
Wheat stem sawfly (*Cephus cinctus* Norton)

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1 Introduction

1.1 Historical distribution

The wheat stem sawfly (WSS), *Cephus cinctus* Norton, has been a major pest of cereal grain production in the Northern Great Plains of North America for well over a century (Beres et al., 2011c; Weiss and Morrill, 1992; Edde, 2022). It was first described from a Colorado grass (Norton, 1872), and Beres et al. (2011c) summarize species characters that may be used to identify this cephid. Currently, damaging populations exist in the contiguous region spanning the states Washington, Idaho, Montana, Wyoming, North Dakota, South Dakota, Utah, Minnesota, Nebraska, Kansas and Colorado and provinces Alberta, Saskatchewan and Manitoba (Fig. 1). These populations are centered on the area of greatest historic damage encompassing Montana, North Dakota, Alberta and Saskatchewan (Beres et al., 2011b).

Wheat stem sawflies are in the family Cephidae (Hymenoptera), which includes all grass-feeding stem sawflies, as well as others that develop in woody plant stems, twigs and branches. Globally, pest members of the Cephidae attacking cereal grains are found exclusively in the northern hemisphere. Three congeners responsible for most of the losses occur in distinct geographic areas. In Eastern Eurasia, the dominant species associated with crop loss is

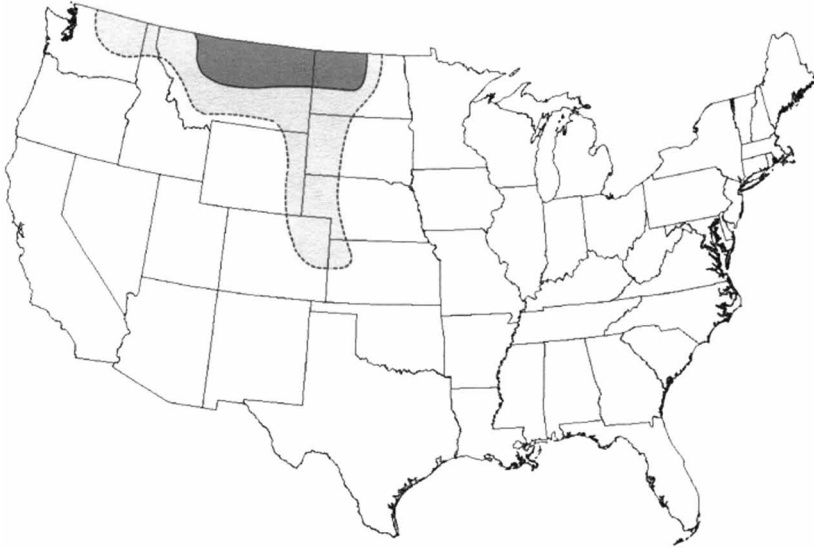


Figure 1 Areas of historical (dark shading) and recent (light shading) damaging wheat stem sawfly populations in the USA. Source: Adapted from: Bekkerman and Weaver (2018).

Cephus fumipennis Eversmann (Chen et al., 2004), while in Western Eurasia and North Africa, the dominant species is *C. pygmaeus* (L.) (Wallace and McNeal, 1966).

The most damaging cephid species in North America is the native WSS, although small populations of introduced *C. pygmaeus* are found in eastern North America (Shanower and Hoelmer, 2004). A fourth species, *Trachelus tabidus* (F.), causes crop losses in North Africa, as well as in the south central and Mediterranean regions of Western Eurasia (Wallace and McNeal, 1966). As for *C. pygmaeus*, small populations of introduced *T. tabidus* have been found damaging wheat grown in the eastern USA (Shanower and Hoelmer, 2004; Filipy et al., 1985). Populations of *C. pygmaeus* and *T. tabidus* in western Eurasia have a longer history of damaging wheat, *Triticum aestivum* L. (Shanower and Hoelmer, 2004). Where wheat was first domesticated, a greater diversity of cephid species is also locally associated with crops (Korkmaz et al., 2010; Çalmaşur and Özbek, 2010; Mutlu et al., 2019). Damaging populations of *C. fumipennis* have been reported in China for approximately 50 years (Chen et al., 2004) and likely have existed for longer in central Asia, although available records are few (Shanower and Hoelmer, 2004).

In North America, the intensification of cereal crop production in the areas where WSS damage occurs is much more recent than where other Palearctic cephids cause losses (Beres et al., 2011a). The recorded distribution of WSS from known host feral and native grasses (Cockrell et al., 2017) also

encompasses a much greater area of North America than where damaging populations in cereal crops are currently found (Ivie, 2001; Olfert et al., 2019). The species was first described from a specimen in native grass collected in Colorado (Norton, 1872) and was subsequently reared from larvae that were collected in grass stems near Alameda, California (Riley and Marlatt, 1891). Ainslie (1920) contains the following prophetic quote from Albert Koebele, who collected the specimens in California: 'The economic importance of this species arises from the fact that it may be expected at any time to abandon its natural food-plant in favor of small grains, on which it can doubtless successfully develop'.

The first record of a member of the Cephidae damaging wheat in North America was in New York in 1887 (Comstock, 1889) and was likely actually introduced *C. pygmaeus*, which is now endemic and rarely occurs in damaging numbers in eastern North America (Ivie, 2001). For WSS, the first record of damage in western wheat crops was in 1895 at locations in southeastern Saskatchewan and southwestern Manitoba (Fletcher, 1896). A historical progression of damaging populations followed the initial westward spread of wheat production first in spring wheat crops in Manitoba, Saskatchewan, Alberta, North Dakota and Montana (Ainslie, 1929). Subsequently, damaging populations emerged in winter wheat, first in Montana in the 1970s (Morrill and Kushnak, 1996) and likely afterward in southern North Dakota, South Dakota and Nebraska, although precise dates are unknown.

1.2 Future range of damaging populations

More recently, damaging populations arose in Colorado winter wheat, with the first observations in 2010 (Cockrell et al., 2021). It is important to note that new, larger populations were found in wheat in southeast Colorado, subsequent to the first records from more northerly counties. This is most likely due to the local adaptation of existing populations from feral grasses (Lesieur et al., 2016) rather than a progression of range expansion by an invasive population shifting southward. Genetic variation within the WSS populations suggests three main haplogroups who are somewhat geographically separated into clusters - with a notable northern cluster of haplogroups spanning the border between the USA and Canada (Lesieur et al., 2016). In Canada, all populations are from the northern haplogroup, while just south of the border in Montana this cluster contains small populations of the two other haplogroups: southern and mountain. Both the mountain and southern clusters contain populations from this northern haplogroup, while the southern cluster in Colorado contains several populations from the northern haplogroup and none from the mountain haplogroup. Grass- and wheat-associated populations exist in all haplogroups (Lesieur et al., 2016), while the southern and northern haplogroups have the

greatest uniformity at the more northern and more southern extremes. Local adaptation to winter wheat progressed southward in Colorado from 2016 to 2021 (Cockrell et al., 2021).

There is a very large area of wheat production where WSS inhabits adjacent grasses only (Ivie, 2001). It is reasonable to assume that the assertion made by Painter (1953) that the life cycles of northwest Kansas populations in grass were too asynchronous from the crop cycle to successfully use large areas of winter wheat is no longer applicable. From the first use of winter wheat by WSS in Montana representing a local change of host use of more than a month sooner (Morrill and Kushnak, 1996) through the southward progression of adaptation in Colorado, this is an ominous scenario. This perspective is further justified by the recent expansion of large damaging populations of WSS into barley (*Hordeum vulgare* L.) in Montana (Varella et al., 2018; Achhami et al., 2020b) representing a further increase in the dryland cropping landscape. Among cereals, hexaploid (*T. aestivum* L.) and tetraploid (*T. durum* Desfontaines) wheat are commonly used as hosts, while another seven species of the genus *Triticum* are reported to be infested to some degree, as well as rye (*Secale cereale* L.) and barley (Wallace and McNeal, 1966). A significant list of host grasses have been recently described by Cockrell et al. (2017) and Peirce et al. (2022) along with Cárcamo et al. (2022), who reported that triticale (\times *Triticosecale*), a hybrid of bread wheat and rye, is a suitable host that could be used as a trap crop or host for parasitoids. Recently, WSS life cycles in grasses are becoming more synchronous with wheat under climate warming coupled with frequent longer-term drought, leading to an ongoing expansion of southern adaptation. It is inevitable that WSS will damage wheat in Oklahoma and New Mexico, followed by Texas and more eastern states. In 2015, damage was reported in Sherman and Wallace counties in Kansas (Colorado Wheat Stem Sawfly Resources, 2020 - <https://coloradowheat.org/2020/08/wheat-stem-sawfly-resources/>).

Equally important is the potential for damaging populations to occur more northerly in Canada under climate warming, with suitable habitat for expanding larger populations also spreading east and west (Olfert et al., 2019). These authors focused on potential impacts in western provinces under specific warming and drying scenarios, with alarming findings of greater suitability for populations over a much larger northerly area than currently impacted. Although not discussed in detail, the potential distribution of WSS suitable habitat illustrated by Olfert et al. (2019) includes parts of North Central Mexico and southeastern USA (Fig. 2). It is imperative that the long-standing, locally adapted presence of the insect in grass, coupled with a capacity to locally adapt to damage wheat quite readily, be recognized as a large and current challenge to wheat production.

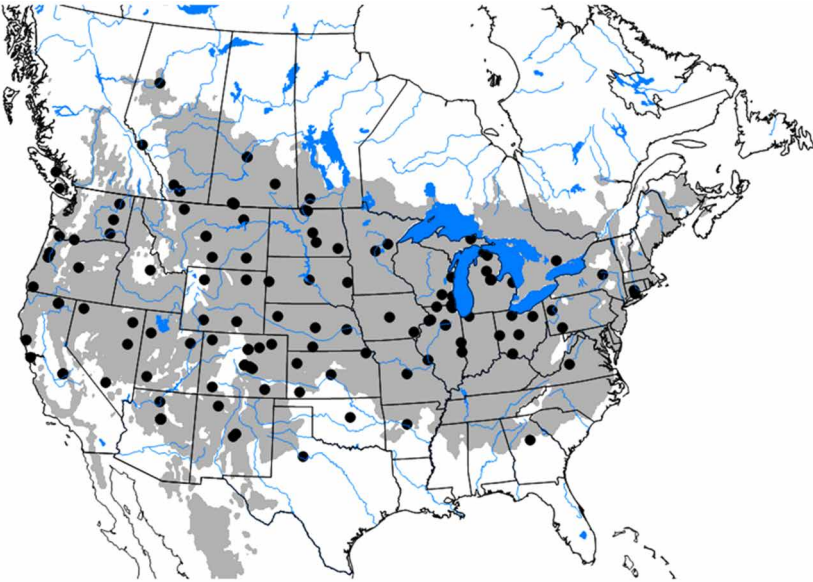


Figure 2 Potential distribution of wheat stem sawfly in North America. Dark points are actual records and dark shading indicates the modeled area where damaging populations might occur. Source: Adapted from: Olfert et al. (2018).

2 Damage

2.1 Unique life cycle-driven losses

The life cycle of WSS is shown in Fig. 3. Unlike most herbivorous pests, the biology of WSS ensures not only decreased yield due to feeding injury, in this case while fully protected inside a stem but also includes obligate cutting of the ripening stem by the larva to provide a secure overwintering chamber for hibernaculum. This is undoubtedly due to an evolved need for protection from exposure to desiccation, excess moisture and pathogens that would occur over up to 8 months of temperate and winter exposure without the frass plug constructed at the time of stem cutting. The frass plugs and diaphanous hibernacula both protect the overwintering larvae and facilitate easy egress of new adults the following year. The stem cutting also allows for a lengthy obligate larval diapause to be accomplished readily within protective hibernacula (Ainslie, 1929), and diapause can be reentered or maintained under unfavorable conditions for an additional year (Holmes, 1982).

In ripening crops, this stem cutting typically leads to lodging with the head of the infested plant on the ground, where it is difficult to recover even with specialized equipment. In practice, it is not possible to recover all lodged

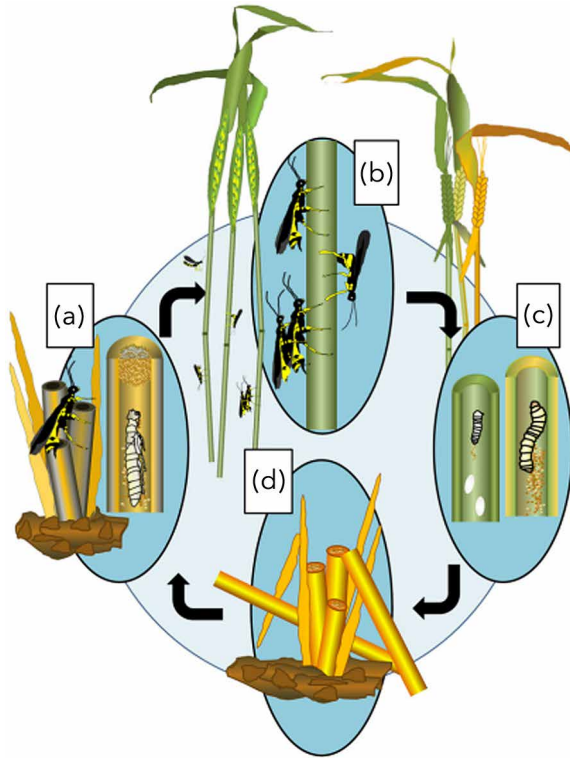


Figure 3 Life cycle of the wheat stem sawfly. (a) Overwintering chambers with pupae and newly emerged adults; mid-May–early July; (b) mating and oviposition; late May–mid-July; (c) eggs, feeding neonate and late-instar larvae with frass and early senescence of injured hosts; June–late July; (d) stems newly cut by late-instar larvae, with larvae in hibernacula inside until metamorphosis; mid-July–late May of the subsequent year. Source: Adapted from: Robertson et al. (2018).

heads that are due to stem cutting by WSS, and the degree of severity of this stem cutting influences the probability that a cut stem will be recovered. Prior to stem cutting, dissection of stems will yield clear evidence of extensive dry frass that is diagnostic of the species. The species is haplodiploid, meaning unmated females can lay eggs that produce male progeny (Holmes, 1982), with new females tending to emerge from larger stems (Morrill et al., 2000) while males are more likely to be found across smaller stems (Morrill and Weaver, 2000). Although each female typically lays a single egg per stem (Holmes, 1982; Buteler et al., 2009), females cannot detect the presence of conspecific eggs or feeding larvae (Buteler et al., 2009). This greatly increases the chances for larval cannibalism within stems (Criddle, 1923; Buteler et al., 2015; Achami et al., 2020a).

2.2 Physiological yield loss

Impaired photosynthetic capacity from feeding damage in infested stems combines with abiotic stress to limit head weight by as much as 30% (Macedo et al., 2005, 2006, 2007; Delaney et al., 2010). This is corroborated by findings of 10–20% yield loss in spring wheat (Seamans et al., 1944; Holmes, 1977) and winter wheat (Morrill et al., 1992). Morrill et al. (1992, 1994) noted that larger stems were more likely to be infested, which can challenge simple estimation of loss because of innate differences in potential yield. Holmes (1977) reported that among infested stems those that were cut had head weights decreased by 17%, while those that were not cut yielded 11% less. Using an extensive dataset, the model of Bekkerman and Weaver (2018) similarly reported a further 9% decrease in yield for stems infested with larger larvae that proceeded through to stem cutting. Early larval feeding is confined to parenchymal tissues, but when these resources are exhausted in an internode the larva bores through the node impacting the vascular architecture. Late infestation is characterized by extensive feeding on parenchyma in all internodes, along with boring injury at most, if not all, nodes. Frass can be densely packed throughout the entire stem by the time a stem is cut, and it is not known whether loss of parenchyma or loss of vascular integrity contributes more to yield loss, since both occur. Morrill et al. (1994) attribute a darkened region below the node of ripening stems to accumulation of assimilate after vascular transport is disrupted.

2.3 Yield loss from unrecovered heads

Growers may not have any easy in-season estimate of potential head weight loss due to WSS feeding, which complicates management, although sampling guidance (Cockrell et al., 2021; McCullough et al., 2020; Nansen et al., 2005a, 2005c; Weaver et al., 2005) and sampling plans exist for characteristic 'edge-effect' populations (Nansen et al., 2005b; Cárcamo et al., 2007; Pesho et al., 1971). In contrast, at harvest, growers readily detect newly cut stems lodging due to the clear disruption of the standing row structure. In heavy infestations, fallen stems are difficult to harvest, especially after a wind event (Ainslie, 1929; Criddle, 1921, 1922, 1923). Early estimates of crop loss due to stem cutting range from 25% of a crop (Criddle, 1922) to 30% of potential yield (Ainslie, 1920), while Beres et al. (2007) estimated losses across cultivars ranging from 6% to 20% due to unrecovered heads. These numbers approximate those derived from the loss of 11 heads per square meter suggested by Holmes (1979) which he determined to be 67 kg/ha and subsequently 53 kg/ha (Beres et al., 2007), due to varietal differences.

2.4 Overall losses

Historical overall crop loss estimates range from over 500 000 tons across the prairies of Canada (Platt and Farstad, 1946) to over 150 000 tons in North Dakota (Davis, 1955), while Beres et al. (2011c) estimate aggregate losses of US\$350 million over the entire impacted area of wheat production in North America. The price of wheat currently would make these economic losses 60% greater, before considering that the area associated with damaging populations has increased in Nebraska, Colorado and Kansas. Calculation of current overall losses due to WSS remains challenged by increasing costs of on-farm inputs, inefficiency and additional operations at harvest associated with fallen stems, plus associated equipment costs and repairs (Beres et al., 2007; Bekkerman and Weaver, 2018). It is also difficult to quantify impacts such as increased soil erosion due to stem lodging that perturbs the wind boundary layer in stubble fields, which are also likely to have lower overall snow retention (Beres et al., 2011a; 2011c). Such environmental costs may decrease the available soil moisture, having a direct impact on crop yield, but estimates of current losses due to WSS considering all interactions with environmental factors are beyond the scope of this review.

3 Management

3.1 Insecticides

Adult WSS are likely to emerge over a period ranging from several weeks to longer than a month (Perez-Mendoza and Weaver, 2006), with variation likely to arise from location and wheat variety, suggesting a role of landscape-level population structure and host suitability (Lesieur et al., 2016). A lengthy adult flight period is not conducive to management using contact insecticides because it requires frequent repeat applications and is not efficacious or cost-effective (Knodel et al., 2009). Larvae feeding inside the stems are fully protected from contact insecticides, and only high rates of the systemic insecticide heptachlor (Wallace, 1962; Holmes and Peterson, 1963; Wallace and Butler, 1967) yielded results worthy of further study. More recently, the Montana Department of Agriculture issued a special local need pesticide registration [Section 24(c)] for phorate (Thimet®20-G), an organophosphate soil and systemic granular insecticide to control WSS larvae (Montana Department of Agriculture, 2015). This was due to a 367 kg/ha average yield increase and an 82% decrease in average stem cutting in winter and spring wheat (Wanner and Tharp, 2015). However, post-crop emergence soil incorporation of this insecticide poses potentially unacceptable health and environmental risks and has a long preharvest interval of 85 days in wheat (Portman et al., 2018). For these reasons, the use of phorate was limited, and the 'special local need'

registration against WSS larvae in wheat in Montana was not renewed after expiration on 31 December 2019.

Research on alternative or low-impact insecticides, such as neem and Azadirachtin®, the plant defense elicitor Actigard® and signaling molecules had variable and limited, inconsistent benefits against WSS (Tangtrakulwanich et al., 2014; Shrestha et al., 2018) except for WSS adults preferring not to settle on Azadirachtin- or Actigard-treated wheat plants when there were untreated control plants available. In the absence of control wheat plants, and under no-choice conditions, adult WSS settled on treated wheat (Shrestha et al., 2018). Preliminary results for two applications of Actigard® in winter wheat during the growing season had greater WSS larval mortality, reduced larval body weight and wheat stem lodging (Shrestha et al., 2018). Current management of WSS relies entirely on integrated pest management without the planned inclusion of insecticides.

3.2 Cultural tactics

Several approaches have been used to potentially destroy WSS larvae. Among these is burning crop residue, suggested in Fletcher (1904), but Ainslie (1929) reported that there was limited impact on larvae due to their location inside cut stems below the soil surface. There was insufficient heating due to the rapid transient nature of the fire, even when excess straw was layered over residue to increase the intensity and longevity of the fire.

It is now generally considered that any process that removes soil residue has a detrimental impact on desirable soil attributes and moisture (Lafond et al., 1996; Lindwall and Anderson, 1981), which would include burning or moldboard ploughing (Mathews, 1945). The heavy erosion associated with the latter practice led to the use of limited disturbance tillage, such as the Noble blade, that was asserted to have increased WSS damage on the landscape (Holmes, 1982). However, it is difficult to find corroborating data; Ainslie (1920) reported that adult emergence was 90% when stubs containing larvae were buried at depths of 10 cm and 65% when buried at a depth of 15 cm. Farstad et al. (1945) stated that good control could be achieved by deep ploughing residue to a depth of 15 cm or more or by deep tillage of summer fallow that buried the developing WSS. The same publication also suggested shallow tillage that exposed the stubs on the soil surface was also effective in causing mortality before adult emergence, which was confirmed by Morrill et al. (1993). These authors also suggest that the high levels of mortality observed were due to the desiccation of the larvae in the arid environment of dryland wheat fields. In a later study, Runyon et al. (2002) observed that the process of burying residue had greater detrimental effects on beneficial parasitoids than on WSS, leading to a surprising observation that fields adjacent to herbicide-managed

no-till cropping had less WSS damage - due to suppression by parasitoids - than heavily tilled fields. More recent WSS publications are replete with declarations that no-till practices have worsened WSS problems due to the loss of mortality caused by tillage, although Weiss et al. (1987) reported no effect of tillage on WSS survival. There is likely some mortality to WSS due to modern tillage operations, especially when stubble is sufficiently exposed or even by direct impact with an implement, but those considering such practices should look for evidence of a reduction of damage in the following crop before undertaking these efforts on a large scale (Morrill et al., 1993).

Historically, considerable attention was also given to trap crops that would intercept and retain immigrating WSS females, thus concentrating infestation on the perimeter of fields (Criddle, 1922). Most recommendations focused on the destruction of infested stems of annual crops such as rye, *S. cereale* L. (Criddle, 1921) or wheat by mowing or tilling (Ainslie, 1929; Farstad et al., 1945). Another observation was that smooth brome, *Bromus inermis* L., was suitable as a permanent trap because it elongated earlier than wheat and was highly attractive while also having limited survival and elevated parasitism (Criddle, 1922; Seamans, 1928; Farstad et al., 1945). Historically, growers may not want to give up productive land to sowing a crop that must be destroyed before harvest - or be willing to concede crop area to a permanent trap (Beres et al., 2011c).

Recently, trap crops such as non-host or resistant traps such as oats or solid-stem wheat have been revisited (Beres et al., 2009; Morrill et al., 2001a). However, Beres et al. (2009) found that this practice was ineffective due to large WSS populations overwhelming any benefits of trapping. Morrill et al. (2001b) used the phenological advantage of planting more favored winter wheat (a resistant solid-stem variety) as a border around hollow-stem spring wheat to demonstrate the efficacy of the concept. One disadvantage was that two separate seeding operations were required, and the benefits may not justify this costly approach. There may be a methodological flaw in how trap cropping is approached, where a potential trap crop is selected without considering variability among cultivars in attractiveness to the sawfly. Several volatile compounds from wheat were found to have behavioral activity for WSS females (Piesik et al., 2008), and these can explain field preferences between cultivars (Weaver et al., 2009). These differences were evident in winter (Buteler et al., 2010; Buteler and Weaver, 2012) and spring wheat (Weaver et al., 2009). Peirce et al. (2022b) found that triticale was a potential trap crop for WSS but was not more attractive than winter wheat to ovipositing WSS. This crop may also be quite suitable as a reservoir for parasitoids of WSS (Cárcamo et al., 2022). Thus, the key to developing effective trap crops remains a characterization of behavioral and oviposition preferences to identify the most attractive cultivars within any germplasm considered for deployment (Weaver et al., 2009; Sharma

et al., 2019), as well as consideration of any impacts on parasitoids. Without more careful screening to assess the suitability of the trap crop and target crop, it will continue to be reported that trap cropping is of limited suitability or only applicable for light infestations (Weiss et al., 1990; Beres et al., 2009; Peirce et al., 2022a).

Swathing is a late-season operation that may be required to windrow heavily infested crops to prevent stem losses due to lodging (McCullough et al., 2020) and can be considered for either field margins or entire fields, depending on the severity of infestation (Nansen et al., 2005b). The practice was evaluated to determine if there is potential to use a swather to manage larval WSS populations by cutting the stem below where they are feeding (Holmes and Peterson, 1965). The authors found that the process was only partially effective when stems were swathed at a moisture content that was too high to maintain quality at harvest and did not recommend it if the WSS population was large. In addition, the idea of recoverable yield only strictly applies to stems that would be cut, overlooking the smaller heads due to physiological yield loss; simulations suggest the practice is costly and less efficient than managing large populations by repeated planting of WSS-resistant solid-stem wheat (Bekkerman and Weaver, 2018).

Wheat is an optimal crop for dryland agriculture and monocultures, whether or not interspersed with fallow fields, which can cause potentially severe WSS damage across large landscapes (Beres et al., 2011a; Weiss and Morrill, 1992; Adhikari et al., 2019a). Early in the last century, crop diversity was recognized as an important component in regulating outbreaks of WSS (Criddle, 1922, 1923). Logically, planting of non-hosts is a key part of the effective management of long-term outbreaks as are numerous other aspects of cropping systems (Beres et al., 2011c; Zentner et al., 2006).

Other considerations, including production type and cropping system (Adhikari et al., 2018; Malone et al., 2020, 2022), impacts of weed populations (Weaver et al., 2004; Perez-Mendoza et al., 2006; Keren et al., 2015; Cockrell et al., 2017), impacts of fertilizer use (Luginbill and McNeal, 1954; Delaney et al., 2010; Beres et al., 2011a; Beres et al., 2012), increased row spacing and seeding rates (Luginbill and McNeal, 1958; Miller et al., 1993; Beres et al., 2011b; Beres et al., 2012), later planting dates (Jacobson and Farstad, 1952; McNeal et al., 1955; Weiss and Morrill, 1992; Morrill and Kushnak, 1999), residue management (Weiss et al., 1987; Beres et al., 2011a; Beres et al., 2012) and harvest operations (Beres et al., 2011a; Bekkerman and Weaver, 2018), must be included when planning wheat cropping strategies in WSS-impacted areas. A thorough review of these is found in Beres et al. (2011a, 2011c), but in general, less disturbance, moderation in the use of inputs and conservation of ecosystem services all are favored in a proactive plan for economically optimal wheat production in the presence of damaging WSS populations.

3.3 Biological control

The management of WSS depends significantly on biological controls, primarily by parasitoids but also by insect predators, pathogens and nematodes.

3.3.1 Parasitoids

Two species of native parasitoids, *Bracon cephi* (Gahan), first described in 1918 (Gahan, 1918), and *B. lissogaster* Muesebeck, first described in 1953 (Muesebeck, 1953), can provide significant biological control of WSS (Buteler et al., 2015; Rand et al., 2017; Rand et al., 2020b). Their biology has been reviewed in detail [*B. cephi* - Nelson and Farstad (1953); *B. lissogaster* - Somsen and Luginbill (1956)]. WSS (late instars) is the only known host of either species, other than for the infrequent occurrence of hyperparasitism in both species (Davis et al., 1955). Although *B. cephi* and *B. lissogaster* were responsible for more than 80% mortality of larval WSS in grasses in Manitoba (Criddle, 1922), WSS in nearby heavily damaged wheat was not parasitized. This was more than 25 years after damaging WSS were first observed in wheat (Ainslie, 1920). Criddle (1923) made the first report of *B. cephi* attacking WSS larvae in wheat and was hopeful that *B. cephi* would eventually move into wheat and provide useful levels of biological control. These first observations (Criddle, 1923) were of first-generation presence in the wheat, possibly only occasional early-season foragers. WSS population suppression by *B. cephi* was recorded in wheat over a period of favorable years in North Dakota (Munro et al., 1949) and the Canadian Prairies (Nelson and Farstad, 1953; Davis et al., 1955; Holmes et al., 1963).

Currently, WSS populations are successfully suppressed by these parasitoids in many areas - with possible parasitism rates of greater than 90% (Holmes et al., 1963; Morrill et al., 1998; Runyon et al., 2002; Weaver et al., 2004; Wu et al., 2011, 2013; Cárcamo et al., 2016). Their bivoltine life cycles on a univoltine host are a major part of the frequently reported successful suppression of WSS. The life cycle of both *B. cephi* and *B. lissogaster* both feature adult emergence at approximately the same time as the host species (Nelson and Farstad, 1953; Somsen and Luginbill, 1956), with females requiring a pre-oviposition period in both species, although it is more protracted in *B. cephi*. This is likely to allow for WSS hosts to feed and develop to late-instar larvae suitable for detection (Somsen and Luginbill, 1956; Mankin et al., 2000, 2004) and subsequent parasitism (Nelson and Farstad, 1953). On the other hand, as first noted by Criddle (1923), the second generation may not be fully successful in wheat crops due to asynchrony, presumably because of early crop ripening and advanced harvest date that occurs under drought conditions that are frequent in these dryland cropping systems (Holmes et al.,

1963; Holmes, 1979; Rand et al., 2014; Peirce et al., 2021). This is difficult to corroborate experimentally. Rand et al. (2020b) conducted experiments with supplemented and constrained annual water limitations in caged wheat systems, but the treatments do not represent landscape-level drought, where WSS larval host availability in standing wheat stems is truncated by very early cutting of prematurely ripening wheat, which ultimately greatly constrains the success of second-generation parasitoids. Thus, the potential for suppression of WSS by these parasitoids is high, with the caveat of population declines as a result of drought, and especially multi-year drought (Holmes et al., 1963).

Changes in WSS life history associated with its attacking wheat necessitate subsequent adaptation for *B. cephi* and *B. lissogaster* (Criddle, 1923; Ainslie, 1929; Nelson and Farstad, 1953; Cárcamo et al., 2012; Peirce et al., 2021). This is especially true for more southerly regions of southern Montana, Colorado, Nebraska and Kansas where both host and natural enemies must utilize earlier maturing crops. For example, the transition to successful parasitism of WSS larvae in winter wheat in Montana was governed by a shift to earlier WSS adult emergence of approximately a month - probably in the 1970s (Morrill and Kushnak, 1996). *B. cephi* and *B. lissogaster* rapidly followed from nearby fields of spring wheat, a long-standing host of WSS and its parasitoids (Morrill et al., 1994). In winter wheat in Nebraska, Colorado and Kansas, where spring wheat is not grown, an equally rapid shift from grasses to winter wheat by the parasitoids is unlikely (Lesieur et al., 2016; Cárcamo et al., 2012) because this requires a shift in host plant species as well as a shift in phenology (Morrill et al., 1994, 1998; Cockrell et al., 2017; Peirce et al., 2021). Similar to the observations of Criddle (1923) and almost a century later, both parasitoids are present in grasses surrounding Colorado wheat fields, but there is as yet no parasitism of WSS in the wheat (Peirce et al., 2021) despite WSS first appearing in Colorado wheat in 2010 (Cockrell et al., 2017). Nonetheless, eventual biological control of WSS by these parasitoids will likely be important for its management in more southern regions where varietal choices on agricultural landscapes can trigger local intensification of WSS populations (Rand et al., 2012, 2014; Peirce et al., 2021), likely due to a massive increase in the density of highly suitable host stems per unit area. The cryptic and secure WSS developing inside wheat stems (Ainslie, 1920; Holmes, 1982; Weiss and Morrill, 1992; Weaver et al., 2005) are protected from natural enemies other than the bivoltine parasitoids (Holmes and Peterson, 1963). Although more than 66% of the stems cut by WSS were reported to be cut below the soil surface (Runyon et al., 2002), reports of elevated, unexpected levels of parasitism were reported in WSS cut stems (Rand et al., 2011; Cárcamo et al., 2011). It is not known whether these parasitized, cut stems were cut above the soil surface, but it does illustrate adaptation by both WSS and parasitoids to the agricultural system. Rand et al. (2017) suggested that 68% parasitism of

WSS larvae were required to suppress population growth, whether larvae were actively feeding or were in chambers created after stem cutting (called winter or summer larvae).

3.3.2 Enhancement of native parasitoids

Success of parasitism could be improved with habitat management. Pre-oviposition stage parasitoids have greater longevity, egg load and egg size when supplemental carbohydrates and amino acids are available (Reis et al., 2019; Rand et al., 2020a; Cavallini et al., 2022). This includes both nectar and honeydew (Rand et al., 2020a), as well as artificially supplemented resources (Reis et al., 2019; Cavallini et al., 2022). Management to provide these resources could improve parasitism. The overwintering strategy of *B. cephi* involves the accumulation of glycerol to enable supercooling and even freeze tolerance for the survival of prolonged exposure above the surface of the frozen substrate during the winter (Salt, 1956, 1959). Nelson and Farstad (1953) report that synovigenic *B. cephi* also foraged yellow flowers for nectar, while Somsen and Luginbill (1956) included honey-water as a nutritional supplement to increase longevity while collecting early data on synovigenic *B. lissogaster*.

Possibly consistent with a reliance on floral resources by these parasitoids, where WSS has had large impacts on intensified production of wheat crops, there has often been very limited cultivation of flowering species (Adhikari et al., 2019a) except for limited acreage of organic wheat production (Adhikari et al., 2018). The trend in crop production in dryland agriculture to favor increased floral diversity, with benefits for native and introduced pollinators (Adhikari et al., 2019b, 2019c), potentially can benefit WSS parasitoids. Although WSS can also benefit slightly from floral resources (Rand et al., 2019), this has no other impact on reproductive parameters. WSS and parasitoid preference for yellow flowers (Wallace and McNeal, 1966) could reflect a need for water [also corroborated in the experiments of Rand et al. (2019)] for greater longevity in the dryland habitat. It has been suggested that efforts to conserve and even mass produce the native braconid parasitoid species have merits (Portman et al., 2018).

3.3.3 Biological control and host plant resistance

The importance of parasitism in solid-stem WSS-resistant wheat (Weaver et al., 2004; Cárcamo et al., 2011) was explored using models to estimate the combined effect of solid-stem wheat-based resistance and parasitism on WSS larvae (Rand et al., 2020a). The findings showed that parasitism at 22% will attenuate WSS population growth in solid-stem wheat, which has great

value for wheat growers. There are concerns about comparison of parasitoid efficiency (Weaver et al., 2004) and numerical responses (Cárcamo et al., 2011; Rand et al., 2012) across resistant and susceptible wheat that warrant further exploration, considering the somewhat concerning findings of Rand et al. (2012). In a recent review, Peirce et al. (2022) tabulate the benefits of host plant resistance, including contradictory reports on the interactions of solid stems with the specialist braconid parasitoids; nonetheless, efforts to increase host plant resistance have great merits.

Parasitism is complementary to host plant resistance because it delivers mortality to late-stage larvae, while mortality to host plant resistance is greater against younger and especially neonate larvae (Nelson and Farstad, 1953; Somsen and Luginbill, 1956; Peterson et al., 2011; Buteler et al., 2015). Mortality by parasitism is irreplaceable because later instars are protected within stems and protected from most other sources of mortality (Rand et al., 2017, 2020a). Although host plant resistance impedes establishment by early instars, the parasitoids have immediate economic value because they are idiobionts that paralyze hosts, preventing further injury to the stem, as shown by Buteler et al. (2008) and corroborated in the model of Bekkerman and Weaver (2018). Losses due to parasitizable late-stage larvae proceed a further 8% if injury continues to stem cutting, while there is a relative increase of 11% for such stems containing parasitized larvae. Thus, to incentivize wheat producers to conserve and enhance parasitoids, both decreased yield losses in the current crop and decreased risks to subsequent crops must be emphasized.

3.3.4 Other parasitoids

Efforts to identify additional parasitoid species for use against WSS have been well summarized (Shanower and Hoelmer, 2004; Hoelmer and Shanower, 2004). Much of this was based on the idea that WSS relatively recently colonized North America (Ivie, 2001). Foreign exploration in its presumed native range in Asia identified *Collyria catoptron* Wahl, which parasitizes *Cephus fumipennis* Eversmann (Wahl et al., 2007) as a candidate for further evaluation against WSS. The results showed that the parasitoid could successfully detect WSS larvae but could not complete development (Rand et al., 2016). Subsequently, it was shown that WSS was likely native to North America rather than a recent colonist (Lesieur et al., 2016) helping to explain why *C. catoptron* failed to develop in WSS. Multiple native parasitoid species attack WSS larvae in grasses, but they are very infrequently found in WSS-infested wheat plants (Davis et al., 1955; Morrill et al., 1998). The reasons for this are unclear, but several of the species are generalists that use multiple stem inhabiting hosts that are abundant in grass, including WSS.

3.3.5 Predatory species

A predatory clerid, *Phyllobaenus dubius* (Wolcott), occasionally causes low levels of mortality of WSS larvae, most often detected in overwintering stubs, as was the case for the specimens used for initial identification (Morrill et al., 2001b). Although there have been reports by others confirming this (Beres et al., 2009; Cárcamo et al., 2011), and alluding to other, related clerid species that could be doing the same thing (Beres et al., 2011c), very little is known of the life cycle of this predatory species or other predators nor are there any estimates of potential impacts on WSS.

3.3.6 Pathogens and nematodes

There has been work on entomopathogenic nematodes (Tangtrakulwanich et al., 2014; Portman et al., 2016, 2018), including efforts to identify native species in WSS habitat (Sandhi et al., 2020). In laboratory experiments, Portman et al. (2016) showed that nematodes were successful in killing WSS larvae in stubs especially with certain adjuvants, but these results did not translate into reliable efficacy in the field (Portman et al., 2016). Further exploration is needed (Portman et al., 2018), perhaps using species isolated from dryland wheat production (Sandhi et al., 2020).

Some fungal pathogens can impact WSS, including a complex of facultative *Fusarium* species isolated from larval cadavers (Wenda-Piesik et al., 2009), and commercially marketed strains of *Beauveria* and *Metarhizium* species (Tangtrakulwanich et al., 2014; Portman et al., 2018). Limited efficacy occurs for commercial pathogens that are applied externally to infested plants, perhaps because persistence is limited in these arid settings, but there may be potential for future development of these as endophytes for commercial use in wheat (Portman et al., 2018). The isolates of the *Fusarium* spp. are facultative entomopathogens that also cause plant disease in wheat and have limited utility unless a strain is found that is asymptomatic in wheat while maintaining the ability to kill WSS larvae (Wenda-Piesik et al., 2006, 2009; Portman et al., 2018).

4 Host plant resistance

The foundation of WSS management is planting rotational crops that are not hosts or are poor hosts of WSS (Weiss and Morrill, 1992). Dryland crops such as legumes and oilseeds may help to curtail persistent large populations of WSS as part of a broad production practice, even in a wheat-focused cropping scenario (Miller et al., 2002). None of the broadleaves are hosts except for one early report of oviposition in flax without successful development (Farstad, 1944). Among grasses, frequently cultivated cereals range in susceptibility

(Cockrell et al., 2017). Hexaploid bread wheat is more susceptible than durum wheat, which is followed by barley (Varella et al., 2018; Achhami et al., 2020c) and finally by oat (Beres et al., 2011c). Oat species are readily accepted for oviposition but are lethal to WSS eggs and larvae (Criddle, 1923; Ainslie, 1929; Weaver et al., 2004). Criddle (1923) attributed mortality to observations of excessive sap production in oat and a possible nutritional deficiency creating an unfavorable environment for larvae. The moisture content of oat is not different from that of either resistant or susceptible wheat, and WSS mortality occurs at an early stage, suggesting that a nutritional deficiency in oat is an unlikely cause (McGinnis and Kasting, 1961).

4.1 Pith containing wheat stems

Kemp (1934) showed that wheat stems containing pith were cut less by WSS larvae. Pith was an early focus on heritability of traits in wheat (Engledow and Hutchinson, 1925), even before potential benefits in WSS suppression were known. This observation and the ability to breed wheat cultivars targeting complete expression in all internodes (Dhariwal et al., 2022) soon led screening and breeding for solid stems rather than tests of resistance to WSS (Sherman et al., 2015; Talbert et al., 2014) because it was possible to readily assay pith in the absence of consistent and vigorous WSS populations. While solid-stem wheat varieties are the foundation of WSS management (Beres et al., 2011a, 2013a, 2013b), it is likely incorrect to strive solely for maximal expression of stem solidness throughout the stem. This is because WSS mortality is caused by several aspects of pith solidness. Simple stem phenotyping does not detect temporal variations such as 'early solidness' (Talbert et al., 2014; Varella et al., 2016) that can influence WSS behavior and survival. Understanding of the effects of pith on WSS oviposition and increased larval mortality has lagged (Varella et al., 2017b). Indeed, according to recent reviews, mortality in solid-stem wheat is reported to be due to physical factors impeding immatures or due to early drying of pith in solid stems (Peirce et al., 2022) or 'crushing' eggs (Beres et al., 2011c). The former is now less common, with only a small proportion of larger larvae dying in pith that impedes their ability to cut the stem for overwintering – and there is limited evidence in the scientific literature that truly supports that early drying of pith causes increased larval mortality. Rather, desiccated pith itself, arising under early, normal, or late drying, becomes a lethal barrier to some larger larvae. The inability to move and consume nutrients in desiccated pith of solid-stem wheat causes mortality and the cadaver dehydrates rapidly, but there is no evidence of larval desiccation as a direct mortality factor (Kasting et al., 1958; McGinnis and Kasting, 1961). In solid-stem pith, unhatched eggs containing embryos that have died appear deflated due to loss of liquid, but the outer surface of such eggs are intact

- there is no evidence that the integrity of the egg is lost via 'crushing' that breaches the chorion. Loss of water in egg or larval cadavers is expected, so the occurrence of dehydrated cadavers does not support desiccation-causing mortality. In a survey of the literature, 'crushing' of the larvae by the stem is only reported for overwintered hibernacula within cut stubs of timothy, *Phleum pratense* L., in which larvae are crushed by early-season 'bulb-like' growth of new plants (Farstad, 1940). This effect is limited, and otherwise timothy is susceptible to stem cutting by WSS (Criddle, 1922; Ainslie, 1929) and should be considered a host.

The key cause of mortality across all resistance to WSS is antibiosis, whether it is 'absolute' as in oat, which has hollow stems (Criddle, 1923; Ainslie, 1929), 'relative' in barley, which also has hollow stems (Varella et al., 2018; Achhami et al., 2020b, 2020c), or 'relative' in solid-stem wheat, which kills more larvae than hollow-stem wheat (Buteler et al., 2015; Varella et al., 2017b). Partial or 'relative' antibiosis, like in solid-stem wheat, has other fitness impacts on surviving larvae that inhibit population dynamics (Cárcamo et al., 2005). The cumulative advantage of the sublethal effects, combined with moderate mortality, has led to research with repeated planting (Holmes and Peterson, 1957) to evaluate longer-term impacts and contributions to population suppression. Data-driven models show that repeated planting of solid-stem wheat to counter large infestations is better than planting agronomically desirable hollow-stem wheat and swathing (Bekkerman and Weaver, 2019). Solid-stem wheat has better yields than hollow-stem wheat under large, damaging WSS infestations (Beres et al., 2007, 2009), despite its perceived agronomic liabilities in the absence of WSS. Yield under moderate-to-heavy sawfly infestation is often a key component of the registration of new solid-stem germplasm (Bruckner et al., 2020) and complements yield data obtained across multiple environments that encompass all levels of WSS infestation.

To further enhance mortality by isolating toxic compounds in the solid-stem pith of wheat, or from other host plant resistance, which could subsequently be targeted in breeding efforts is difficult. It is not possible to rear WSS larvae on an artificial diet (Kasting and McGinnis, 1958; McGinnis and Kasting, 1962; Macedo et al., 2005) long enough to quantify the mortality of candidate toxic compounds in bioassays. The potential for solid-stem pith components to cause antibiosis in WSS was inferred using a surrogate pest cutworm species (McGinnis and Kasting, 1959; Kasting and McGinnis, 1961), which showed a clear inhibition of growth when solid-stem pith was incorporated into an artificial diet, relative to other tissues. Molecular methods are being used to identify other traits that could confer WSS resistance (Biyiklioglu et al., 2018). Of interest are miRNAs as well as short- and long-noncoding RNAs that may differentially regulate the expression of host plant responses within infested plants (Akpınar et al., 2023; Cagirici et al., 2017; Biyiklioglu et al., 2018; Brant

and Budak, 2018; Budak et al., 2020; Muslu et al., 2021; Robertson et al., 2018). The goal of hollow-stem wheat lethal to immature WSS (as in oat) based on classical breeding with non-wheat sources of resistance seems remote. The ability to scrutinize mechanisms causing mortality by comparing the relative expression of genes and metabolites in infested versus uninfested stems may provide insights (Biyiklioglu et al., 2018; Peirce et al., 2022).

4.2 Loci conferring stem solidness in wheat

Breeding for solid-stem wheat can be enabled by determining quantitative trait loci contributing to stem solidness (Dhariwal et al., 2022). These include loci on the 3B chromosome in hexaploid and tetraploid wheat (Cook et al., 2004; Lanning et al., 2006; Houshmand et al., 2007) and the 3D chromosome in hexaploid wheat (Lanning et al., 2006). Allelic variations at the 3B locus confer early solidness or lack of pith (Cook et al., 2017; Wong et al., 2022). Exploration of resistance in targeted populations or broad screening of landraces (Varella et al., 2015, 2017a, 2019a, 2019b; Cook et al., 2017; Peirce et al., 2022) in hexaploid and tetraploid wheat identified several other loci conferring useful stem solidness on chromosomes 1B, 2A, 3A, 4A, 5A, 5B, 5D and 6B (Sherman et al., 2010; Varella et al., 2017a; Nilsen et al., 2017; Cook et al., 2017; Varella et al., 2019a, 2019b), most of which were corroborated using WSS infestation and mortality data. Recently, genes on different chromosomes have been identified that are associated with stem solidness, including those expressed primarily in the basal or lower internodes, which may govern lignification processes that result in greater stem strength (Kebrom et al., 2012; Hyles et al., 2017; Oiestad et al., 2017). Nilsen et al. (2020) identified that copy number of *TdDof*, encoding a Dof zinc finger protein, controls stem solidness at the 3B locus in tetraploid and hexaploid wheat. Greater copy number was associated with increased retention of solid-stem characteristics. There is a great need for a comprehensive review of stem solidness and WSS resistance in wheat, focusing on consolidating information across publications focusing on genetics and molecular mechanisms.

4.3 Maximizing stem solidness in crops in the field

Early solid-stem varieties expressed pith inconsistently under environmental conditions that reduce light levels (Beres et al., 2017; Subedi et al., 2021). Thus, a major goal for breeding remains complete solidness across all internodes that is maintained even under low light levels (Dhariwal et al., 2022; Liang et al., 2022). Meanwhile, current recommendations to growers using existing germplasm may include cultivation practices such as avoiding high seeding and fertilizer rates to reduce undesirable autoshading within the crop that

reduces stem solidness (Luginbill and McNeal, 1954, 1958; Beres et al., 2011a, 2011b; De Pauw and Read, 1982). Equally important is the comparative field assessment of solid-stem commercial cultivars (Beres et al., 2013a) and all other germplasm that has potential utility (Beres et al., 2013b) under the conditions imposed by large and damaging WSS populations. Often, it is not possible to combine agronomic and host plant resistance studies over a large geographic area, which makes those studies that do this all the more important (Subedi et al., 2021). Ideally, it will be possible to someday deploy wheat varieties with resistance levels more like those found in barley or even oat.

4.4 Other considerations for host plant resistance

Modern comparative techniques also show great promise in understanding underlying mechanisms for resistance. These include comparative metabolomics of leaf surface compounds (Lavergne et al., 2018), which may play a role in antixenosis, or non-preference, for ovipositing WSS. These, along with volatile attractants, may play a critical role in oviposition choices made by females (Weaver et al., 2009; Lavergne et al., 2018; Varella et al., 2017b). Equally important are those studies that have compared transcriptomic responses to WSS infestation (Biyiklioglu et al., 2018) as well as proteomic and metabolomic responses to infestation (Lavergne et al., 2020). These studies provide important insights into candidate germplasm for mechanistic exploration of relative responses to infestation across cultivars (Lavergne et al., 2020). For example, the relatively susceptible cultivar 'Hatcher' had the greatest number of induced changes in expression, while more resistant 'Conan' germplasm had fewer changes (Lavergne et al., 2020), suggesting underlying useful genetic traits are available even in more susceptible wheat germplasm. Multitrophic interactions could also be exploited. A *Spiroplasma* symbiont was recently characterized from larval and adult wheat stem sawflies from grass and crop populations (Yeoman et al., 2019). Wheat germplasm could be evaluated for its effects on this symbiont as an avenue for a novel type of host plant resistance.

5 Future trends in research

5.1 Distributions

There is evidence that WSS will continue to spread by local adaptation of populations in grasses to wheat. Climate warming could influence ripening synchronization between endemic grass populations and wheat, facilitating this colonization. Although there are extensive records for WSS at the level of states or provinces (Ivie, 2001), there have been no strategic surveys of local populations since the extensive Northern Great Plains surveys led by Davis (1948, 1952, 1953, 1955). Given recent reports from Washington, Minnesota

and Kansas (Bekkerman and Weaver, 2018; Peirce et al., 2022) as well as recent outbreaks in Colorado and Nebraska, a combination of efforts from state-level extension personnel and even citizen scientists (Maistrello et al., 2016) could be employed to document where populations are occurring in grass adjacent to wheat fields and in the wheat crop. Sampling locations could be guided or supplemented by remote-sensed distributions, and the models evaluated in Lestina et al. (2016) using Moderate Resolution Imaging Spectroradiometer (MODIS) imagery may be informative. Sweep net sampling the distinctive adults in late spring to early summer, as well as dissection of wheat and grass stems on the interface of crop edges in mid-summer, would provide valuable information. Sampling near the edges of the current range of WSS could look for smaller larvae in wheat stems on the field edge that may not be viable but indicate the potential for further range expansion.

5.2 Basic research needs

The last major review on WSS (Beres et al., 2011c) and a recent concise review (Peirce et al., 2022) mention the need for work on the chemical ecology of plant-insect interactions across tritrophic levels made feasible by technological advances since early work on the chemical basis of WSS oviposition choice (Holmes and Peterson, 1960). Understanding of the sensory mechanisms used by WSS during the selection of wheat or barley, including responses to host odors (Gress et al., 2013; Robertson et al., 2018) and contact cues (Varella et al., 2017b; Robertson et al., 2018), and knowledge of variability in key volatile attractants that facilitate the use of multiple hosts (Weaver et al., 2009; Achhami et al., 2021) are needed. This should be augmented by efforts to determine whether plant-plant communication (Piesik et al., 2013) occurs when WSS feeds within the wheat stem. Inducible compounds and chemical messengers are not yet known for the type of plant injury caused by WSS larval feeding.

Sensory ecophysiology could also help improve biological control. It is not known how *B. cephi* and *B. lissogaster* detect WSS larvae that are hidden inside stems. The size of the infested stem relative to the much smaller and hidden WSS larva and the diminutive female parasitoid makes it likely that acoustic cues (Mankin et al., 2000, 2004) are important for localized search while induced volatile compounds, and possibly reflected wavelength differences (Nansen et al., 2009), provide cues to which stem is infested.

In many regions, *B. cephi* and *B. lissogaster* are spatially and temporally sympatric (Morrill et al., 1998; Peirce et al., 2021; Cárcamo et al., 2012), and it is not known what maintains species integrity and how these species might partition the host resource (Runyon et al., 2001). Mechanisms facilitating species isolation in these congeneric braconids are not known, including any potential pheromones - nor is the pheromonal system of the

host WSS itself fully understood (Bartelt et al., 2002; Cossé et al., 2002). The mechanisms of incapacitation of hosts by the braconid species have not been elucidated, although differences in Dufour's gland hydrocarbon content in the sting complexes of the two species have been reported (Baker et al., 2005). Care should be taken to avoid the convenience of only reporting on one species in areas where both are present (Rand et al., 2012; Cárcamo et al., 2012), especially when working with adults because the key to separate these based on external characters (Runyon et al., 2001) is not difficult (Peirce et al., 2021).

There has been a large amount of research conducted on host plant resistance mechanisms, with a major focus on stabilizing and maximizing the expression of stem solidness in WSS-resistant wheat (Dhariwal et al., 2022; Liang et al., 2022) and equally on better understanding stem solidness (Nilsen et al., 2020). However, other sources of resistance are possible, given the consistent inability of WSS to complete development in oat that has been known for over a century. Recently, an increase in the use of barley by WSS allowed for the identification of relatively resistant and susceptible cultivars (Achhami et al., 2020a, 2020b), but mortality, and in particular neonate mortality, in barley still exceeds that in solid-stem wheat (Achhami et al., 2020c). This could enable crossing experiments to identify genes and loci that confer resistance. The ability to produce putative toxic compounds by barley may be latent and conserved in more distantly related wheat. It may also be possible to modify an oat population to be more susceptible to WSS so that a similar approach to scrutinizing the cause of mortality can begin.

Better understanding of what makes solid-stem wheat pith moderately toxic to WSS may allow for greater expression of resistance in commercial wheat varieties (Peirce et al., 2022). To achieve this, a careful study of mortality is key (Buteler et al., 2015; Varella et al., 2017b; Achhami et al., 2020c). Historically, reports suggested that pith obstruction of large larvae attempting to descend to cut stems was the dominant form of mortality (Holmes, 1954; Holmes and Peterson, 1962; Platt and Farstad, 1946; Morrill et al., 1992, 1994), but there was a debate on the relative importance of this and neonate mortality (Roberts, 1960; Holmes and Peterson, 1961; Kasting and McGinnis, 1961). Roberts (1960) indicated that the cause of mortality varied with plant stage and when infestation occurred (Fig. 4). Neonate mortality and plant response (Buteler et al., 2015) evidenced by the 'oviposition scar type' mortality of Roberts (1960) seem more important in modern datasets. Further exploration of how critical the newly identified symbiont (Yeoman et al., 2019) is to the survival of WSS, especially when feeding interactions include resistant germplasm, is needed.

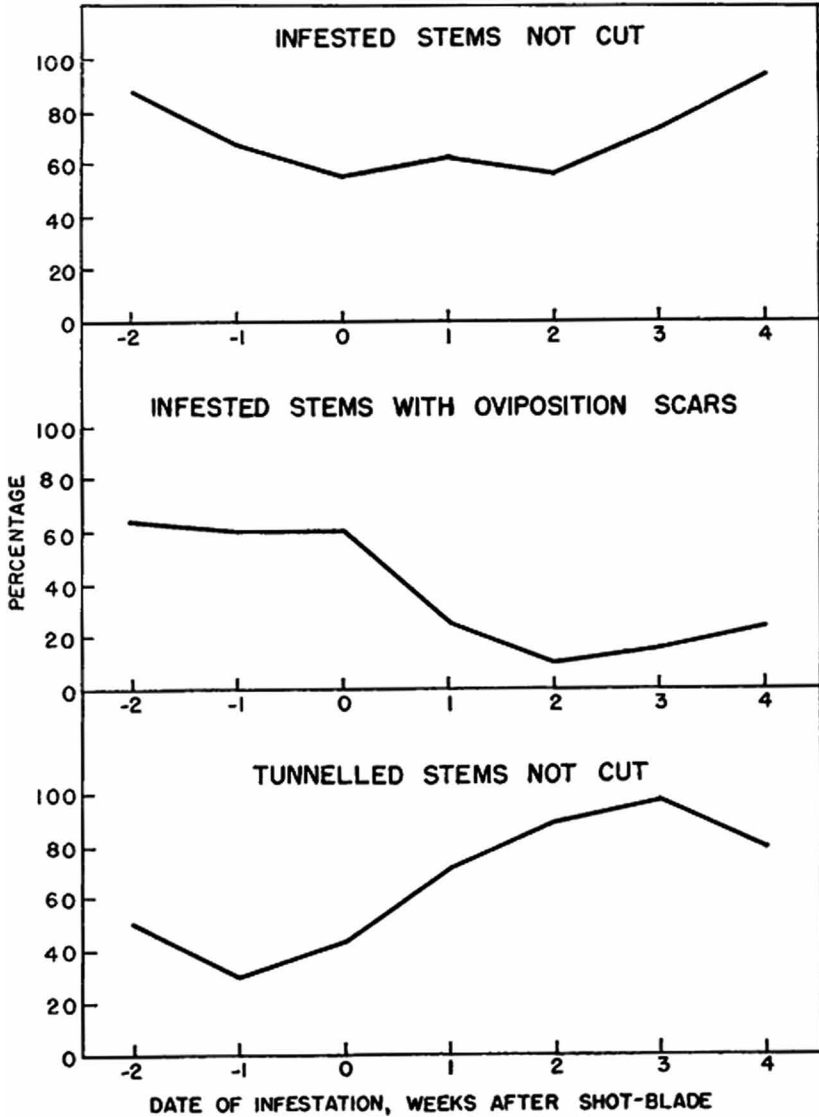


Figure 4 Mortality of wheat stem sawfly larvae from specific infestation over weeks after full emergence of the flag leaf (called 'shot-blade' below) of 'Rescue' solid-stem wheat. In this image, -2 weeks would correspond to the first possible infestation at the beginning of stem elongation. Top graph: the percentage of stems infested that were not cut for each infestation interval. Middle graph: stems with oviposition scars over the same interval. These scars occur for dead eggs and newly hatched larvae. Lower graph: stems tunneled by late-instar larvae from the same infestation interval showing the effect of desiccated pith. There is greater mortality of neonates in early infestations and greater mortality of late-instar larvae in later infestations. Source: Adapted from: Roberts (1960).

5.3 Applied research needs

The only two systemic insecticides effective against WSS larvae feeding in wheat stems, phorate and heptachlor, are no longer available for use in wheat. All new systemic insecticides should be evaluated for potential activity against WSS larvae, especially if the systemic expression extends to the interior lining of the wheat stem. In contrast, targeting WSS adults with repeated applications of contact insecticides is not viable, because of the protracted period of adult emergence and flight driving up costs of repeated applications (Knodel et al., 2009).

Cultural tactics that could target WSS include revisiting the use of cultivation implements to expose WSS larvae on the soil surface in their overwintering chambers inside stubs causing desiccation and mortality. Tillage to achieve this can cause undesirable disturbance of the soil surface, leading to loss of soil water and erosion and additional production costs which must be a consideration. Effectiveness must be assessed in terms of not only WSS destruction by tillage activity but whether the WSS populations are significantly smaller the following year. Use of tillage should also consider detrimental negative outcomes for parasitoids.

Harvest technology in dryland cropping has changed, where header stripper-type harvesters are used more frequently. These are desirable because they maximize the residue structure after harvest, ensuring better moisture retention and protecting the soil surface from erosion. It is unlikely that parasitoids can survive passing through the implement in straw processed at harvest by a conventional combine, while the header stripper may leave more parasitoids undisturbed to overwinter in tall standing stubble. A researchable question is whether these parasitoids survive the gentle harvest process. In addition, there may be ancillary value in the use of solid-stem wheat to manage WSS, which provides a standing stubble structure to retain moisture and limit erosion. It was recently shown that there is no advantage to this tactic when comparing solid- and hollow-stem wheat (Simão et al., 2021) using typical harvest implements under unknown (or perhaps limited) WSS numbers. More study is needed to make more meaningful comparisons when sufficient populations of WSS occur. Greatly increased stem cutting by abundant WSS will reduce the standing stubble structure considerably in susceptible cultivars relative to solid-stem cultivars.

More research is needed on conservation biological control for *B. cephi* and *B. lissogaster*. Beres et al. (2011a) outlined a plausible cropping system to minimize losses due to WSS, but additional effort is required to provide adjacent nectar-providing species that will benefit these parasitoids. This could be accomplished by cropping systems or rotations that have spatially staggered arrays of wheat and flowering crop species. Provisioning must consider the

foraging ecology of these parasitoids (Rand and Waters, 2020), which may access nectar more readily from more open and shallow floral structures, from extrafloral droplets or from honeydew, when available. Research is needed on late-ripening grass species like smooth brome (*Bromus inermis* L.) that harbor WSS larvae as reservoir hosts for the parasitoids (Criddle, 1922a; Seamans, 1928). These reservoirs will be especially important when second-generation crashes occur during historical and frequent drought (Holmes et al., 1963; Holmes, 1982).

Pathogens are likely to be greatly challenged in the arid conditions that allow WSS populations to thrive, but more investigation of the possible endophytic establishment of candidate pathogens early in the growing season might identify a vehicle to deliver these organisms in drylands (Portman et al., 2018). However, caution needs to be exercised when considering endophytic organisms because of the feeding habits of WSS larvae. The principal diet of the larvae is the layer of tissue lining the stem lumen as well as vascular conduits consumed when boring through nodes. Thus, the establishment of an endophyte in host plant leaves will not necessarily provide a mode of action against WSS larvae, just as most systemic insecticides fail to reach feeding larvae. In the case of WSS, it will help if the organism colonizes interstitial spaces such as the stem interior by localizing on the surface of the inner stem lining.

Trap crops merit further consideration, especially if research can identify both highly attractive and less attractive cultivars (within and across species) to be deployed in a push-pull scenario (Khan et al., 2016) where immigrating female WSS are retained on a preferred cultivar on the crop periphery. This was previously demonstrated by using a phenologically more desirable winter wheat crop planted around spring wheat (Morrill et al., 2001a), but growers would rather not have two temporally separated seeding operations for the same field. There may also be an opportunity to use a WSS-preferred solid-stem cultivar to concentrate the pest and cause mortality as a 'dead-end' trap crop. Current technology should allow for the rapid collection of volatile compounds as part of this effort under controlled conditions, but field evaluations will be more challenging.

Finally, the single greatest challenge is providing growers information that allows them to maximize use and benefits from planting solid-stem WSS-resistant wheat varieties, which remains the single best management strategy for WSS (Beres et al., 2011a, 2011c). Fundamental to this is the recommendation for plant solid-stem wheat varieties, which growers are reluctant to do. The elite solid-stem germplasm currently available is typically slightly lower yielding than comparable hollow-stem cultivars, but the gap between these lessens with the continual efforts made by solid-stem variety development programs. There is an urgent need for nurseries specifically targeting yield characterization under large and damaging WSS populations. The reason for this is twofold. First,

solid-stem wheat is intended for use when WSS problems occur, but not when the populations of the pest are small or non-existent. The yield of solid-stem wheat in the absence of WSS is unimportant but appears as tantamount in the way data are presented. Second, and equally critical, accurate and detailed data are urgently needed to demonstrate that susceptible cultivars have poor agronomic performance when damaging WSS populations exist, even when very successful swathing of ripened crops recovers nearly all of the smaller heads caused by WSS feeding (Bekkerman and Weaver, 2018).

6 Conclusion

It is very likely that WSS will become an even greater focus for wheat and barley growers in western North America. Local adaptation of populations in grassy areas near wheat fields will continue, resulting in spread of damaging populations. The natural regulation of WSS in such areas by specialist parasitoids appears to lag behind the host but can provide significant suppression of damaging populations when conditions are right. The foundation of management remains host plant resistance, and major efforts are underway to incorporate existing germplasm into crop production areas where outbreaks are expected, or where they may worsen. Ongoing production practices can be continually adapted to minimize losses as much as possible - and need to be supported by careful research. Exploratory efforts targeting new sources of host plant resistance and alternative biological control approaches will get additional attention. Outreach efforts should continue to remind growers of proactive management benefits and should also include resources to increase familiarity with the pest and the damage it causes.

7 Where to look for further information

There are a number of good resources listed in the following References. Additional on-line resources would include web pages of institutions leading research on this insect. Here are a few examples to get started:

- Edde, P. A. (2022). Chapter 9: Arthropod pests of small grains: Wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.). In: Edde, P. A. and Crop, F. (Eds.), *Arthropod Pests of Economic Importance*, pp. 536-611. doi: 10.1016/B978-0-12-818621-3.00001-X.
- Beres, B. L., Dosdall, L. M., Weaver, D. K., Cárcamo, H. A. and Spaner, D. M. (2011). Biology and integrated management of wheat stem sawfly and the need for continuing research. *The Canadian Entomologist* 143(2): 105-125. doi: 10.4039/n10-056
- Peirce, E. S., Cockrell, D. M., Mason, E., Haley, S., Peairs, F. B. and Nachappa, P. (2022). Solid stems and beyond: Challenges and future directions of

resistance to wheat stem sawfly (Hymenoptera: Cephidae). *Journal of Integrated Pest Management* 13(1). doi: 10.1093/jipm/pmac023.

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