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A Review of the Wheat Stem Sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae)

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A review of the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae)

by

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on

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Abstract

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae) is a native stem-mining insect pest of significant economic importance within the Northern Great Plains of the United States and the prairie provinces of Canada (Criddle, 1923). *Cephus cinctus* adult females specifically attack large-stemmed grasses, originally feral and later adapted to cultivated grasses, with dryland wheat, *Triticum aestivum* L. (Poaceae), as the most notable host (Morrill & Kushnak, 1996). As all but two weeks of the sawfly's lifecycle is contained within a host-grass, understanding the ecological history, biological interactions, and economic impacts between *C. cinctus* and *T. aestivum* is crucial to implementing effective pest management strategies.

Chapter 1: Ecological Impacts of *Cephus cinctus*

Distribution of *Cephus cinctus* across North America

The first *C. cinctus* specimen was collected in 1872, a sole male from Colorado (Ivie, 2001). The specimen was described by Edward Norton (Norton, 1872). *Cinctus* is Latin for ”belted, banded, encircled” (Moisset, 2009), referring to “an irregular dentate band widest at sides, on the first, second and fourth and on the sides of the third, fifth and sixth, and apical segments of the tergum, and on the apical edge of each segment of vertex, yellow” highlighting the distinctive black and yellow banded pattern across the tergum (Norton, 1872).

In the United States, collections indicate a geographic distribution of *C. cinctus* as far south as California (1890), Nevada (1872), Utah (1894), and Colorado (1872), as spread northward as far as Washington (1901), Idaho (1935), Montana (1890), and North Dakota (1906) and spread as far east as far as Iowa (1910) and a decade later in Michigan (Riley & Marlatt, 1891; Ivie, 2001). In Canada, the geographic range of *C. cinctus* was located along the southern edges of Saskatchewan and Manitoba from specimens collected in 1895, with the sawfly later spreading westward into Alberta in 1909 (Ashmead, 1898; Ivie, 2001).

While the first documentation of a *C. cinctus* specimen was in Colorado, a theory has been suggested that the wheat stem sawfly may not be endemic to North America. Rather, the geographic origin of the wheat stem sawfly may be from Southeast Asia, accidentally introduced to the West (Ivie, 2001). Such introduction may be from wheat stubble and culms holding sawfly larvae and pupae used as packing material, ballast, and domestic livestock bedding on intercontinental ships (Ivie, 2001). In the late eighteenth century, Russian ships transported goods to Alaska and California, including glassware and stoneware packed in straw for safekeeping (Lightfoot et al, 1993). Once populations of *C. cintus* potentially became established in California, the wheat stem sawfly could traverse North American transcontinentally through the railroad eastward, giving a false impression of its nativity. In addition to *C. cinctus,* 30 other sawfly species are hypothesized to have been introduced across the Atlantic following the Asian trade route (Benson, 1962).

While circumstantial evidence following 17th Century human migration may lead one to assume a non-native status for *C. cinctus*, a genomic study of populations of the genus *Cephus* across North American and northeastern Asian *Cephus* provided further insights to the evolutionary origin of the wheat stem sawfly (Lesieur et al., 2016). Within North America, three distinct geographically separated haplotypes were identified (Lesieur et al., 2016). The first group's distribution spanned Canada and eastern Montana feeding on spring wheat, the second haplogroup inhabited the Rocky Mountains in western Montana and Idaho feeding on spring and winter wheat, and the third group was spread across eastern Montana into North Dakota, Wyoming, Nebraska, and Colorado feeding on both spring and winter wheat. The molecular data supports the original theory of a native North American origin for *C. cinctus*, with populations later spreading west across the Pacific Ocean into Asia, as the North American specimens had a much greater genetic diversity in the mtDNA and microsatellite markers than their Asian counterparts (Lesieur et al., 2016). While it is currently unknown when the divergence between these Cephidae populations occurred between the North American and Asian continents, *C. cinctus* and the closest living relative *Cephus hyalinatus* of China and Russia are indeed distinct species (Lesieur et al., 2016).

Invasive trajectory from native to cultivated grasses

Historically, *Cephus cinctus* was known to infest native *Agropyron* spp. grasses, selected for their taller height and wider, hollow stem diameter, providing optimal conditions for the stem-tunneling larvae living and feeding within (Criddle, 1923). By the 21st Century, the wheat stem sawfly infested moved from native grasses into cultivated wheat, with populations thriving in nearly every wheat-growing US state and Canadian province in North America (Fulbright, 2017). This transition from native to cultivated grains was not unexpected, as in 1890, Mr. Albert Koebele, whom first reared wheat stem sawfly larvae from native grass stems in Alameda, California, prophetically and correctly stated that "the economic importance of this species arises from the fact it may be expected at any time to abandon its natural food-plant in favor of the small grains, on which is can doubtless successfully develop (Ainslie, 1890)."

As wheat cultivation spread across North America, so in succession was the wheat stem sawfly able to expand its feeding grounds. Large sawfly populations inhabiting fields of *T. aestivum* cultivars are expected, as these modern cereal crop monocultures are consistently producing high-quality host plants. Cultivated wheat is often a prime selection, as the crop has been genetically modified for low anatomical and physiological variation between plants, enabling the crops to withstand greater drought pressure and potentially possess larger stems than nearby native grasses (Ainslie, 1890; Morrill & Kushnak, 1996; Beres, 2011).

Cephus cinctus originally preferred cool season, perennial, native wheatgrasses, including *Agropyron tenerum,* smooth brome (*Bromis inermis*), Canada wild rye (*Elymus canadensis*), bearded wheatgrass (*E.* caninus), quackgrass (*E.* repens), slender wheatgrass (*E. trachycaulus*), foxtail barley (*Horduem jubatum*), western wheatgrass (*Pascopyrum smithii*), and timothy (*Phleum pratense*; Ainslie, 1920). The transition from native wheatgrasses to cultivated small grains was opportunistic, as cultivated grains were planted in the same locations where native grasses historically thrived (Ainslie, 1920; Morrill & Kushnak, 1996). Initially infested cultivated grains included oats (*Avena sativa*), barley (*Hordeum vulgare*), rye (*Secale cereale*), durum *(T. durum*), and spelt (*T. spelta*) in addition to *T. aestivum* (Ainslie, 1920; Criddle, 1923). The phenology of over 15 genera of non-cultivated grass species and many additional cultivated small grains provide a suitable habitat able to provide the spatial and nutritional needs for wheat stem sawfly to successfully develop in North America (Cockrell et al., 2017).

Within *T. aestivum*, both spring wheat and winter wheat are cultivated in North America (United States Department of Agriculture, 2023a). Spring wheat and winter wheat are differentiated by the season in which the seeds are sown and later sprout (Klein et al., 2020). Spring wheat is planted in spring and harvested the following fall, while winter wheat is planted in the fall and harvested the following summer (Klein et al., 2020). Winter wheat production utilizes a period of cold dormancy before the plant tillers and heads, requires fewer herbicides during the winter, and lowers soil erosion and moisture loss, taking advantage of the favorable moisture and temperature conditions in late winter and early spring (Entz & Fowler, 1991; Klein et al., 2020). Spring wheat is grown primarily in Canada and the northern United States, where the colder winter temperatures would kill any dormant winter wheat seedlings (Vocke & Ali, 2013).

Initial crop damage by the wheat stem sawfly was limited to spring wheat, due to the sawfly's ovipositional success coinciding with the temporal and nutritional needs of the feeding larva relative to the maturity of the culm (Wallace & McNeal, 1966). Spring wheat development most closely coincided with the growth habits of the cool season wheatgrasses (Morrill & Kushnak, 1996). Meanwhile, the earlier maturing winter wheat was a less suitable host; not allowing the larva enough time to fully mature and form a hibernaculum within the culm before the host plant desiccated, subsequently killing the larva within (Painter, 1953). However, during the mid-late 20th Century, local sawfly populations adapted to winter wheat fields through earlier seasonal activity (Morrill & Kushnak, 2006). Wheat stem sawfly emergence has expanded temporally from early-June to early-May, ending as late as early-July, expanding once again the viable grass host range for the invasive nature of this native sawfly temporally and subsequently geographically (Criddle, 1923; Morrill & Kushnak, 1996).

Population dispersal and density of *Cephus cinctus* in the surrounding landscape

The dispersal of *C. cinctus* is influenced by the surrounding landscape, where insect distribution patterns vary between grassland prairies of wheatgrasses and farmed fields of small grains. In the indigenous grassland prairies of North America, the ecological conditions for *C. cinctus* and their co-evolved grass hosts selected for female wasps to oviposit a high number, as many as 50, single eggs per female (Buteler et al., 2009). The eggs are laid in scattered clusters of suitable wheatgrasses, commonly found growing in bunches (Criddle, 1917; Nansen et al., 2005b). The native grasslands which once predominated the landscape were spatially segregated, with of grasses suitable for females to oviposit in existing in small clumps, as most native grass species present had unfavorable stems due to the dense pith and smaller stem sizes (Sing, 2002; Nansen et al., 2005b).

Historic female flight behavior for oviposition was directed by the prevailing winds, where females emerging from the stub would then come across a patch of suitable bunchgrasses and oviposit a high density of eggs (Sing, 2002). As the bunchgrass hosts would be sparse across the landscape, selection pressure would prioritize morphological host suitability selection, but a poor ability for discrimination between stems containing conspecifics, as female sawflies are either unable to detect or disregard the presence of other sawfly eggs and larvae within the stem (Nansen et al., 2005b). Sawfly larvae complete their entire development within the interior of a single stem; in cases where multiple viable eggs are laid in a single stem, cannibalism occurs, as the host can only provide enough nutritional matter for a single sawfly to successfully reach adulthood (Wallace & McNeal, 1966; Buteler et al., 2009).

In present day wheat fields, high host availability supports female sawflies ovipositing their entire clutch of eggs in close vicinity of their emergence point, resulting in heightened localized infestations (Sing, 2002; Nansen et al., 2005b). The interrelationship between agricultural intensification and sawfly population size has led to increased numbers of *C. cinctus* in agricultural landscapes compared to undisturbed grassland prairies due to suitable host plant density (Rand et al., 2014). Even though the wheat stem sawfly will feed on both native and cultivated small grains in the same geographic location, landscapes composed of a greater number of acres dedicated to cultivated *T. aestivum* result in greater *C. cinctus* infestation rates, i.e. more wheat, more wheat stem sawflies (Rand et al., 2014). Inversely, increased amounts of landscape-level natural habitats did not influence *C. cinctus* infestation (Rand et al., 2014).

Within-field *C. cinctus* distribution

The distribution of *C. cinctus* adults and their eggs is not evenly spread across wheat fields (McCullough et al., 2020). The wheat stem sawfly co-evolved with bunching wheatgrasses in grassland prairies, where high species richness led to a further physical distribution of the same species of plant (Sing, 2002). Female sawflies would advantageously oviposit eggs in close physical proximity to the stem they emerged from (Sing, 2002, Nansen et al., 2005). Wheat fields typically display an edge effect, where the greatest density of the sawflies, from eggs to adults, are found in the perimeter of the crop, more apparent along the side of the field nearest to sawflies emerging from neighboring feral rangeland grasses or stubble from the previous year's crop (Nansen et al., 2005; McCullough et al., 2020). Sawfly infestation rates significantly decreased up to 20 meters in distance into the field, with both males and females found in greater densities along the edge of the field (McCullough et al., 2020).

However, the decreased dispersal of *C. cinctus* adults into the center of the field is not uniform between males and females, as males had a more significant decline in density approaching the center of the field (McCullough et al., 2020). The male sawflies exhibited a stronger edge effect, where the highest density was the one meter into the field (McCullough et al., 2020). Even as sawfly infestation levels increase, the spatial distribution pattern retains the edge effect through weak flight and high intraspecific competition (Nansen et al., 2005b).

Starting from the edge, the deeper into the center of the field sampled, the lesser the density of males were found, with only 7% of males found 30 meters into the field (McCullough et al., 2020). Adult males concentrating closer together near the edge of a field may have been an evolutionary advantage in native wheatgrasses, where a larger group of males emitting the sex-attracting pheromone 9-acetyloxynonanal could potentially lure in more females emerging further away (Cossé et al., 2002).

In comparison, female density across a field did not have the same stark decline towards the center of the field as was seen with males (Cárcamo et al*.,* 2005; McCullough et al., 2020). While females were also the densest at the field's edge, 30 meters into the field, 20% of adult females were found (McCullough et al. 2020). The wider density of adult female *C. cinctus* density may be from females responding to the competitive risk of ovipositing eggs close to other females, physically separating themselves to potentially locate uninhabited stems, as they either do not have the ability to differentiate between already occupied stems or choose to overlook that factor while selecting a host grass (Buteler et al., 2009). Females may choose to move deeper into the *T. aestivum* field rather than move into the fallow or sparser native grasses adjacent to the field (McCullough et al., 2020). As males emerge a few days before females, they die soon after copulation, whereas females have a few more days to venture further into the field center (Cárcamo et al., 2005).

The development stage of wheat during the sawfly's flight period may also impact the edge effect, causing a more pronounced effect in winter wheat than spring wheat (Sing, 2002). When *C. cinctus* females search wheat stems for oviposition susceptibility, the earlier matured winter wheat has a greater proportion of matured elongated stems allowing for immediate infestation, while spring wheat's developmental delay forces females to distribute further throughout the field in search of stems which seasonally mature later (Sing, 2002).

Cephus cinctus larval density was also the most prominent along the edges of the field (McCullough et al., 2020). Highest larval density was observed within the first meter, decreasing 40-60% when sampled up to 40 meters within the field (McCullough et al., 2020). As females ventured further into the field from the edge, this led to a more gradual dispersal of larvae in the wheat stems toward the center of the field. A more extensive region for oviposition would lead to a greater number of successful progenies, as female sawflies do not distinguish between conspecifics (Buteler et al., 2009).

Sex ratios influenced by host stem diameter

While female wheat stem sawflies do not differentiate between stems already inhabited by sawfly eggs and larvae, females do select stems with a larger diameter (Buteler et al., 2009; Cárcamo et al., 2020). Female sawflies, and thereby female eggs, are larger than their male counterparts, where females have a greater chance of successfully completing development hosted in a larger stem (Cárcamo et al., 2005). Female sawflies may have the ability to select if the egg oviposited is a fertilized female egg or an unfertilized male egg (as *C. cinctus* is in the family Hymenoptera, the haplodiploid chromosomes determine sex), allowing grass-host size to influence which sawfly sex lives within (MacKay, 1955; Cárcamo et al., 2020).

Seeding rates influence stem diameter, where fields with a higher density of seeds produce more wheat stems per acre (Pelton, 1969). More individual wheat plants give rise to a larger number of stems competing for the same water and nutrient resources, leading to thinner wheat stems and lower grain weight (Pelton, 1969). Seeding rates of spring and winter wheat fields can thereby influence the sex ratios within-field, where denser seeded fields typically produce a larger percentage of male sawflies (Cárcamo et al., 2020). Even a difference of only 0.3 mm larger in stem diameter could subsequently increase the proportion of females to males by 80% (Cárcamo et al., 2020). The break-even point in wheat tillers for even male to female sex ratios is approximately 2.0-2.2 mm in stem diameter for triticale and wheat cultivar Lillian (Cárcamo et al., 2020).

Chapter 2: Biology of *Cephus cinctus*

Taxonomy

The wheat stem sawfly (*Cephus cinctus*) belongs to the order Hymenoptera, containing more than 146,000 described species of ants, bees, and wasps (Huber et al., 2009; Axel et al., 2013). Hymenopterans can be phytophagous, predatory, or parasitic, often forming complex eusocial colonies (Axel et al., 2013). Hymenoptera is divided into two suborders: Apocrita (possess a tapered wasp-waist between the prostomium and peristomium) and Symphyta (without a wasp-waist) which contains sawflies and woodwasps (Axel et al., 2013). There are approximately 8,000 described species of sawfly in Symphyta, split into six families (Taeger et al., 2010). Sawfly larvae are phytophagous and adult females possess a saw-like ovipositor for inserting eggs inside of plant stems, leaves, or twigs (Wallace & McNeal, 1966).

Of the six families contained in Symphyta, *C. cinctus* is found in the tribe Cephini contained in the family Cephidae (Wallace & McNeal, 1966). Adults in the Cephini tribe bore primarily into grasses, are slow-fliers, remain amongst foliage during rain or high wind events, and are usually dark-colored with long and cylindrical or laterally compressed abdomens (Wallace & McNeal, 1966; Benson, 2009). The primary regions of cephid diversity are found in the grasslands of the Mediterranean and the Eurasian steppes, but cephids can be found throughout the entire globe in grass-dominated ecological regions (Benson, 1946).

Adult morphology

Cephus cinctus adults are long and slender, approximately 10 times as long as wide (Wallace & McNeal, 1966). The adult body is about 7 to 12 mm long and a glossy black, juxtaposed with two to three bright yellow bands transverse across the dorsal side of the abdomen (Ainslie, 1920; Ries, 1937, Beres et al., 2011). Adults have a solid black head, large prominent eyes, and club-shaped antennae with approximately 19-20 segments and are one-half the body length (Ries, 1937; Wallace & McNeal, 1966; Beres et al., 2011). Legs are long, thin, and yellow, and the wings are a light smoke-color and approximately 6 mm long that extend beyond the end of the body (Ries, 1937, Wallace & McNeal, 1966).

As in other Symphytans, the abdomen is not constricted, but broadly connected to the thorax (Wallace & McNeal, 1966). When distinguishing *C. cinctus* from closely related species, the base of the thorax and abdomen is black, while the mesepisternum of the thorax is yellow, femora mostly yellow, and apical tergite and venter of the of the abdomen are yellow (Wallace & McNeal, 1966). However, abdomen color variation between black to yellow can be highly variable depending on the ecoregion of the wheat stem sawfly specimen (Ries, 1937).

Some differences occur between male and female specimens. Adult female wheat stem sawflies are considerably larger than their male counterparts, as their energy needs are greater for egg production, enabling larger females to produce and carry more eggs (Ries, 1937; Leonard, 2007). The legs of female *C. cinctus* are also yellow, except for the base, whereas male legs have black patches on the femora (Ries, 1937). As in all Hymenopterans, male wheat stem sawflies are haploid with nine chromosomes, hatching from unfertilized eggs, while females are diploid, hatching from fertilized eggs (Beres et al., 2011). Female *C. cinctus* also have an ovipositor, where the ovipositor sheaths when viewed dorsally, tapering towards its apices (Wallace & McNeal, 1966).

Behavioral habits of adult *Cephus cinctus*

When either *C. cinctus* sex is at rest, typical adult behavior in the crisp morning or after sundown is lying flat against the grass stem, tucking their head downward and closely folding their wings against their body (Ainslie, 1920). While sun-bathing midday, adult sawflies lie on the side of the grass facing the sun, with wings and legs partially stretched out to absorb the warmth of the sun (Ainslie, 1920). The wheat stem sawfly heavily prefers sunny, calm days to any form of cloud-cover and subsequent precipitation (Ainslie, 1920).

When flying, sawflies infrequently traverse great distances, preferably to stay quite close to the grass stem in which they emerged from (Wallace & McNeal, 1966). During moments in time with little to no wind, sawflies will hover in the air, even occasionally partaking in a mating dance (Ainslie, 1920). Once the wind picks back up again, the sawfly will quickly veer downward, back to the protection provided by a tuft of grass (Ainslie, 1920).

During late spring to early summer, the univoltine (one brood of offspring per year) adult sawfly emerges from its obligate overwinter diapause hibernaculum inside the wheat stubble leftover from the previous year’s harvest (Criddle, 1923; Morril & Kushnak, 1996). Mating between a male and female sawfly occurs soon after emergence, where the male grasps the back of the female, with his abdomen curved under her ovipositor (Wallace & McNeal, 1966). Male infighting for dominance has been observed, where males bite its opponent’s antennae (Wallace & McNeal, 1966). Copulation occurs quite briefly, usually taking no more than a minute (Ainslie, 1920; Ries, 1937). As the adult lifespan is only about one week and has a singular brood, copulation and ensuing egg oviposition occurs in quick succession (Ainslie, 1920; Wallace & McNeal, 1966).

Ovipositional behavior of adult *C. cinctus*

Post-copulation, female sawflies use chemoreceptors to detect volatile compound cues released by suitable host plants in search of the large-stemmed graminoid hosts (Weiss et al., 1992; Piesik et al., 2008). The potential grass hosts are then morphologically inspected by the female (Ainslie, 1920). She first hovers around potential grass hosts, lands and preens herself, then walks up and down, encircling, and grasping candidate stems, preferentially detecting taller and wider hollow stems (Ainslie, 1920; Buteler et al., 2009). Grass hosts are susceptible to oviposition from the appearance of the first stem node during the elongation period to anthesis and are not known to be chosen while the stem has a grain head (Ainslie, 1920; Morrill & Kushnak, 1996).

Once an oviposition location has been selected through antennal tapping, the saw-like ovipositor is gradually inserted into the lumen, occupying the chosen location for about a minute (Ainslie, 1920; Buteler et al., 2009). The female sawfly is facing downward, parallel to the stem, thrusting the ovipositor in and out of the stem between the cell walls, until a wide enough opening is formed (Ainslie, 1920; Wallace & McNeal, 1966). The egg is most frequently inserted about an inch above the second node from the top of the stem (Ainslie, 1920; Criddle, 1923). However, through dissections, eggs have been known to be found in all hollow portions of the grass stem, female sawflies prefer the more delicately walled, actively elongating internodes during the grass's transition phase (Ainslie, 1920; Wallace & McNeal, 1966; Simon & Park, 1983). The softer stem wall tissue influences earlier emerging females to oviposit closer to the base of the stem than later emerging females, in succession with directional development of the stem: bottom to top (Wallace & McNeal, 1966). If a hollow pith is not detected, the sawfly will select a new location (Criddle, 1923).

After inserting a single egg during oviposition inside the stem, the female sawfly then flies away in search of a new grass stem to repeat the process (Ainslie, 1920). The date in which oviposition occurs changes with latitude, with earlier adult emergence and subsequent mating occurring sooner the closer the wheat stem sawfly population is to the equator and at a lower elevation (Ainslie, 1920). Oviposition generally occurs at temperatures between 68º F and 90º F, with wind speed under 20 mph (Wallace & McNeal, 1966).

The egg

Dissections of female sawflies indicate each has the capability of bearing up to 50 individual eggs, indistinguishable in size and maturity (Ainslie, 1920). The egg's appearance is symmetrical, crescent-shape, rounded and slightly tapered on the end (Ainslie, 1920). Milk-white to translucent in color, with a shiny cast, the egg also has faint, small, longitudinal lines (Ainslie, 1920). The size of the egg varies in correlation with the size of the female, ranging between 1.0-1.25 mm long and 0.33-0.56 mm wide at its thickest point (Ainslie, 1920; Ries, 1937). Placed in the hollow of the stem, the egg is free-standing, not physically bound to the plant it is encased within (Ainslie, 1920). In agroecosystems with higher wheat stem sawfly population densities, it is not uncommon to find multiple eggs in a single stem, leading to competition among conspecifics where there is a sole victor (Criddle, 1923; Buteler et al., 2009). Even though taller, more succulent grasses can receive a greater number of *C. cinctus* eggs, each host plant can only nutritionally support a single sawfly (Criddle, 1923; Buteler et al., 2009).

The primary factors which lead to the healthy development of a *C. cinctus* egg are proper temperature and moisture (Ainslie, 1920). On the first and second day, the cells within the egg coalesce along the central axis, where on the third day the physical shape of the developing larva becomes slightly visible, with the region which will become the head slightly swelling (Ainslie, 1920). On the fourth day, an irregular heartbeat can be detected, where over the next few days becomes more regular, reaching 120 beats per minute, and the musculature system allows the egg to shift and move from within (Ainslie, 1920). By day six, the head has the outline of a jaw forms and darkens, and the eyespots appear, also darkening, and the egg is no longer crescent-shaped, but oval to kidney-shaped (Ainslie, 1920; Ries, 1937).

The larva

After the five to eight days of development post-oviposition, the egg hatches, where the developing larvae undergoes four instars in the stem over a period of about 60 days (Ainslie, 1929). The emergent larva has a translucent body, large brown head possessing very strong four-pointed mandibles, and a comparatively weak body with well-defined segments, ready to voraciously feed on the parenchymatous tissue lining the pith (Ainslie, 1920; Wallace & McNeal, 1966). Thoracic tubercles reside where legs will form in later stages of development (Wallace & McNeal, 1966). The brown caudal horn and stout bristles on the trunk assist the larva in crawling inside of the grass host (Ainslie, 1920).

The size of the larva is variable, largely dependent on the stem width and amount of nutritional host-plant material available for consumption, with an average length of 8-14 mm and width of 1-2 mm (Ainslie, 1920). Throughout development, the larva takes on a characteristic S-shape both in and out of the host stem (Ainslie, 1920) and tints greenish yellow from the plant material ingested (Wallace & McNeal, 1966).

While the larva may choose to first go either upwards or downwards to feed, eventually the larva will feed through the downward node and form a feeding gallery on the interior of the entire stem (Ainslie, 1920). As the larva feeds, a trail of densely packed “sawdust” frass is left behind, typically a few inches above the active boring (Ainslie, 1920). If other *C. cinctus* larvae are found within the stem, ordinarily the oldest, and thereby largest, larva cannibalizes all other conspecifics (Buteler et al., 2009). As the larva feeds upon the parenchyma and vascular tissues throughout the stem interior, the stem is girdled, causing physiological stress via a reduction of water and photosynthate translocation and subsequent yield loss during the grain fill period for the host plant (Wallace & McNeal, 1966; Morrill et al., 1992; Talbert et al., 2001).

Around August, once anthesis begins and the host plant undergoes desiccation, the mature larvae bore downward through the stem nodes to the basal portion of the stem (Criddle, 1923; Wallace & McNeal, 1966). *Cephus cinctus* larvae form a hibernaculum, where the larva cuts a V-shaped notch within the interior perimeter of the stem, and plugs the stem lumen with frass (Holmes, 1975). The severance of the grass stem may differ in up to three weeks between *C. cinctus* in the same location, dependent on the maturity of the host plant (Criddle, 1923). The frass plug is about 3-5 mm long and fills the width of the stem (Wallace & McNeal, 1966). While the sawfly does not sever the stem completely during this process, the weakened cut stem may still lodge (Shanower & Hoelmer, 2004). Underneath the frass plug, the larval gallery is empty, say for the larva, known as a pupation cell (Ainslie, 1920; Ries, 1937). Inside of this chamber the wheat stem sawfly's head up towards the top, still able to move up and down with the caudal horn (Ainslie, 1920). Nearing the end of summer to mid-fall, the sawfly will then form a cocoon in its hibernaculum for overwintering (Ainslie, 1920).

In preparing for winter, the larva forms a cocoon by spinning a nearly transparent tube of silk (Ainslie, 1920). The silken tube is longer than the enclosed larva, entirely closed at both ends, and freestanding within the stub, enabling the larva to move freely inside (Ainslie, 1920; Wallace & McNeal, 1966). During the winter, the enclosed sawfly can completely freeze, but slowly thaws out in the spring as the external temperatures gradually warm (Ainslie, 1920). The cocoon remains intact until the sawfly decides to emerge from its obligatory diapause (Ainslie, 1920; Wallace & McNeal, 1966). Most emergence periods occur the following year, but extremely rare cases have shown sawflies to survive three years in the hibernaculum (Ainslie, 1920).

The plant material left behind is the anchored stub near or below ground level, providing optimal temperature and humidity conditions for the enclosed larva through diapause, and an easy escape channel the following spring (Ainslie, 1920; Shanower & Hoelmer, 2004). The size of the stub can vary between a half of an inch to 4 inches aboveground (Ainslie, 1920). Unless disrupted by outside forces, such as mechanical tillage, the stub will remain in its place until the following growing season, allowing the sawfly to remain undisturbed (Ainslie, 1920).

The pupa

The sawfly develops for eight to nine months until temperature, humidity, and photoperiod indicators break diapause and post-diapause development continues (Perez-Mendoza & Weaver, 2006). Inside of the hibernaculum's cocoon, the sawfly larva molts into its pupal stage around May (Ainslie, 1920; Wallace & McNeal, 1966). Once the prepupal stage has begun, the wheat stem sawfly will not re-enter diapause (Wallace & McNeal, 1966). The pupa is a milky-white and slightly larger than its previous larval form, with a length of 12mm and width of 1.5mm (Ainslie, 1920). The pupa also now has short wing pads and is encased in a translucent envelope, which is often broken by the movements of the insect within (Wallace & McNeal, 1966). After pupation, the *C. cinctus* pupa remains motionless for the initial few days, until resuming activity (Ainslie, 1920). Like its larval form, the pupa's head remains near the top of the hibernaculum (Ainslie, 1920).

The pupal stage is incredibly brief, only about one to two weeks long (Ainslie, 1920; Criddle, 1923). During this developmental stage, the body and legs of the sawfly begin to pigment and turn black, the eyes blacken, and the wings elongate, inflate, and harden (Wallace & McNeal, 1966). Once the pupa reaches full maturity, the sawfly may emerge in its adult form immediately capable of flight (Ainslie, 1920; Perez-Mendoza & Weaver, 2006). After the adult wheat stem sawflies emerge, their yearly cycle of life repeats itself once again (Wallace & McNeal, 1966).

Chapter 3: Economic Impact

Economic losses to the wheat production industry

In 2022, 792 million metric tons of wheat, *Triticum aestivum*, (Shabendeh, 2023) were grown on 531 million acres of farmland across 120 countries (Ernstein et al., 2022), feeding 2.5 billion people (International Maize and Wheat Improvement Center, 2020). Wheat is the dominant staple food crop for North Africa, West Asia, Central Asia, and Europe (Shaikh, 2023), supplying one-fifth of all food calories consumed globally (Ernstein et al., 2022) as the second-most consumed grain worldwide (Shaikh, 2023). Wheat is the first-most internationally traded grain (Shaikh, 2023), where from the United States nearly $50 billion worth in wheat is traded globally annually (United States Department of Agriculture, 2023b). As one of the oldest domesticated food crops, the protection of this dietary staple is of the utmost importance for global human health (Erstein et al., 2022).

The wheat stem sawfly is currently the most economically important pest of dryland wheat in the northern Great Plains (Beres et al., 2011; Shrestha at al., 2018). The annual economic loss due to *C. cinctus* damage across Canada and the United States is more than $400 million (Beres et al., 2017). In Montana, from 2010 to 2014 the associated economic losses for spring wheat and winter wheat were estimated between $52.2-$80.0 million (Fulbright et al., 2017). In North Dakota, the economic loss to wheat producers was between $25-$70 million in 2009 (Knodel et al., 2010). The economic loss in Colorado for 2022 was estimated to be $41 million (Pierce & Nachappa, 2022). As the wheat stem sawfly's infestation geographically widens across the northern Great Plains and local populations increase in density, the economic damage is also expected to increase (Olfert et al., 2019).

Plant injury caused by *Cephus cinctus*

The most destructive part of a wheat stem sawfly's life cycle is during its larval stage (Beres et al., 2011). As the larva feeds on the host plant's pith and vascular system, the plant is less efficient at transporting water and photosynthate to the upper portions of the plant, thereby lowering photosynthetic capabilities by 12%, CO_2 exchange rate, and transpiration (Macedo et al., 2007). Larvae feed in the spring and early summer during the grain fill period for grasses, reducing grain yield by upwards of 35% (Holmes, 1977). The sawfly impacts the grain head by reducing the head's overall grain weight by 10-17% (Holmes, 1977; Morrill et al., 1992), grain protein content, number of kernels per head (Holmes, 1977; Shanower, 2004), and accelerating senescence (Macedo et al., 2007). The impact of *C. cinctus* damage is also skewed toward plants with a higher yield potential, as female sawflies select larger diameter stems which normally bear heavier bigger seed heads with larger kernels (Morrill et al., 1992; Beres et al., 2011).

These effects on cultivated wheat can be widespread across the field, as infestation levels may exceed 88% (Rand et al., 2014) and potential entire field-crop losses due to a high proportion of stem lodging and subsequent inability to harvest (Knodel et al., 2016). As the larva forms its hibernaculum for overwintering, the insect cuts a V-shaped notch which destabilizes the top of plant, where moderate to high winds will cause the stem to fall over (Achhami et al., 2020; Starinieri et al., 2022).

Impact of *Cephus cinctus* on harvest operations

At 2011 fuel prices, a 50% stem cutting loss would equivalate to approximately $74 dollars per acre in extra fuel costs from the slower driving speeds necessary to pick up the fallen heads (Beres et al., 2011). The implement attached to the harvester would also need to be set lower to the topsoil, causing fewer wheat stubs to remain attached to the ground, escalating soil erosion and reducing soil moisture content from the lack of snow capture (Beres et al., 2011). The lower cutting table also increases the likelihood of damaging the equipment, as more soil and rocks will be sucked up into the shears, causing greater machine wear and tear (Starinieri et al., 2022).

Different harvesting equipment may need to be purchased, such as a swather or stripper header, to collect the infested stems, incurring additional costs to the farmer (Bekkerman & Weaver, 2018; Pierce et al., 2022). Swathing is the practice of cutting down (windrowing) the wheat once it has reached physiological maturity, accelerating the drying process (Bekkerman & Weaver, 2018) and trapping and subsequently killing *C. cinctus* in the wheat stem before it moves to the crown of the root for overwintering (Carlson, 2019). The stripper header strips the grain head from the wheat plant, leaving the stem standing in the field (Lysber, 2020). As a complete harvest of lodged plants is impossible, stem lodging always causes additional yield losses (Pierce & Nachappa, 2022), often between 10-25, but sometimes up to 80% (Knodel et al., 2010).

Chapter 4: Integrated Pest Management Strategies

Chemical control

Currently, chemical pest management practices are considered inadequate for effectively controlling *C. cinctus* populations and are not recommended in the northern Great Plains (Shanower & Hoelmer, 2004). As sawflies spend the majority of their life cycle enclosed within their host stem, the period in which chemical application is effective is relatively short (Wallace & McNeal, 1966; Knodel et al., 2010). If the chemical was applied too early during the emergence period, only males would be extinguished, but if the chemical was applied too late, females would be killed but the majority of the eggs would already be deposited (Beres et al., 2011). As insecticides must come in direct contact with adult *C. cinctus*, current net chemical application costs far exceed wheat yield cost benefits (Shanower & Hoelmer, 2004; Bekkerman & Weaver, 2018). Grain quality may also be compromised due to the direct chemical application, further deterring its usage (Beres et al., 2011).

Biological control with *Bracon cephi* and *Bracon lissogaster*

Two bivoltine parasitoids, *Bracon cephi* (Gahan) and *B. lissogaster* Mues. (Hymenoptera: Braconidae), can serve as natural biological control agents against *C. cinctus* (Runyon et al., 2002). Both species are native to the northern Great Plains (Nelson & Farstad, 1953; Somsen & Luginbill, 1957). *Bracon* cephi was first described as *Microbracon cephi* by Arthur Burton Gahan in 1918 from five females and two males found in native grasses from North Dakota and Manitoba (Gahan, 1918). *Bracon lissogaster* was first described by Carl

Frederick William Muesebeck in 1953 from 17 females and 28 males reared from wheat stems in Montana (Muesebeck, 1953).

Bracon cephi and *B. lissogaster* are, like *C. cinctus*, Hymenoptera, but are in the suborder Apocrita (Nelson & Farstad, 1953; Morrill et al., 1998). These braconids reside in the family Braconidae, where all described members are known to be protelean parasitic wasps (Quicke & van Achterberg, 1990). Protelean organisms are parasites as juveniles, which consume or kill their hosts, later emerging as free-living adults (Quicke & van Achterberg, 1990).

Original descriptions state *B. cephi* males are around 3.5 mm long and females are 4.1 mm long, with *B. lissogaster* females around 3.5mm long (Gahan, 1918; Muesebeck, 1953). Both *Bracon* spp's faces, frons, and thoraxes are smooth, polished, and black, distinctly long antennae, ovipositors extend less than half the length of the abdomen, tarsi and stigmas are blackish, wings fumate with brownish venation, and predominately possess yellowish-orange abdomens (Gahan, 1918; Muesebeck, 1953). *Bracon cephi* have 38-40-jointed antennae, a finely shagreened metasoma, and vein *r* near middle of stigma (Gahan, 1918; Runyon et al., 2001), while *B. lissogaster* have 27-39-jointed antennae, smooth and polished metasoma, and vein *r* before middle of stigma (Muesebeck, 1953; Runyon et al., 2001).

Both parasitoids are ectoparasites and larval idiobionts that sting and paralyze the sawfly larvae (Nelson & Farstad, 1953; Somsen & Luginbill, 1956). To locate the sawfly larva, the female parasitoid walks up and down a suspect stem, tapping the stem with her antennae, occasionally holding perfectly still to feel for movement within the stem (Somsen & Luginbill, 1956). *Bracon cephi* and *B. lissogaster* can parasitize *C. cinctus* larva in both cultivated and non-cultivated grasses (Somsen & Luginbill, 1956). Once the sawfly larva has been detected, the ovipositor is repeatedly inserted into the stem and injects venom into the larva, partially paralyzing the sawfly (Somsen & Luginbill, 1956; Beres et al., 2011). Upon sawfly paralization, *B. cephi* will lay one egg per sawfly larva, while *B. lissogaster* often lays multiple eggs, up to four, per sawfly larva, oviposited nearby or stuck onto the larva's integument (Nelson & Farstad, 1953; Somsen & Luginbill, 1956). Parasitoid eggs are cylindrical, elongate, slightly curved, approximately 0.5-.74mm long and 0.9-1.2mm wide, and a shiny light grey (Somsen & Luginbill, 1956; Shanower & Hoelmer, 2004).

After about 3-5 days, the parasitoid larva hatches from its egg (Somsen & Luginbill, 1956; Shanower & Hoelmer, 2004). The sex ratio appears to be two males for every one female, as unfertilized eggs produce males, but fertilized eggs produce equal male and female eggs (Somsen & Luginbill, 1956). The resulting braconid larvae then tear open the sawfly integument with mandibular incisions and feed on the eviscerating fluids, leaving only the head capsule and integument after about 10 days (Runyon et al., 2001; Beres et al., 2011).

Both parasitoids normally complete pupal development in 12-20 days in a single season, growing from 0.6 mm after hatching to 4.2 mm long and 1 mm wide during its final larval stage (Somsen & Luginbill, 1956; Runyon et al., 2001). The larva undergoes three (*B. lissogaster*) or five (*B. cephi*) instars, where the larva is elongate and slightly curved, evenly covered in short setae, and possesses mandibles which sclerotize by the third instar (Somsen & Luginbill, 1956; Shanower & Hoelmer, 2004). When 3-4 larva feed on the same host, the development time can be shorted to 6-8 days, as each smaller larva has a more limited amount of food (Somsen & Luginbill, 1956).

Both *B. cephi* and *B. lissogaster* may undergo a partial second generation, where one part of the *B. cephi* population may enter diapause while the other part pupates and emerges as adults later in the summer (Nelson & Farstad, 1953; Somsen & Luginbill, 1956). The first generation emerges late-June to early-July and oviposits one week after emergence, while the second generation emerges mid-August and oviposits within a day after emergence (Somsen & Luginbill, 1956).

These braconids diapause throughout winter within silken cocoons in the host plant stem and post-harvest stubble (Runyon et al., 2001; Runyon et al., 2002). The first generation spins a light brown, loosely woven cocoon, formed with two padded ends and physically attached to the inner stem wall (Somsen & Luginbill, 1956). The second generation forms a dull white, tightly woven cocoon, better adapted for the colder winter climate (Somsen & Luginbill, 1956). Each cocoon takes a day and a half to construct, is about 6.1 mm long and 1.9 mm wide, and is spun in close proximity to the deceased *C. cinctus* host (Somsen & Luginbill, 1956).

The prepupal and pupal stage for both *Bracon* spp. is 12-20 days long, where the 4 mm long and 1 mm wide pupa is a glassy white with antennae first to appear (Somsen & Luginbill, 1956; Shanower & Hoelmer, 2004). The pupa has two compound eyes, three ocelli which turn reddish brown, three pairs of legs, and wings extending to 0.5 mm (Somsen & Luginbill, 1956). By the end of pupal development, the free-standing parasite turns black and emerges by cutting a hole out of the top of the cocoon (Somsen & Luginbill, 1956). The adults live up to three weeks, are relatively week fliers, and are most active on calm, sunny days (Somsen & Luginbill, 1956).

Bracon cephi and *B. lissogaster* reside in the northern Great Plains in both Canada and the United States (Nelson & Farstad, 1953; Somsen & Luginbill, 1956; Morrill et al., 1994). Conversely from *C. cinctus*, these parasitoids are not as evenly distributed throughout the wheat dominant agroecosystems, rather exhibiting drastic density fluctuations between isolated populations in the same geographic region, with some areas having no parasitism pressure

(Morrill et al., 1998; Clarke & Walter, 2011; Rand et al., 2014). In cultivated wheat, parasitism rates have reached up to 98% of available *C. cinctus* in Montana (Morrill et al., 1998).

For *Bracon* spp. to suppress *C. cinctus* population growth, 68% of the host sawfly population must be parasitized (Rand et al., 2017). Parasitism effectiveness may also fluctuate inversely with *C. cinctus* infestation rates, where greater than 60% grass-host infestation could result in lower parasitism rates (Holmes et al., 1963). At high-host densities, female parasitoids can place their eggs in stems with multiple *C. cinctus* larva, where the largest *C. cinctus* larva would then consume its conspecifics and their parasitoids (Holmes et al., 1963). Second generation parasitoids may then have greater success rates, as by mid-summer normally one final sawfly resides in each infested stem (Beres et al., 2011).

Greater parasitism rates have been shown in later maturing wheat, as the parasitoid is more likely to have a successful second generation (Morrill et al., 1998) and in wheat fields bordering untilled summer fallow, where the overwintering parasitoid cocoons are less disturbed (Runyon et al., 2002). More braconid parasites may be expected in agroecosystems composed of both cultivated and native grasslands, as the second generation may have better success overwintering in the sawfly populations in the un-harvested native grasses, however, that is not always the case (Rand et al., 2014). *Bracon* spp. seem to not be significantly influenced by greater grassland or cultivated wheat areas, indicating *T. aestivum* may be considered the dominant habitat for these native parasitoids (Rand et al., 2014). The conservation of these parasitoids may then be best directed to within-field approaches (Beres at al., 2011; Rand et al., 2014).

Host Plant Resistance

Cultivated wheat, *T. aestivum*, is commonly bred as either hollow-stemmed or solid-stemmed cultivars, as the solidity of the stem can range from 0-100% depending on genetic and environmental factors (Berzonsky et al., 2003). Conventional spring and winter wheat varieties were hollow-stemmed, where the central cavity of the stem is hollow, anatomically structured from completely hollow to resembling a honeycomb of thin-walled, open cells loosely adjacent to each other (Pluta et al., 2021). In mature wheat stems, as the vascular system continues to differentiate in the cortex, the parenchyma cells in the central cavity collapse and breakdown, forming the hollowed-out pith (Nilsen et al., 2020). As the majority of *C. cinctus'* lifecycle is contained within the hollow of a grass stem, the integrity of an unfilled culm is vital for sawfly development (Pluta et al., 2021). Hollow stems with large stem diameters maximize sawfly fitness, producing larger females able to produce maximal quantities of eggs (Morrill et al., 2000).

The original solid-stemmed variety was produced in 1946, aptly named Rescue (Platt et al., 1948). Currently, most of the spring and winter wheat *C. cinctus*-resistant varieties planted in the northern Great Plains are descended from Rescue (Cook et al., 2017). Solid-stemmed varieties of wheat are bred for increased pith expression, genetically raising the number of undifferentiated parenchyma cells to either partially or completely fill the central cavity of the culm of the stem (Kemp, 1934; Nilsen et al., 2020). For fields with greater than 15% *C. cinctus* infestation, solid-stemmed wheat is recommended for planting (Knodel et al., 2010). The solid stem cultivars increase resistance to *C. cinctus* by deterring oviposition, impeding larval development inside of the stem, delay adult emergence, and shift sex ratios to produce more males (Hayat et al., 1995; Cárcamo et al., 2011; Cárcamo et al., 2020). Fewer wheat stem sawfly larvae in the wheat stem decreases potential yield losses by reducing larval stem boring and the number of cut stems, as larvae often die before the formation of the hibernaculum is initiated (Talbert et al., 2014; Varella et al., 2018).

Even though a greater percentage of the culm is filled with pith, solid-stem cultivars do not appear to adversely influence parasitism rates by *B. cephi* and *B. lissogaster,* as braconid eggs and larvae are smaller than that of *C. cinctus* and are able to complete development in stems where *C. cinctus* has been able to survive (Morrill et al., 1994; Knodel et al., 2010). A blend of hollow-stemmed and solid-stemmed cultivars is also recommended for increasing within-field parasitoid populations (Cárcamo et al., 2016). However, parasitoid success may still be influenced by plant morphology, as increased stem solidity and the wheat genotype itself has been shown to have a negative impact on parasitism rates of *C. cinctus* (Rand et al., 2012; Cárcamo et al., 2016).

Despite the wheat stem sawfly mortality benefits, solid-stemmed cultivars come with trade-offs, as solid stem seeds are more expensive and have lower harvested yields comparatively to hollow stem cultivars, as the plant uses a greater percentage of its net energy for bolstering the stem's pith instead of increasing the number, size, and protein content of the seeds (Beres et al., 2007; Bekkerman & Weaver, 2018). The lower maximum yield potential from solid-stemmed cultivars significantly deters the widespread usage of the agronomic practice, especially in fields with lower sawfly infestation rates (Cárcamo et al., 2005; Bekkerman & Weaver, 2018), however newer developed cultivars have improved grain quality in comparison with the original cultivars (DePauw et al., 2005).

The solid-stemmed varieties also incur greater transportation costs, as the stems have a higher mass and volume which take more time to compress and transport the bales (Edet, 2015).

Solid-stemmed wheat varieties also have more inconsistent degrees of stem solidness from the same variety planted at different locations, as pith expression was environmentally influenced by light intensity, temperature, nutrient availability, soil moisture content, and seed spacing (Knodel et al., 2010). Heavy cloud cover and shortened photoperiods negatively affected pith expression in solid-stemmed wheat (Holmes, 1984). An overapplication of Phosphorus and Nitrogen, above what the plant physiologically needs, can also reduce pith expression in solid-stemmed wheat, as the plant directs its biomass energy to excess vegetative growth, increasing the effects of shading (Beres et al., 2012).

Hollow-stem and solid-stem cultivars have been blended, creating intermediate-stemmed or semi-solid-stemmed cultivars, potentially capitalizing on beneficial traits from both main breeding lines (Bowden et al., 2001). However, semi-solid cultivars are not as resistant to the larval growth of the what stem sawfly as solid-stemmed cultivars (Biyiklioglu et al., 2018). Semi-solid stemmed cultivars have fewer genes modifying their phenotype than solid-stemmed cultivars, conferring the semi-solidness, stabilizing said solidness, and are more variable (Bradley, 1991). However, some semi-solid stemmed cultivars can exhibit lower levels of *C. cinctus* damage than expected (Weaver et al., 2009).

Cultural control methods: trap cropping, swathing, crop rotation, and tillage

Within-field cultural control strategies to mitigate the proliferation of *C. cinctus* populations infesting cultivated wheat include trap cropping, swathing, crop rotation, and tillage (Bekkerman & Weaver, 2018). Each risk management strategy utilizes either alternative planting strategies or using specific types of machinery at key points in the wheat stem sawfly's lifecycle to maximize sawfly mortality and thereby minimize *T. aestivum* yield loss (Knodel et al., 2010;

Bekkerman & Weaver, 2018). These management strategies can be used in tandem with biological control and host plant resistance to effectively suppress *C. cinctus* crop damage.

Planting strategies support using solid stem cultivars on the field's perimeter surrounding the central hollow stem cultivars, employed for its decreased stem cuttings and sawfly larval survivorship, trapping the sawflies within the thicker stems (Cárcamo et al., 2005; Beres et al., 2009). Trap cropping can be used to deceive adult sawflies in search of a suitable host plant and minimize dispersal, where a perimeter of wheat can be planted in strips in fallow adjacent to a wheat field planted for that growing season (Beres et al., 2011). The trap strip should be planted about 2-3 feet from the wheat field, enticing the sawflies to remain above the stubble they just emerged from, rather than move to the next crop of wheat grown (Beres et al., 2009; Beres et al., 2011). Then in mid- to late-July, the trap crop should be plowed under, killing the sawflies trapped within (Beres et al., 2011). Feral grasses can also be planted or conserved adjacent to wheat fields, not only attracting emerging sawflies but also conserving parasitoid populations within the un-harvested grasses (Criddle, 1922; Weaver et al., 2004).

While alternative spatio-temporal harvest practices, i.e. swathing instead of standard straight-cutting methods, may allow for a minimal increase in harvested yield, the solution is neither efficient nor cost effective, and is rather quite labor intensive (Nansen et al., 2005a; Weaver et al., 2005). However, swathing practices may be limited to the highest infested regions of the field, where the edges containing the highest percentage of lodged stems may be swathed while the central portion is left untouched by the swather (Knodel et al., 2010). Swathing or stripper heading is recommended for fields with greater than 15% wheat stem sawfly infestation (Knodel et al., 2010). The swathing should occur when the wheat kernel moisture is below 40%, timing the implementation when the kernels have fully developed and before the sawfly larvae have moved towards the bottom of the stem to create their hibernaculum (Knodel et al., 2010).

However, swathing may have a negative impact on beneficial parasitoid populations, as parasitoid larvae would also be killed while living in the upper portions of the wheat stem (Knodel et al., 2010; Bekkerman & Weaver, 2018). Increasing the swathing height, at minimum to two-thirds of the way down the stem, in fields to conserve the amount of residue left in the field may help conserve these parasitoids (Weaver et al., 2005; Rand et al., 2014). Stripper heading may be a better option for parasitoid conservation, as much of the wheat stem is left behind and only the seed heads are collected, allowing the parasitoids to overwinter in the stem and emerge the following year (Knodel et al., 2010).

Crop rotation may help decrease wheat stem sawfly populations, as sawfly populations are limited to laying crops in hollow-stemmed native grasses and cereal crops, such as wheat, barley, and rye (Knodel et al., 2010). Planting corn, soybeans, potatoes, sunflowers, or other broadleaf crops can reduce the within-field sawfly populations, as emerging *C. cinctus* adults won't be able to immediately find a suitable host plant (Knodel et al., 2010). However, as many agroecosystems can become dominated by a single crop, in areas with multiple wheat fields bordering each other, if wheat was planted in a neighboring field, the adult wheat stem sawflies could potentially still infest neighboring fields or feral grasses bordering the fields in ditches of pastureland (Knodel et al., 2010).

Traditionally, no-till strategies have many beneficial impacts for soil health and structure through a reduction of soil compaction, soil erosion, and the amount of soil moisture lost to evaporation, while improving nutrient cycling, nutrient stratification, and the buildup of organic matter (Creech, 2022). Not having to till the soil also reduces fuel and labor costs, allowing the farmer to focus on other necessary work during the spring and fall seasons (Creech, 2017). The current trend for government programing is focused on conservation tillage measures, highly promoting no-till production practices for soil conservation, especially in areas with low annual precipitation (Silva et al., 2017).

Drawbacks to no-till include a lack of mechanical weed control in the spring when the soil is warming up necessitating the usage of more herbicides (Hirsch, 2013), increasing the need for quality weed free seeds (Silva et al., 2017). Foliar and soilborne diseases are also more likely to transfer to the new season of crops when the residue is left unburied (Hirsch, 2013), providing a green bridge for diseases such as powdery milder, take-all, tan spot, strawbreaker foot rot, and dryland root rot in wheat (Silva et al., 2017). No-till practices also disturb soil-dwelling insects less than conventional tillage methods, where the mechanical soil disruption can kill pests living in the soil or crop residue (Silva et al., 2017).

Pertaining to the wheat stem sawfly, no-till management strategies on wheat may inadvertently preserve overwintering sawfly larvae in the crown of wheat stubble left behind from the previous year's harvest (Knodel et al., 2010). Tillage aids in the death in sawfly pupae by disrupting the pupal chamber (Runyon et al., 2002). As the blades break up the soil, wheat tiller clumps are flipped upside down. Inverted sawflies become disoriented, unable to climb "upwards" out of hibernaculum, and subsequently die still inside of the tiller (Thomas & Bradshaw, 2019). Tillage can also break open wheat tillers, exposing *C. cinctus* to greater temperature fluctuations and a higher risk for desiccation (Runyon et al., 2020).

No-till practices can however help suppress *C.* cinctus populations, as no-till management strategies can increase the survivorship of parasitoid populations within wheat fields (Rand et al., 2014). As most parasitoids attack sawfly larva in the upper portion of the stem, tillage would disturb the parasitoid's cocoon (Runyon et al., 2002). Tillage can break the wheat stems, exposing the overwintering parasitoid to too cold of temperatures or burying the stem under soil, leaving the emerging parasitoid adult unable to escape the soil surface (Runyon et al., 2002). In comparing no-till and conventionally tilled wheat fields in Montana, 75% of no-till fields had higher parasitoid population numbers and lower wheat stem sawfly infestation numbers than neighboring tilled fields, as tillage disrupts *Bracon* spp. cocoons inside of the wheat stems (Knodel et al., 2010).

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