C.P. Alexander Review / Revue C.P. Alexander[1]

Biology and integrated management of wheat stem sawfly and the need for continuing research

B.L. Beres, L.M. Dosdall, D.K. Weaver, H.A. Cárcamo, D.M. Spaner

Abstract—The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), is historically one of the most important economic insect pests in the northern Great Plains of North America. Within this geographical region, the areas subjected to greatest attack are southern Alberta and Saskatchewan, southwestern Manitoba, eastern and northern Montana, North Dakota, northern South Dakota, and western Minnesota. Cumulative grain-yield losses and annual economic losses associated with this pest can exceed 30% and $350 million, respectively. Solid-stemmed cultivars of common wheat, *Triticum aestivum* L. (Poaceae), tolerant of infestation, are critical for *C. cinctus* management, but outbreaks of this pest continue to occur even after six decades of cultivar development. Furthermore, chemical control (a primary control option for other cereal (Poaceae) insect pests) has proven ineffective; this underscores the need to integrate resistant cultivars into a comprehensive integrated pest management program. We provide overviews of wheat stem sawfly biology, recent advances in applied research, the efficacy and integration of cultural and biological management strategies, and future directions for global research activities to manage wheat stem sawfly.

Resume—Le cèphe du blé, *Cephus cinctus* Norton (Hymenoptera : Cephidae), est historiquement l'une des espèces de ravageurs de la plus grande importance économique dans le nord des Grandes Plaines d'Amérique du Nord. Au sein de cette région géographique, les zones qui ont subi la plus forte attaque sont le sud de l'Alberta et de la Saskatchewan, le sud-ouest du Manitoba, l'est et le nord du Montana, le Dakota du Nord, le nord du Dakota du Sud et l'ouest du Minnesota. Les pertes cumulatives de rendement en grain causées par ce ravageur peuvent dépasser 30 % et les pertes économiques annuelles peuvent excéder 350 millions $. Les cultivars de blé, *Triticum aestivum* L. (Poaceae), à tige solide et tolérants à l'infestation sont d'importance critique dans la gestion de *C. cinctus*, mais des épidémies de ce ravageur se produisent toujours même après six décennies de développement de cultivars. De plus, le contrôle chimique (une méthode importante de lutte contre les autres insectes ravageurs des céréales (Poaceae)) s'est

---

Received 4 August 2010. Accepted 19 November 2010.

[1] This series is supported by a fund established in memory of the late Charles P. Alexander. The Entomological Society of Canada uses the fund to support the publication of invited articles or reviews on topics that broaden the scope of *The Canadian Entomologist* and (or) are of current significance to entomology.
Cette série est financée par un fond établi à la mémoire de feu Charles P. Alexander. La Société d'entomologie du Canada utilise les fonds afin de supporter la publication d'articles ou de revues sur invitation portant sur des sujets qui élargissent le champ de *The Canadian Entomologist* et (ou) sont présentement pertinents en entomologie.

B.L. Beres,[2] Agriculture and Agri-Food Canada, Lethbridge Research Centre, Box 3000, 5403 1st Ave. S., Lethbridge, Alberta, Canada T1J 4B1, and University of Alberta Department of Agricultural, Food, and Nutritional Sciences, 410 Ag/Forestry Building, Edmonton, Alberta, Canada T6G 2P5
L.M. Dosdall, D.M. Spaner, University of Alberta Department of Agricultural, Food, and Nutritional Sciences, 410 Ag/Forestry Building, Edmonton, Alberta, Canada T6G 2P5
H.A. Cárcamo, Agriculture and Agri-Food Canada, Lethbridge Research Centre, 5403 1st Avenue South, Lethbridge, Alberta, Canada T1J 4B1
D.K. Weaver, Montana State University Department of Land Resources and Environmental Sciences, P.O. Box 173120, Bozeman, Montana 59717-3120, United States of America

[2] Corresponding author (e-mail: brian.beres@agr.gc.ca).

doi: 10.4039/n10-056

avéré inefficace; cela souligne la nécessité d'intégrer les cultivars résistants dans un programme complet de lutte intégrée contre le ravageur. Nous présentons un exposé général de la biologie du cèphe du blé, des progrès récents en recherche appliquée, de l'efficacité et de l'intégration des stratégies de gestion basées sur la culture et la biologie et des avenues futures des activités globales de recherche nécessaires pour gérer le cèphe du blé.

[Traduit par la Rédaction]

Introduction

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), has been a major pest of common wheat, *Triticum aestivum* L. (Poaceae) (hereinafter referred to as wheat), in the northern Great Plains of North America for more than 100 years. Within this geographical region, the areas subjected to greatest attack are southern Alberta and Saskatchewan, southwestern Manitoba, eastern and northern Montana, North Dakota, northern South Dakota, and western Minnesota. The species was described from a specimen collected from native grass in Colorado (Norton 1872; Davis *et al.* 1955), and adults were reared from larvae collected in Alameda, California (Ainslie 1920; Holmes 1979). Comstock (1889) first reported a species of stem sawfly as a wheat pest in northern New York State. *Cephus cinctus* was first observed infesting wheat in Canada in 1895 near Souris, Manitoba, and Indian Head, Saskatchewan (Fletcher 1896). Reports of *C. cinctus* infestations followed the westward movement of wheat production across the Canadian prairies and the northern states of North Dakota and Montana (Fletcher 1904; Ainslie 1920). By 1910, infestations of wheat stem sawfly were reported as far west as Claresholm, Alberta (Holmes 1979).

There are dissenting views from the common assumption that *C. cinctus* is indigenous to North America. Ivie and Zinovjev (1996) proposed that *C. cinctus* is a senior synonym of the Siberian species *Cephus hyalinatus* Konow. Ivie (2001) described inconsistencies in the ecological relationships between *C. cinctus*, native hosts, and native parasitoids. He noted that stems of native host plants often are of insufficient diameter to support *C. cinctus* pre-imaginal development, and stated that parasitoids were poorly synchronized with their hosts. This seems unlikely, however, because a strong oviposition preference for an introduced marginal host with very narrow stems has been documented (Perez-Mendoza *et al.* 2006). Ivie (2001) also argued that early insect collectors in North America did not encounter *C. cinctus* and suggested that introduction could have occurred through the transport of straw or crowns from plants containing live larvae. The probability of introducing straw containing living larvae is low, however, because most larvae overwinter near the crown (Ainslie 1929). Larvae would also have been at risk for destruction by pathogens (Criddle 1922*b*) because of the likelihood of very humid transport conditions. In addition, crowns (commonly imported for medicinal purposes early in the 20th century) would likely have been stored indoors. Thus, completion of obligate low-temperature diapause (and subsequent adult emergence) (Holmes 1982) prior to crown pulverization for medicinal extractions (Ivie 2001) seems improbable. Other unpublished work shows that it is relatively unlikely that *C. cinctus* is of recent Eurasian origin (M.C. Bon, personal communication). This debate will likely continue.

The economic importance of wheat stem sawfly was evident early in the settlement of the Prairies. The first recorded severe infestation and damage to wheat occurred in 1922 in western Canada (Criddle 1923). Criddle (1923) characterized the extensive damage and economic losses as the sawfly's "free hand" that evolved from the elimination of natural population checks such as the limited food supply associated with native grass host abundance and health, and because natural enemies of the sawfly had not successfully adapted to this shift in host preference.

Wheat stem sawfly outbreaks were historically short-lived because wheat crops were often destroyed by rust epidemics, eliminating preferred host plants (Platt and Farstad 1949) and parasitoids reduced sawfly populations

(McGinnis 1950). The development of rust-resistant wheat cultivars that served as healthy hosts for *C. cinctus* (McGinnis 1950), coupled with the severe drought of the late-1930s, favoured sustained increases in wheat stem sawfly populations in the northern Great Plains (Morrill 1983). Cultural practices to mitigate soil erosion (most notably the introduction of the low-disturbance Noble blade to replace the mould-board plough, as well as strip-farming as an alternative to farming large blocks of land) provided undisturbed overwintering habitat, facilitating the increase of wheat stem sawfly populations and leading to dispersal of sawflies across entire fields instead of localization at field margins (McGinnis 1950). The urgency for adoption of cultural control practices to mitigate damage is clear in a "War-Time Production Series" report (Farstad *et al.* 1945): descriptions synonymous with warfare were used to describe management strategies (*e.g.*, "drive out", "kill", "protect", and "salvage") and upper-case lettering in some sentences underscored the message (*e.g.*, "ALL TRAPS MUST BE DESTROYED ABOUT MID-JULY TO KILL THE MILLIONS OF SAWFLY GRUBS IN THEM"). In theory, the recommended cultural practices to manage wheat stem sawfly had potential for reducing infestation levels, but the rate of adoption of cultural control methods during that time is unknown.

In the same period, efforts to develop a wheat cultivar resistant to wheat stem sawfly infestation were initiated. Dominion of Canada researchers from Swift Current and Lethbridge evaluated germplasm from New Zealand, Spain, Morocco, and Portugal that expressed greater amounts of pith within the culm of the stem than varieties grown in western Canada at the time (Kemp 1934). The interaction between wheat stem sawfly and solid-stemmed hosts was assessed because Kemp (1934) believed that mechanical restriction within solid stems could be detrimental to larvae. Additional tests were performed that identified line S-615, originally selected from Portugal (Platt and Farstad 1949), as a suitable parent with considerably reduced of stem-cutting caused by mature larvae (Platt and Farstad 1946). A cross between S-615 and Apex, a hollow-stemmed and rust (*Puccinia sp.* (Pucciniaceae))-resistant variety, produced the first solid-stemmed commercial variety aptly named 'Rescue' (Platt *et al.* 1948). The development of this variety, however, did not prove to be a "magic bullet" and damage from wheat stem sawfly was still severe through 1954 (Holmes 1982).

Several factors during the 1950s resulted in reductions of wheat stem sawfly populations, including heavy rainfall and a severe wheat stem rust (caused by *Puccinia graminis* Pers.: Pers. f. sp. *tritici* Eriks. & E. Henn.) outbreak during the 1954 growing season. Additionally, in 1956, rates of parasitism were very high and subsequently reduced infestations (Holmes 1982). Periods of resurgence that followed were generally short-lived and sporadic through the entire wheat stem sawfly distribution area (Holmes 1977, 1982; Morrill 1983). Damage in Montana, however, increased significantly in the mid-1990s (Morrill *et al.* 1998), and a major resurgence of *C. cinctus* occurred in southern Alberta in 1998–1999, and soon after in Saskatchewan (Meers 2005; Beres *et al.* 2007). Currently, extensive damage to wheat caused by *C. cinctus* persists throughout the northern Great Plains, particularly in Montana, southern Alberta, and Saskatchewan.

Our review comes more than a century after the first report of wheat stem sawfly attacking wheat in Canada. *Cephus cinctus* remains one of the most economically important insect pests of wheat in the northern Great Plains in spite of enormous efforts to control it in Canada and in the United States of America. This serves as a testament to the resiliency of this insect and the difficulty of developing successful strategies for its management. We provide overviews of wheat stem sawfly biology, the efficacy of cultural and biological management strategies, and future directions for global research activities to manage wheat stem sawfly.

Wheat stem sawfly life cycle

Timing of emergence is influenced by temperature (Perez-Mendoza and Weaver 2006) and thus, latitude. In Manitoba, adults have been observed emerging from 10 June through 10 July from previous-year host plants, usually wheat stubble (Criddle 1922*a*). Adults are shiny black and approximately 12 mm long with yellow abdominal bands, they have large prominent eyes, club-shaped antennae with approximately 20 segments, and a slightly compressed abdomen (Fletcher 1904). Males are haploid with nine chromosomes and typically emerge before females (Holmes 1979). Copulation takes place immediately after emergence unless environmental conditions such as wind or rain inhibit activity (Wallace and McNeal 1966). Some competition exists between males; males have been observed nipping at the antennae of challengers (Wallace and McNeal 1966). Fertilized eggs produce diploid females and unfertilized eggs produce male offspring. Therefore, most early eggs deposited produce female offspring, and most laid toward the end of the flight period (when males are less abundant) produce male offspring (Holmes 1979).

Oviposition occurs a few days after adult emergence. An ovipositing female uses her sawlike ovipositor to slice an opening into the elongating internode of a wheat stem and inserts an egg. The female selects an oviposition site, usually a hollow region (Seamans 1945) historically reported to be between the second and fourth internodes, by first climbing to the apex of the top leaf, where she turns and points downward to the most suitable site on the stem just above the node. Stems that are succulent and from which the spike has not yet emerged (boot stage) are preferred (Holmes and Peterson 1960). There is also a preference for larger diameter stems. The sex ratio of offspring is female-biased in larger stems, whereas ratios from smaller stems are male-biased (Wall 1952; Morrill *et al.* 2000; Cárcamo *et al.* 2005). Most oviposition occurs about midday during a 4-day period and each female deposits only one egg per stem (Holmes 1979). However, multiple eggs often occur in stems because subsequent females are unaware of earlier oviposition (Criddle 1923; Buteler *et al.* 2009). Nansen *et al.* (2005*b*) proposed that females may possibly detect chemical signals emitted from host plants containing larvae and avoid them, but this proved to be incorrect (Buteler *et al.* 2009).

Female behaviour suggests that a number of host attributes must be present before oviposition will occur (Buteler *et al.* 2010), at least when host plants are abundant. When hosts are scarce, however, females may be less discriminating; Holmes and Peterson (1960) observed that in laboratory conditions females will attempt to oviposit in glass rods, desiccated wheat stems, or wooden rods.

Each female is capable of carrying up to 50 eggs, which are usually equal in size and maturity (Ainslie 1920). Each egg is crescent-shaped, milky white or translucent, and usually 1.00–1.25 mm long, depending upon the size of the female that produced it (Ainslie 1929). Each egg lies freely within the cavity of the stem or in a hollow created by the ovipositor during egg deposition (Ainslie 1929). Larvae develop rapidly and begin to take shape by the third day. By the sixth or seventh day after oviposition, each larva breaks free of its egg sac and enters the stem cavity (Ainslie 1920).

Newly hatched larvae are transparent and colourless (Criddle 1923; Ainslie 1929), but appear yellowish-brown soon after feeding begins. In stems containing more than one larva, the first larva to hatch is usually the one that survives, although the lowermost larva has an advantage over others in the same stem (Criddle 1923). Stem-boring activity begins immediately after hatching. Newly hatched larvae destroy other eggs (and each other) until usually only one larva remains in a stem (Criddle 1923; Holmes 1982). It is not known whether destruction of eggs and larvae is the result of intentional cannibalism or an indirect consequence of indiscriminate feeding activity. Although multiple larvae in a stem are usually reduced to a single survivor within a few weeks (Criddle 1923), two or more larvae have been recovered from post-harvest stems and stubs at Lethbridge, Alberta (B. Beres, personal observation).

Cephus cinctus exhibits a distinct spatiotemporal pattern of distribution. It begins with the concentration of adults at field edges as they emerge from stubble and migrate to the nearest suitable hosts, which are usually plants within an adjacent wheat field (Holmes 1982). Females oviposit first within the field margin, which usually results in more severe damage along edges than in the field interior. Infestations are initially clustered, a behavioural trait that might relate to oviposition strategies when only native grasses were available and spatially dispersed in bunches (Nansen *et al.* 2005*a*, 2005*b*). Oviposition gradually moves toward the center of the field and there is a more uniform distribution of eggs in the field as the flight period progresses (Nansen *et al.* 2005*a*). Nansen *et al.* (2005*a*) hypothesized that signalling compounds are released from plants after larval eclosion and commencement of herbivory; this would deter further infestation and motivate females to seek out uninfested hosts. However, females cannot differentiate between infested and uninfested stems (Buteler *et al.* 2009) and other evidence for this mechanism is lacking. Interestingly, uniformity of egg distribution does not lead to a more uniform larval distribution; larvae remain mainly concentrated at field margins (Nansen *et al.* 2005*a*). Survival of larvae in the interior of fields may be inconsistent because most of these larvae hatch from eggs deposited later in the flight period and may not have sufficient time to prepare for overwintering before the onset of host senescence (Nansen *et al.* 2005*c*).

The larva feeds within the stem until the plant is nearly mature; the duration of this period varies with host plant phenology. Toward the end of the growing season, an obligatory diapause is triggered by two environmental cues. The first cue occurs when host plants are sufficiently mature that visible and infrared light penetrate the stem wall (Holmes 1979), inducing the larva to move downward to the base of the plant. The second cue occurs when whole plant moisture content drops and the moisture content of the kernels falls to 41%–51% (Holmes 1979), inducing the larva to prepare its hibernaculum. A neat V-shaped groove is made around the entire inside of the stem at ground level, weakening the stem so that it topples easily when exposed to wind (Ainslie 1929). The larva fills the girdled section with frass, creating a solid plug in the pith cavity that seals the stub after the stem topples. Below the plug the larva encases itself in a silken cocoon and overwinters as a mature fifth instar (Holmes and Peterson 1960).

As long as the chamber and cocoon remain sealed, the larva is well protected from environmental degradation or predation. A larva within a sealed hibernaculum can survive months of immersion in water (Ainslie 1929) and the larval supercooling point ranges from −20 to −28 °C (Holmes 1979). Overwintering larvae remain very near host root crowns. Temperatures at the crowns are generally 9–28 °C higher than ambient winter air temperatures (Morrill *et al.* 1993) and more stable than the air temperatures 15 cm above the crowns (B. Beres, unpublished data), allowing larvae to withstand consecutive days of low temperatures. Cárcamo and Beres (2006) reported almost 100% survivorship of larvae exposed to −20 °C for 10 or fewer consecutive days. However, the rate of mortality increased sharply when exposure was longer than 10 days (Cárcamo and Beres 2006), or if wheat stubs (and cocoons) had been disturbed by tillage (Morrill *et al.* 1993). Mortality rates were high after a few hours of direct exposure to −22 °C.

Diapause is completed after 90 days of exposure to 10 °C, usually by mid- to late-spring. Prior to pupation, if temperatures approach 35 °C (Salt 1947), or conditions are extremely dry (Holmes 1979), larvae re-enter diapause and will remain in that state until the following spring. However, if these conditions arise after pupation has occurred, diapause cannot be re-entered and malformed prepupae or pupae will result (Holmes 1979). An extremely dry winter and spring in 1937 caused a resumption of diapause in many larvae across the Canadian prairies (Holmes 1979). There are no known reports of this occurrence in recent decades even though the western prairies endured extreme drought and high temperatures in 2001 and 2002. Possibly this is because the current adoption of conservation tillage practices (as opposed to the extensive cultivation of the 1930s) may limit exposure of wheat stubs to desiccation and high temperatures through lower evapotranspiration rates (Lindwall and Anderson 1981).

Usually, pupation occurs over no more than 21 days (Criddle 1923). The prepupal period begins in early- to mid-May and the first pupae develop in late May (Holmes 1979). After pupation, each newly eclosed adult chews through the frass plug or the side of the stub (Holmes and Peterson 1960).

Plant injury caused by wheat stem sawfly larvae

Adult sawflies inflict little injury on host plants but the stem-boring activity of larvae is destructive and can result in severe losses. The first damage occurs soon after a larva hatches from an egg and begins boring through parenchyma tissue and vascular bundles of its host, causing a significant reduction in photosynthetic capacity (Macedo *et al.* 2005). The stem can be thoroughly bored in a few weeks, as the larva feeds both downward and upward in the stem (Criddle 1923). There may be little external evidence of boring activity unless the stem is opened longitudinally to check for the presence of frass (Holmes 1979). Macedo *et al.* (2007) observed 12% higher photosynthetic rates in uninfested than in infested wheat plants and this appears to be linked to further reductions in yield resulting from abiotic influences and plant variety (Delaney *et al.* 2010). Seamans *et al.* (1944) found that stem boring associated with heavy sawfly infestation resulted in a 10% yield loss in heads of 'Marquis' wheat. Holmes (1977) separated cut from uncut infested spring wheat stems and found that head weight was reduced by 17% and 11%, respectively. Winter wheat is also a host for wheat stem sawfly, particularly in western Montana where sawflies have synchronized emergence patterns to exploit this host. Morrill *et al.* (1992) reported a range of 2.8%–10.0% in winter wheat head weight loss and noted that infestation rates were higher in larger diameter stems, which also normally produce heads bearing seed of greater kernel weight.

The initial phase of herbivory is only evident upon close examination of the subnodal region immediately below one or more nodes, which can appear discoloured or spotted after larval boring (Morrill *et al.* 1992). However, late-season stem girdling by mature larvae is readily apparent because this causes stems to topple easily in windy conditions (Ainslie 1920). This stem cutting results in additional yield losses because it is difficult to harvest fallen stems effectively. Ainslie (1920) and Criddle (1922*b*) estimated losses from stem cutting at approximately 30% of attainable yield and about 25% of the 1921 crop, respectively. In subsequent outbreaks prior to the release of the first solid-stemmed cultivar, annual losses in the Canadian prairies exceeded 544 000 tonnes (Platt and Farstad 1949). Losses in the 1950s in Montana and North Dakota were 61 000 and 154 000 tonnes, respectively (Davis 1955). In more recent years, damage and losses in Montana in the mid-1990s were projected to exceed 402 000 tonnes annually (Blodgett *et al.* 1997). In a European study, Ozberk *et al.* (2005) concluded that yield losses from *Cephus pygmaeus* (L.) would be $69 · ha^{-1} for durum and bread wheat. Beres *et al.* (2007) used their strong positive correlation to show that grain losses could be estimated based on stem cutting. Using this approach, and based on modern commodity prices, close to 50% stem cutting could result in economic losses in excess of $100 million annually across the Canadian prairies. Recovery operations to minimize losses typically involve using a swather equipped with a pickup reel and crop lifters. The added energy cost of a recovery operation is likely to exceed $30 · ha^{-1} at current fuel prices, and the fixed cost of equipment purchase and installation is close to $10 000 (Alan Gajdostik, personal communication). The recovery of toppled stems also requires a very low table cutting height, which leaves little anchored stubble and exposes fields to increased risk of soil erosion and reduced snow capture.

Cultural control

Wheat stem sawflies spend up to 10 months of the year as larvae within host plants; thus, early control tactics targeted the larva through destruction of the stub. Fletcher (1904) recommended burning any stubble that was not turned over in the fall, but Ainslie (1920) concluded that larvae housed within the bunchgrass stems suffered little, if any, damage from burning. Ainslie (1920) also described Criddle's (1907) experiments to test the effects of increased heat intensity through burning a deep layer of straw previously spread over infested stubble. No larvae were killed by Criddle's treatments (Ainslie 1920) and the negative effects of burning can be severe. Serious soil erosion may result from removal of residue (Lal 1997; Lafond *et al.* 1996) and natural enemies of the sawfly, housed within stems but above ground, could perish.

Tillage was another early recommendation for wheat stem sawfly control. Criddle (1922*b*) recommended ploughing infested stubble to a depth of at least 15 cm and completely burying all stubs between 1 August and 5 June of the following year (fall tillage was preferred because of increased potential for pathogens to rot stubs and destroy larvae). Criddle (1922*b*) also recommended packing of ploughed furrows to seal the soil and prevent successful emergence of adults from stubs. Although tillage was believed to provide effective control during this period, the method did not destroy all sawflies. In spite of increasing larval mortality as burial depths increased to 15 cm or more, some adult emergence still occurred (Ainslie 1920). Furthermore, ploughing under wheat stubble significantly increases the mortality of the *C. cinctus* parasitoids *Bracon lissogaster* Muesebeck and *Bracon cephi* (Gahan) (Hymenoptera: Braconidae) (Runyon *et al.* 2002).

When it became apparent that ploughing left fields prone to soil erosion during periods of drought and high winds, farmers began to adopt cropping practices to mitigate soil erosion and replaced the plough with low-disturbance tillage equipment such as the Noble blade (Mathews 1945). Although this was thought to enhance the survivorship of *C. cinctus* (McGinnis 1950), because the practice did not sufficiently bury stubs (Morrill *et al.* 1993), stub burial is not critical for killing overwintering larvae. Shallow tillage can provide effective wheat stem sawfly control if the operation fully exposes host plant root crowns by uprooting and removing all soil from them (Holmes and Farstad 1956). Furthermore, the practice should be performed in the fall or late May, after larvae have pupated and cannot return to diapause (Holmes and Farstad 1956). Tillage operations that did not free the soil from the crown produced the same rate of spring larval survival as did non-tilling treatments (Goosey 1999). Goosey (1999) also reported that a rotary harrow operation following tillage was usually more effective for removing soil from crowns than the Noble blade or not harrowing after cultivation. Morrill *et al.* (1993) performed tillage in fall and in mid-May and reported that the spring operation did not cause the larvae to return to diapause. It was recommended that only field margins should be tilled to minimize soil drift. Other studies have reported no effect of tillage on *C. cinctus* survivorship (Weiss *et al.* 1987). Moreover, factors such as larval development time or operational implements may not be as important as environmental conditions; efficacy of tillage and harrowing to uproot and remove soil from crowns is influenced by soil moisture and texture.

Field configurations were modified in many areas to mitigate soil erosion. Large tracts of monoculture were replaced with alternating strips of crop and fallow land. This increased the abundance of *C. cinctus*, which easily dispersed across the narrow strips, caused widespread stem cutting, and greatly impeded harvest operations (McGinnis 1950; Morrill *et al.* 2001*b*; Weaver *et al.* 2004). An early approach to minimize dispersal beyond field edges involved the use of trap crops or border management. The earliest trap crop was rye grass, *Lolium perenne* L. (Poaceae), planted in ditches and headlands of wheat fields so that invading *C. cinctus* would deposit most eggs into rye grass stems, which would then be destroyed by mowing in July (Criddle 1922*a*). Criddle (1922*a*) noted that brome grass, *Bromus inermis* Leyss. (Poaceae), might be a superior trap crop because larvae generally did not survive in brome grass and mowing would not be required. Also, brome grass elongates earlier in spring than does wheat, thus becoming the primary host if situated beside a wheat field (Seamans 1928). Cutting of native grasses or brome grass surrounding wheat field edges and headlands was not recommended because parasitism rates of *C. cinctus* were generally higher in the native grasses than in wheat or rye grass (Criddle 1922*a*).

Annual crops have also been used as trap crops. Volunteer wheat in fallow strips has higher infestation rates than adjacent wheat fields (Seamans 1928). A perimeter of wheat could also be planted on a fallow field adjacent to a wheat field to attract adults emerging from the previous year's crop. A space between the trap strip and the wheat field equal to the width of the trap strip ("2–3 rod widths" or 10–15 m) was left bare to entice adult sawflies to remain in the trap crop (Farstad *et al.* 1945). The trap crop was then ploughed under in mid- to late-July to destroy larvae. There is still potential for this strategy to work in regions with a wheat–fallow cropping system. In the southern prairies of Canada, however, many producers favour continuous cropping practices and prefer not to fallow fields.

An updated approach to trap strips involves within-field border management; *i.e.*, sowing the perimeter of a wheat field to an immune or resistant crop and then planting the interior of the field to a hollow-stemmed wheat cultivar. The goal of this strategy is to intercept incoming sawflies from adjacent infested stubble so that most infestation occurs within the trap perimeter (Beres *et al.* 2009; Morrill *et al.* 2001*b*) and beneficial insects are conserved (the trap crop is harvested rather than destroyed). Trap effectiveness is maximized when insect and trap-crop phenologies are in synchrony and the main crop developmental stage lags behind. This is achieved by seeding trap and main crops at different dates or selecting trap and main cultivars that differ significantly in growing day-degree requirements. One approach used in Montana is to plant solid-stemmed winter wheat trap borders around fields that will be seeded to a hollow-stemmed spring wheat cultivar (Morrill *et al.* 2001*b*). The strategy requires multiple seeding operations in the same field and, therefore, may be considered impractical for large farm operations. Beres *et al.* (2009) used a single seeding operation for fields and borders and reported the traps to be generally ineffective, owing to high wheat stem sawfly pressure and higher than expected stem cutting in the solid-stemmed wheat treatments.

Certain cropping practices that were incompatible with deep tillage led to development of alternative trap crops. Ainslie (1920) noted that tillage of infested stubble was not adopted in regions where producers grew winter cereals (Poaceae) because the practice of planting into standing stubble was advocated for increased winter cereal survival. However, improved survivorship of overwintered sawflies was partially offset because winter cereals are usually too advanced to be preferred hosts for *C. cinctus* at more northern latitudes (Criddle 1922*b*). Fall rye, *Secale cereale* L. (Poaceae), was the dominant winter cereal of this time, although winter wheat was also grown. The use of fall rye was considered an effective cropping strategy because its relatively early harvest in late summer had the potential to kill larvae in the stem before they moved to the base of the stem to overwinter. Samples collected from harvested fall rye showed 85% mortality of larvae infesting the crop (Criddle 1922*a*).

Other crops recommended as alternatives to bread wheat for wheat stem sawfly management included oats (*Avena sativa* L.), barley (*Hordeum vulgare* L.), and durum (*Triticum turgidum* L.) (Poaceae), as well as non-cereals such as flax (*Linum usitatissimum* L. (Linaceae)) and sweetclover (*Melilotus officinalis* (L.) Lam. (Fabaceae) (Criddle 1922*a*). The mechanism of resistance for oats has not been fully elucidated. One explanation is that larvae succumb shortly after hatching because of excess sap produced by host oat plants (Criddle 1923). Larval death in oats could also be a form of antibiosis and is currently under study at Montana State University. The response of barley and durum to wheat stem sawfly attack is genotype-specific. Durum was initially considered immune but field damage was noted in Canada (Criddle 1922*a*) and the United States of America (Ainslie 1920). In other studies it was determined that some varieties of durum and barley were less prone to infestation and produced significantly fewer larvae than did wheat (Farstad and Platt 1946; Goosey *et al.* 2007). It is now known that *C. cinctus* can complete its life cycle in all cereal crops except oats, and therefore cereal crops can be a source of inoculation in the following year even if little damage was observed in the previous fall. Durum wheat and barley are not as susceptible to stem lodging as is the bread wheat class, thereby masking stem cutting-damage caused by larval activity. Lodging susceptibility is largely a function of straw strength and composition (J. Clarke, personal communication).

The risk to crop harvests when only using cereal crops is high because infestations as low as 10%–15% in one year can lead to rates as high as 80% in the following year (Farstad *et al.* 1945; Holmes 1982). Non-cereal crops provide the best alternative cropping strategy. Opting out of growing wheat for 2 years was recommended but considered drastic in the 1920s through the 1940s when few cropping alternatives existed (Criddle 1923; Farstad *et al.* 1945). Recent cropping systems research in the Canadian prairies has shown the benefit of rotational diversity. A rotation of canola (*Brassica napus* L. (Brassicaceae)), wheat, and field pea (*Pisum sativum* L. (Fabaceae)) optimized production of all three rotational phases in Saskatchewan (Brandt *et al.* 2008); compared with continuous wheat, grain protein and yield of wheat improved following pulse (Fabaceae) crops (Miller *et al.* 2002). It should be noted that these studies were agronomic and did not attempt to determine wheat stem sawfly infestation during the wheat phase of the rotation.

Wheat row spacing and seeding rates can influence *C. cinctus* infestation rates, and the response varies between solid- and hollow-stemmed cultivars. Luginbill and McNeal (1958) reported that narrow row spacing and high seeding rates reduced stem cutting in 'Thatcher', a hollow-stemmed cultivar, but the same treatments reduced pith expression and led to increased levels in 'Rescue', a solid-stemmed cultivar. Wider row spacing and lower plant densities create more opportunity for light to penetrate the canopy, which leads to greater pith expression (B. Beres, R. McKenzie, H. Cárcamo, L. Dosdall, M. Evenden, R.-C. Yang, D. Spaner, unpublished data) and a resultant increase in water-soluble carbohydrates and drought tolerance (Saint Pierre *et al.* 2010). For hollow-stemmed cultivars, high seeding rates and narrow row spacing resulted in a lower whole-plant moisture level, which is less attractive to ovipositing females than plants with higher moisture content (Luginbill and McNeal 1958). Similar results for the interaction of seeding rate and pith expression were observed in a study in Syria, but effects from row spacing were inconsistent (Miller *et al.* 1993). Faris and DePauw (1981) observed optimum seeding rates as high as 675 seeds $\cdot$ m^{-2} for cultivars with high yield potential, whereas check cultivars such as 'Neepawa' did not respond to seeding rates above 300 seeds $\cdot$ m^{-2}.

Seeding date can also influence *C. cinctus* infestations. An early recommendation was to delay seeding wheat and to plant immune crops such as oats or non-cereals first (Criddle 1922*a*; Farstad *et al.* 1945). Jacobson and Farstad (1952) reported that seeding after 21 May reduced high infestation levels to as low as 13%, and also resulted in significantly more males, which could disrupt mating habits in successive years (Holmes and Peterson 1963*a*). Other studies reported that consistently lower infestation levels were only realized with planting dates after 1 June, but this seriously reduced potential crop yields (McNeal *et al.* 1955; Morrill and Kushnak 1999). Therefore, a realistic approach for "safe" planting dates is for fields prone to attack to be planted last (Morrill and Kushnak 1999).

Crop nutrient management can influence *C. cinctus* infestation rates through effects on crop canopy architecture and overall plant health. Luginbill and McNeal (1954) observed that application of nitrogen and phosphorus to wheat generally resulted in an increase in stem cutting. Nitrogen applied separately did not influence stem cutting, whereas a slight increase in cutting was observed when phosphorus was applied alone. In contrast, phosphorus-deficient wheat plants in a Montana greenhouse study were most susceptible to sawfly damage (Delaney *et al.* 2010). In a Saskatchewan study, no effects of nitrogen or phosphorous could be detected owing to the strong influence of environmental factors (DePauw and Read 1982). Similarly, significantly more stem cutting in fertilized plots was observed in only one of eight experiments in a North Dakota study (O'Keeffe *et al.* 1960). The disparity between these study results underscores the stochastic nature of site-specific, soil–plant fertility dynamics.

Actions taken prior to harvest can reduce the severity of losses from unrecovered lodged stems at harvest. Swathing heavily infested wheat ensures that stems are collected in a windrow before stem cutting (Criddle 1915). A Montana study reported stem cutting reductions of 33% and 23% when infested wheat was swathed at 41% and 48% grain moisture, respectively, with no apparent reductions in crop value (Goosey 1999). However, the early swathing resulted in lowered grain test weight and higher protein levels, suggesting that starch formation (*i.e.*, grain-filling) was incomplete. A swathing operation, however, does not usually affect sawfly survival because most larvae have migrated to the base of the plant to prepare for overwintering). Other studies have reported that swathing prior to physiological maturity (*i.e.*, >35% kernel moisture) can reduce yield and grain weight, and swathing at >58% kernel moisture results in severe yield losses (Molberg 1963). Early swathing of wheat may have some effect on *C. cinctus* survival, but is impractical because larval mortality was only observed when moisture of swathed grain was between 55% and 61%, and stem cutting occurred when grain moisture declined to 40% (Holmes and Peterson 1965). Holmes and Peterson (1965) noted that greater efficacy can be achieved when grain moisture is high by cutting longer stems, thus reducing stubble height, and suggested that early swathing may be appropriate if it is restricted to field edges or severely infested fields.

Chemical control

Several studies have investigated the efficacy of insecticidal applications to manage *C. cinctus*, but few results have been published because most have been negative. Several unpublished studies in Montana reported that systemic seed treatments of imidacloprid applied at varying rates and foliar-applied chlorpyrifos, carbofuran, and cyhalothrin-lambda had no significant effects on sawfly survivorship (Goosey 1999). A study conducted in Lethbridge, Alberta, and Swift Current, Saskatchewan (B. Beres, R. DePauw, H. Cárcamo, unpublished data), showed no differences in infestation or stem cutting after application of thiamethoxam at rates of 0, 20, and 90 g active ingredients (a.i.) per 100 g seed.

Heptachlor is the only tested insecticide that has consistently caused significant larval death. In a Montana study, 75%–86% of sawfly larvae were killed following application of heptachlor at 20 g a.i. per 100 kg seed (Wallace 1962). A Canadian study validated these results but noted that control was usually restricted to times when larvae were active in the first two internodes and where the insecticide was more concentrated (Holmes and Peterson 1963*b*). A third study examined the systemic activity of heptachlor through host-plant phenological stages; higher application rates resulted in trace amounts in grain but the lowest rate (20 g a.i. per 100 kg) resulted in residues in straw but not grain (Wallace and Butler 1967). However, heptachlor has been banned in the United States of America since 1988 because it is persistent in soil and has been found in crops 15 years after application (Anonymous 1999) (this chemical is also no longer registered in Canada).

Cephus cinctus spends most of its life cycle protected within host stems so it is doubtful that a pesticide can be developed that will target larvae without compromising grain safety or killing beneficial insects that attack larvae. Foliar applications to field edges (where the greatest amount of adult activity occurs) might be efficacious but would require extremely careful monitoring of adults and timing of spray applications because of the extended period of adult emergence. Sprays applied too early would likely kill only males; later applications would increase female mortality but likely after most eggs have been deposited. The tactic would also be detrimental to parasitoids because the first generation of *B. cephi* would be in flight and mainly concentrated along the field edge.

Host-plant resistance

Gene deployment

Although two other sources exist, all solid-stemmed spring and winter wheat cultivars developed prior to 2010 derive resistance from the line S-615. Resistance in 'Golden Ball', a durum cultivar, is superior to, and more stable than, resistance in cultivars derived from S-615 (Platt and Farstad 1949). Resistance in tall wheatgrass, *Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang (Poaceae), also shows promise but attempts to transfer this resistance to wheat have failed (Platt and Farstad 1949).

Stem solidness is a qualitative trait controlled by three or four primarily recessive genes in the S-615 source (Cook *et al.* 2004; Lanning *et al.* 2006), but only a single dominant gene in 'Golden Ball' (Platt and Farstad 1949; McKenzie 1965; Clarke *et al.* 1998). The recessive nature of the S-615 genes controlling resistance leads to inconsistent pith expression in the field (Hayat *et al.* 1995). This was acknowledged shortly after the release of 'Rescue' (containing resistance derived from the S-615 source) when high susceptibility to stem cutting was noted at Regina, Saskatchewan (Platt and Farstad 1949). It was later determined that genes conferring pith development in plant stems are influenced by photoperiod: intense sunlight results in maximum expression and pith development; shading or cloudy conditions inhibit pith development (Eckroth and McNeal 1953; Holmes 1984). The dominant gene resistance in 'Golden Ball' results in good pith expression across a range of environmental conditions (Platt and Farstad 1949). Therefore, efforts began in the 1940s to transfer the source of resistance from 'Golden Ball' (durum wheat) to wheat (Platt and Larson 1944), but the genes for solidness were suppressed and only hollow-stemmed offspring were produced. This gene suppression was overcome by crossing 'Golden Ball' with a species of goatgrass, *Aegilops* L. (Poaceae), to create a synthetic hexaploid, and then backcrossing the offspring to the hexaploid wheat cultivar, 'AC Elsa' (Clarke *et al.* 1998, 2002). Two germplasm lines were developed using this method and have been released (Clarke *et al.* 2005).

Cultivar development

Solid-stemmed cultivars available in 2010 in the Canada Red Western Spring class are 'AC Eatonia', 'AC Abbey', and 'AC Lillian' (DePauw *et al.* 1994, 2000, 2005). Solid-stemmed spring wheat cultivars available in Montana include 'Fortuna', 'Lew', and 'Choteau'. Montana historically classified the 'Amidon', 'Glenman', 'Conan', 'Corbin', and 'Scholar' cultivars as semi-tolerant to *C. cinctus*, but these cultivars are not favoured, owing to significant risk to efficacy when facing heavy sawfly pressure.

Resistance in winter wheat is also important because of a biotype of *C. cinctus* in Montana that has gradually adapted to become synchronous with winter wheat phenology by emerging 10–20 days earlier than normal. The adaptation seems to have occurred as a response to a shift in Montana from spring to winter wheat production (Morrill and Kushnak 1996). Solid-stemmed winter wheat cultivars available to Montana producers include 'Vanguard' (Carlson *et al.* 1997), 'Rampart', and 'Genou' (Bruckner *et al.* 1997, 2006).

The use of solid-stemmed cultivars helps mitigate crop losses but can also affect the survivorship of *C. cinctus*. The mechanical pressure of developing pith in solid stems can result in egg mortality and the degree of mortality is influenced by cultivar. In studies of egg and larval mortality (Holmes and Peterson 1961, 1962), mortality was highest in 'Golden Ball' (*versus* 'Rescue') but not affected in hollow-stemmed cultivars and, in oats, eggs survived but all larvae died. In other work, hollow-stemmed cultivars with large stem diameters maximized sawfly fitness and solid-stemmed cultivars reduced female mass, size, and fecundity (Morrill *et al.* 2000; Cárcamo *et al.* 2005). Holmes and Peterson (1957) studied the long-term effects of wheat cultivar on *C. cinctus* and reported that sawfly populations restricted to the solid-stemmed cultivar 'Rescue' declined over a 5-year period to almost zero.

Solid-stemmed cultivars generally exhibit lower grain yield and quality than hollow-stemmed cultivars. There is also a concern of additional wear on machinery because solid stems require more energy to thresh and reduce ground speed of combines (B. Buckman, personal communication). Inconsistent pith expression, as influenced by photoperiod during stem elongation, has resulted in higher than expected levels of stem cutting in solid-stemmed cultivars. Beres *et al.* (2007) reported that solid-stemmed cultivars could produce grain yield and protein content levels comparable or superior to those of hollow-stemmed cultivars in an environment of moderate to high *C. cinctus* pressure. 'AC Lillian', a solid-stemmed cultivar released in Canada in 2006, has provided superior yields even in the absence of sawfly pressure. Although inconsistent pith expression (first noted with the release of 'Rescue') has been observed with 'AC Lillian', many producers have continued with this cultivar because *C. cinctus* pressure is currently high in Saskatchewan and Alberta (B. Beres, personal observations).

Cultivar blends

Blending two cultivars (one hollow-, one solid-stemmed) with compatible maturity, market class attributes, and complementary strengths (Bowden *et al.* 2001) may be a feasible approach to management of wheat stem sawfly. This practice is commonly used in Kansas to achieve yield stability because abiotic and biotic stresses can be inconsistent and unpredictable. A Montana study reported that the strategy was successful at minimizing damage at low to moderate levels of sawfly pressure, but not at high levels (Weiss *et al.* 1990). Similarly, a 1:1 blend of solid-stemmed 'AC Eatonia' and hollow-stemmed 'AC Barrie' resulted in an 11% increase in yield potential in comparison with a monoculture of 'AC Barrie' in Alberta (Beres *et al.* 2009). Quality was also improved by using a blend of cultivars with contrasting protein accumulation potential (Beres *et al.* 2007).

Biological control

Nine species of Hymenoptera are known to parasitize *C. cinctus* (Morrill *et al.* 1998; Meers 2005). The shift of host preference of *C. cinctus* from native and exotic grasses to wheat was rapid, but the parasitoids have been slow to follow. Ainslie (1920) and Criddle (1923) reported parasitoids of *C. cinctus* in larvae in grass stems but not in wheat stems, and only two of the nine parasitoids have been recorded in *C. cinctus* populations in wheat (Morrill *et al.* 1998).

Criddle (1923) suggested that *Bracon cephi*, a sympatric idiobiont ectoparasitoid (Runyon *et al.* 2001), had great potential for wheat stem sawfly control because it was largely responsible for larval parasitism rates as high as 85% in grasses. Criddle (1923) speculated that the inability of parasitoids to adapt to wheat was due to tillage and harvest practices and, in the case of *B. cephi*, because of its bivoltine life cycle. Emergence of the first generation of *B. cephi* and of sawfly adults is approximately synchronous, but the second generation emerges in August when early harvest and subsequent ploughing can negatively impact the parasitoids. In wheat, Criddle (1923) only observed parasitism from the first generation.

Bracon cephi eventually adapted to parasitizing sawfly larvae in wheat and has become the most important parasitoid of *C. cinctus* in Canada (Nelson and Farstad 1953) and North Dakota (Meers 2005). A female locates a host larva by traversing a stem and then, if she senses the presence of a host larva, straddles the stem at the place where she will insert her ovipositor. The ovipositor is used to inject venom to immobilize the larva and then deposit an egg near it. Upon hatching, the parasitoid larva searches for, and attaches itself to, the paralyzed *C. cinctus* larva and immediately begins feeding. The host is consumed in approximately 10 days, at which point the fully developed larva spins a cylindrical cocoon where it pupates and enters diapause. Adults of the second generation emerge in August by chewing a circular hole through the stem (Nelson and Farstad 1953).

Parasitism of wheat stem sawfly larvae by the first generation can significantly reduce further yield loss (Buteler *et al.* 2008), although host stem size preferences of adult female sawflies complicate the assessment, just as they do for yield losses. Successful parasitism by the second generation is dependent on crop maturity and the timing of host larva overwintering preparations (Holmes *et al.* 1963). If wheat crops are delayed and maturity is not reached until mid-August, the rates of parasitism by the second generation can be very high. If crops mature early, stems have usually toppled from cutting, and host larvae are safely housed within hibernacula before the second generation of *B. cephi* has completely emerged (Holmes *et al.* 1963). Later seeding would enhance *B. cephi* success but, in many parts of southern Alberta, seeding is now more common in April than in May. This is partially offset by the adoption of later maturing, high-yielding cultivars. Success of *B. cephi* is therefore variable. Low efficacy of *B. cephi* occurs when activity of the second generation is low and when the first generation, overwintering in the upper internodes of the wheat crop, is lost during harvest and threshing (Holmes 1979).

Bracon lissogaster, the second major parasitoid of *C. cinctus* in wheat, also was slow to shift to sawfly populations in wheat but is now active in Montana and North Dakota (Meers 2005) and was recently found in southern Alberta (H. Carcamo, S. Meers, D. Weaver, B. Beres, A. Mauduit, unpublished data). Its life cycle is similar to that of *B. cephi* but it can more readily complete a second generation in late fall, which is attributed to immediate oviposition by adult females after they emerge (Somsen and Luginbill 1956). The second generations of *B. cephi* and *B. lissogaster* are also less likely to be cannibalized by *C. cinctus* larvae than are the first generations. First-generation females of both species will often oviposit in stems containing multiple *C. cinctus* eggs. This can result in a significant reduction in parasitism rates because of cannibalism of parasitized larvae by other *C. cinctus* larvae (Weaver *et al.* 2005).

A predatory beetle, *Phyllobaenus dubius* (Wolcott) (Coleoptera: Cleridae), attacks larvae of *C. cinctus* (Beres *et al.* 2009; Morrill *et al.* 2001*a*). The life history and biology of *P. dubius* has not been detailed but its geographic range could be extensive (Meers 2005). Clerid beetles are most often associated with forest ecosystems but 18 species have now been recorded in prairie ecosystems (Mawdsley 2002). Most prairie clerids have annual life cycles with adult emergence, mating, and oviposition in spring or early summer, larval development in the summer, and pupation in either fall or spring (Mawdsley 2002). Most clerids are prey generalists, but some may be more specialized (Mawdsley 2002). *Phyllobaenus dubius* is small (4.5–5.0 mm long) and adults and larvae can forage within wheat stems. *Phyllobaenus dubius* was first observed in large numbers in wheat stem sawfly-infested fields in 1997; the beetle larvae were overwintering in wheat stubs in cocoons along with cadavers of larval *C. cinctus* (Morrill *et al.* 2001*a*). Most aspects of *P. dubius* biology, as well as its potential for controlling *C. cinctus* populations, remain unknown.

Crop management practices can significantly influence the abundance and efficacy of *C. cinctus* parasitoids. Reduced tillage resulted in higher rates of parasitism and less stem cutting than in adjacent fields that were aggressively tilled (Runyon *et al.* 2002). The use of solid-stemmed cultivars in zero tillage cropping systems conserved parasitoids and reduced sawfly populations (Weaver *et al.* 2004). Conservation of parasitoids can also be accomplished by increasing stubble height at harvest and by restricting insecticide use during peak flight periods of the adult parasitoids (Meers 2005; B. Beres, unpublished data).

Introduction of foreign biocontrol agents can improve the efficacy of biological control. *Collyria calcitrator* (Gravenhorst) (Hymenoptera: Ichneumonidae), a parasitoid of European wheat stem sawfly, *Cephus pygmaeus* L., and was the first biological control agent released to manage *C. cinctus* in North America. However, establishment attempts in Saskatchewan (Smith 1931), Montana, and North Dakota (Davis 1955) were unsuccessful. Specimens of *Collyria coxator* (Villers), another parasitoid of *C. pygmaeus*, were collected in England and a population has become established in eastern North America (Shanower and Hoelmer 2004). Exploration in China identified *Collyria catoptran* (Wahl) as a potential candidate for introduction to North America (Shanower and Hoelmer 2004; Wahl *et al.* 2007). Evaluation of this species is underway to determine its suitability as a potential biocontrol agent of *C. cinctus.*

Pathogens can be used as biocontrol agents to manage insect pests (Lacey *et al.* 2001) and studies of pathogens and their efficacy for the control of *C. cinctus* have reported some success (Piesik *et al.* 2009; Wenda-Piesik *et al.* 2006, 2009). However, many pathogens seem to occur as secondary parasites of dead larvae and, therefore, lack potential as agents for the biological control of *C. cinctus*.

Pheromone monitoring and host-plant semiochemicals

The effectiveness of trap-cropping or border management for control of *C. cinctus* could be enhanced through the development of sawfly attractants (Hardin 2001). Research into the pheromone components of wheat stem sawfly is a complex task because the primary compounds are present but variable in both sexes and host volatiles; other factors are also involved (Hardin 2001). Cossé *et al.* (2002) and Bartelt *et al.* (2002) were the first to describe pheromones of *C. cinctus*; most compounds identified were present in both genders but the quantity differed significantly between males and females. For example, males produced three times the amount of 9-acetyloxynonanal found in females (and males in groups produced significant quantities of phenylacetic acid), whereas hexadecanal was the primary compound in females (Cossé *et al.* 2002).

Cossé *et al.* (2002) used coupled gas chromatographic–electroantennographic detection (GC-EAD) to study the effects of pheromone components on the behaviour of adult *C. cinctus*. They also conducted field assays to determine if 9-acetyloxynonanal could be used as a female attractant in traps. Trap catch was dose-dependent and there was no signficant difference in the sex ratio of trapped individuals (Cossé *et al.* 2002). Bartelt *et al.* (2002) noted the complexity of the *C. cinctus* pheromone system and that it may be influenced greatly by field behaviour and is driven by natural oxidation of cuticular waxes. Future research could benefit from a focus on collecting a female-specific chemical signal that is driven by the various environmental factors (Cossé *et al.* 2002).

Semiochemical-based pest management could influence oviposition behaviour of *C. cinctus* if a bait and trap can be developed that would attract and capture females prior to oviposition. Rather than using a synthetic male-produced pheromone, the synthesis and use of a plant host volatile naturally attractive to ovipositing females could be effective. Studies have been successful in discriminating synthetic wheat volatiles that elicit responses from individual female *C. cinctus* (Piesik *et al.* 2008). Also, in a comparison between 'Reeder', a hollow-stemmed cultivar, and 'Conan', a solid-stemmed cultivar, of the emission of (*Z*)-3-hexenyl acetate and the attractivity of this behaviourally active host volatile to female *C. cinctus*, Weaver *et al.* (2009) noted greater emission by, and greater attractivity to, 'Reeder'. This host preference could be exploited in a trap-cropping strategy (Weaver *et al.* 2009). Subsequent research using RILs from the two parent varieties has identified the quantitative trait loci in wheat that are associated with preference (Sherman *et al.* 2010). Efforts are now underway to develop markers to aid in breeding efforts.

Future research needs

Although wheat stem sawfly currently has regained outbreak status in many parts of the northern Great Plains, resources to study the pest are limited. In Canada, maintenance breeding is all that officially remains of a major research effort to manage this pest and illustrates the tendency to rely upon a single strategy to address an insect pest problem. A holistic approach involving multiple institutes representing several disciplines of research would be preferable (Anderson 2005, 2008).

Cultural methods will remain critical for managing wheat stem sawfly (Weaver *et al.* 2004). Our review underscores the need to encourage producers to adopt practices that reduce sawfly infestations and enhance beneficial insect populations (Weaver *et al.* 2004). Integrated approaches are lacking, and too often the adoption of a "resistant" variety is assumed to solve the problem in a single growing season. Moreover, solid-stemmed cultivars are only available in the bread wheat class in Canada. Five other classes of wheat are grown within the geographical range of *C. cinctus,* and there is currently a trend to reduce production of bread wheat in favour of general purpose markets such as the ethanol feedstock market. Furthermore, the entire production area for durum wheat lies within the geographic range of *C. cinctus*, and durum wheat production is also expected to increase and displace bread wheat. Breeding objectives should be expanded so that solid-stemmed durum, soft white spring wheat, and winter wheat cultivars are available. Pheromone- and semiochemical-based research and plant breeding efforts should be merged, as there may be opportunity to develop cultivars with specific volatile emissions that attract or repel female *C. cinctus* (Weaver *et al.* 2009). Research is also needed to evaluate the use of cultivar blends, or combinations of solid- and hollow-stemmed wheat that can be seeded strategically in a field based on predicted patterns of infestation. Thus, cultivar selection should be considered a management tool that provides the foundation on which an integrated pest management (IPM) strategy is built, and which contributes to the higher goal of optimizing an integrated crop management (ICM) strategy.

What are some considerations for the development of IPM and ICM strategies for the wheat stem sawfly? Unlike other serious cereal pests such as orange wheat blossom midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae), or the clear-winged grasshopper, *Camnula pellucida* (Scudder) (Orthoptera: Acrididae), insecticidal control has proved ineffective for wheat stem sawfly control. Therefore, successful management requires greater complexity. The appropriate selection of cultivars prior to seeding can have positive effects throughout the growing season if that cultivar is managed properly. Not only should market opportunities or abiotic–biotic pressure influence selection, but so should the enhancement of beneficial insects. For example, cultivars or even classes of cereals that require more growing day-degrees (Blake *et al.* 2007) should be favoured because this allows completion of the second generation of *B. cephi* or *B. lissogaster*; which has long-term benefits on population dynamics (Holmes *et al.* 1963) and potential immediate impacts (Buteler *et al.* 2008). An additional advantage is that the later-maturing cultivars recently released have higher yield potential because there is usually a positive correlation between yield and time to maturity (Blake *et al.* 2007). However, the risks of early frost and reduced yield from delayed seeding often outweigh the benefit derived from reduced *C. cinctus* infestation; an effective compromise might be early-seeded, long-season cultivars. Target densities of plant populations must vary with cultivar selection. Solid-stemmed wheat varieties are more efficacious at lower densities (Luginbill and McNeal 1958), but higher densities of hollow-stemmed wheat may increase grain yield, reduce infestation of *C. cinctus*, and decrease the competitive ability of weeds. Cultivar development and genetic gain has advanced considerably in recent decades and a review of seeding rates for modern hollow- and solid-stemmed cultivars is warranted. Thus, research is needed to better define target plant populations so that an appropriate balance between yield potential, wheat stem sawfly management, and overall crop competitiveness is achieved.

Cultivar selection is key to a successful IPM strategy for wheat stem sawfly, and the inconsistency in pith development (the trait that confers ‘‘resistance’’ in solid-stemmed cultivars) in solid-stemmed cultivars should not dissuade producers from growing this cultivar in areas prone to attack. Enhanced efficacy of solid-stemmed wheat could result if modelling is developed based on precipitation-related parameters to predict the in-season tolerance level of solid-stemmed wheat cultivars to wheat stem sawfly. A model that can accurately predict pith expression could serve as a vital quality-assurance tool to prevent losses by alerting producers if in-season precipitation patterns have caused less than ideal pith expression in a solid-stemmed cultivar. Such a tool would allow for preventative measures to be deployed such as swathing ahead of harvest to prevent the loss of cut stems (B. Beres, B. Hill, D. Weaver, H. Cárcamo, unpublished data).

Plant nutritional requirements can change as seeding rates are modified, and may deviate from traditional requirements where fertilizer response rates are known, but more research is needed to investigate this relationship. The inconsistent results from studies of macronutrients and lack of information regarding micronutrients warrant further investigation. For example, recently there has been emphasis on the potential benefit of micronutrient fertilizer, but little is known about benefits to a solid-stemmed wheat system. Fertilizer management and plant density can dramatically alter crop canopy architecture, which warrants the integrated study of multiple factors to better predict effects on pests in modern cropping systems (Anderson 2005; Dosdall *et al.* 1999).

The effects of crop residue management prior to seeding, or residue alteration from seeding operations, are either unknown or generally considered to be ineffective (Runyon *et al.* 2002; Weiss *et al.* 1987), particularly if soil is not completely removed from root crowns (Goosey 1999). These conclusions were drawn from studies that did not incorporate residue management and direct seeding systems typical of modern farming operations. However, the shift toward zero tillage, direct seeding systems, and continuous cropping requires that an alternative to tillage be developed as a sustainable tool for the management of *C. cinctus*. A wheat–fallow cropping system still exists in many parts of the *C. cinctus* distribution area (Weaver *et al.* 2004), and financial pressure from increased input costs has resulted in shifting of some continuously cropped hectarage back to crop–fallow.

Low-disturbance seeding systems and fallowing of infested wheat fields should enhance overwintering populations, but to what degree? Would a better strategy be to re-crop infested wheat stubble and fallow another crop phase instead? If the proper cultivar, or combination of cultivars, is selected and appropriately managed, there is greater opportunity to lessen the impact of harvest operations on beneficial insects, because cutting heights may be increased in response to lower rates of stem cutting. Future studies should validate this approach and determine the effect of chopping straw residue at harvest as opposed to windrowing intact stems for subsequent use as livestock bedding or bioprocessing.

Furthermore, there is a need to couple agronomics with biocontrol release programs. When agronomic and biocontrol strategies are employed together in an ICM system, the incremental benefits of each approach may have an overall additive effect that reduces wheat stem sawfly populations, and would contribute to a sustainable crop production system. Rather than eradication of *C. cinctus*, the management goal should be achievement of a level of coexistence that optimizes crop productivity and maintains the abundance of natural enemies.

Acknowledgements

We are honoured to have this manuscript supported by the C.P. Alexander fund of the Entomological Society of Canada. The manuscript was greatly improved by the input provided by three anonymous reviewers. Special thanks are given to Robb Bennett and Kevin Floate for their editorial support and positive feedback throughout the review process. Lastly, we dedicate this review to the generations of scientists that have contributed to our knowledge of wheat stem sawfly. This article is LRC contribution no. 387-10053.

References

Ainslie, C.N. 1920. The western grass-stem sawfly. USDA Technical Bulletin No. 841.

Ainslie, C.N. 1929. The western grass-stem sawfly: a pest of small grains. USDA Technical Bulletin No. 157.

Anderson, R.L. 2005. A multi-tactic approach to manage weed population dynamics in crop rotations. Agronomy Journal, **97**: 1579–1583. doi:10.2134/agronj2005.0194.

Anderson, R.L. 2008. Diversity and no-till: keys for pest management in the US great plains. Weed Science, **56**: 141–145. doi:10.1614/ws-07-007.1.

Anonymous. 1999. Heptachlor [online]. Available from http://www.epa.gov/wastemin/factshts/hepchl.pdf [accessed 23 April 2008].

Bartelt, R.J., Cossé, A.A, Petroski, R.J., and Weaver, D.K. 2002. Cuticular hydrocarbons and novel alkenediol diacetates from wheat stem sawfly *Cephus cinctus*: natural oxidation to pheromone components. Journal of Chemical Ecology, **28**: 385–405. PMID:11925075 doi:10.1023/A:1017994410538.

Beres, B.L., Cárcamo, H.A., and Byers, J.R. 2007. Effect of wheat stem sawfly damage on yield and quality of selected Canadian spring wheat. Journal of Economic Entomology, **100**: 79–87. PMID:17370813 doi:10.1603/0022-0493(2007)100[79:EOWSSD]2.0.CO;2.

Beres, B.L., Cárcamo, H.A., and Bremer, E. 2009. Evaluation of alternative planting strategies to reduce wheat stem sawfly (Hymenoptera: Cephidae) damage to spring wheat in the Northern Great Plains. Journal of Economic Entomology, **102**: 2137–2145. PMID:20069842 doi:10.1603/029.102.0617.

Blake, N.K., Lanning, S.P., Martin, J.M., Sherman, J.D., and Talbert, L.E. 2007. Relationship of flag leaf characteristics to economically important traits in two spring wheat crosses. Crop Science, **47**: 491–496. doi:10.2135/cropsci2006.05.0286.

Blodgett, S.L., Johnson, G., Kemp, W.P., and Sands, J.K. 1997. Developing an extension pest management program using the needs-assessment process [online]. Journal of Extension, **35**. http://www.joe.org/joe/1997february/a1.php [accessed July 2010].

Bowden, R., Shroyer, J., Roozeboom, K., Claassen, M., Evans, P., Gordon, B., *et al.* 2001. Performance of wheat variety blends in Kansas. *In* Keeping up with research. Kansas State University, Manhattan, Kansas. p. 6.

Brandt, S.A., Kutcher, H.R., and Smith, E.G. 2008. Agronomic implications of more intensive canola rotations. *In* Proceedings of FARMTECH 2008: 136.

Bruckner, P.L., Berg, J.E., Kushnak, G.D., Stougaard, R.N., Eckhoff, J.L., Carlson, G.R., *et al.* 2006. Registration of 'Genou' wheat. Crop

Science, **46**: 982–983. doi:10.2135/cropsci2005.07-0188.

Bruckner, P.L., Kushnak, G.D., Berg, J.E., Wichman, D.M., Carlson, G.R., Stallknecht, G.F., *et al.* 1997. Registration of 'Rampart' wheat. Crop Science, **37**: 1004. doi:10.2135/cropsci1997.0011183X003700030052x.

Buteler, M., Weaver, D.K., and Miller, P.R. 2008. Wheat stem sawfly-infested plants benefit from parasitism of the herbivorous larvae. Agricultural and Forest Entomology, 10: 347–354; *Corrigendum* 11:123. doi:10.1111/j.1461-9563.2008.00396.x.

Buteler, M., Weaver, D.K., and Peterson, R.K.D. 2009. Oviposition behavior of the wheat stem sawfly when encountering plants infested with cryptic conspecifics. Environmental Entomology, **38**: 1707–1715. PMID:20021767 doi:10.1603/022.038.0624.

Buteler, M., Weaver, D.K., Bruckner, P.L., Carlson, G.R., Berg, J.E., and Lamb, P.F. 2010. Identification of winter wheat cultivars suitable as trap crops for the wheat stem sawfly based on screening using agronomic traits and semiochemical production. The Canadian Entomologist, **142**: 222–233.

Cárcamo, H.A., and Beres, B.L. 2006. Does wheat host affect overwintering survivorship of the wheat stem sawfly? *In* Proceedings of the Annual Meeting of the Entomological Society of Alberta, **54**: 1.

Cárcamo, H.A., Beres, B.L., Clarke, F., Byers, R.J., Mundel, H.H., May, K., and DePauw, R. 2005. Influence of plant host quality on fitness and sex ratio of the wheat stem sawfly (Hymenoptera: Cephidae). Environmental Entomology, **34**: 1579–1592. doi:10.1603/0046-225X-34.6.1579.

Carlson, G.R., Bruckner, P.L., Berg, J.E., Kushnak, G.D., Wichman, D.M., Eckhoff, J.L., *et al.* 1997. Registration of 'Vanguard' wheat. Crop Science, **37**: 291. doi:10.2135/cropsci1997.0011183X003700010060x.

Clarke, F., Aung, T., and DePauw, R. 1998. Simplifying the inheritance of resistance to wheat stem sawfly (*Cephus cinctus* Nort.). *In* Proceedings of the Ninth International Wheat Genetics Symposium. A.E. Slinkard. University Extension Press, University of Saskatchewan, Saskatoon, Saskatchewan. pp. 240–242.

Clarke, F.R., Clarke, J.M., and Knox, R.E. 2002. Inheritance of stem solidness in eight durum wheat crosses. Canadian Journal of Plant Science, **82**: 661–664.

Clarke, F.R., DePauw, R.M., and Aung, T. 2005. Registration of sawfly resistant hexaploid spring wheat germplasm lines derived from durum. Crop Science, **45**: 1665–1666. doi:10.2135/cropsci2003.0607.

Comstock, J.H. 1889. On a saw-fly borer in wheat. Cornell University, Ithaca, New York.

Cook, J.P., Wichman, D.M., Martin, J.M., Bruckner, P.L., and Talbert, L.E. 2004. Identification of microsatellite markers associated with a stem solidness locus in wheat. Crop Science, **44**: 1397–1402. doi:10.2135/cropsci2004.1397.

Cossé, A.A., Bartelt, R.J., Weaver, D.K., and Zilkowski, B.W. 2002. Pheromone components of the wheat stem sawfly: identification, electrophysiology, and field bioassay. Journal of Chemical Ecology, **28**: 407–423. PMID:11925076 doi:10.1023/A:1017946527376.

Criddle, N. 1915. The Hessian fly and the western wheat stem sawfly in Manitoba, Saskatchewan and Alberta. Canadian Department of Agriculture, Entomology Branch Bulletin, **11**: 1–23.

Criddle, N. 1922*a*. The western wheat stem sawfly and its control. Dominion of Canada Department of Agriculture Pamphlet No. 6 New Series: 1–8.

Criddle, N. 1922*b*. The western wheat stem sawfly in Canada. The Report of the Entomological Society, **36**: 18–21.

Criddle, N. 1923. The life habits of *Cephus cinctus* Nort. in Manitoba. The Canadian Entomologist, **55**: 1–4. doi:10.4039/Ent551-1.

Davis, E.G. 1955. Status of the wheat stem sawfly in the United States in 1954. North Dakota Agricultural Experiment Station Bimonthly Bulletin, **17**: 171–175.

Davis, E.G., Benton, C., and Somsen, H.W. 1955. Natural enemies of the wheat stem sawfly in North Dakota and Montana. North Dakota Agricultural Experimental Station Bimonthly Bulletin, **28**: 63–65.

Delaney, K.J., Weaver, D.K., and Peterson, R.K.D. 2010. Photosynthesis and yield reductions from wheat stem sawfly (Hymenoptera: Cephidae): Interactions with wheat solidness, water stress, and phosphorus deficiency. Journal of Economic Entomology, **103**: 516–524. PMID:20429469 doi:10.1603/ec09229.

DePauw, R.M., and Read, D.W.L. 1982. The effect of nitrogen and phosphorus on the expression of stem solidness in Canuck wheat at four locations in southwestern Saskatchewan. Canadian Journal of Plant Science, **62**: 593–598. doi:10.4141/cjps82-089.

DePauw, R.M., McLeod, J.G., Clarke, J.M., McCaig, T.N., Fernandez, M.R., and Knox, R.E. 1994. AC Eatonia hard red spring wheat. Canadian Journal of Plant Science, **74**: 821–823.

DePauw, R.M., Clarke, J.M., Knox, R.E., Fernandez, M.R., McCaig, T.N., and McLeod, J.G. 2000. AC Abbey hard red spring wheat. Canadian Journal of Plant Science, **80**: 123–127.

DePauw, R.M., Townley-Smith, T.F., Humphreys, G., Knox, R.E., Clarke, F.R., and Clarke, J.M. 2005. Lillian hard red spring wheat. Canadian Journal of Plant Science, **85**: 397–401.

Dosdall, L.M., Dolinski, M.G., Cowle, N.T., and Conway, P.M. 1999. The effect of tillage regime, row spacing, and seeding rate on feeding damage by flea beetles, *Phyllotreta* spp. (Coleoptera: Chrysomelidae), in canola in central Alberta, Canada. Crop Protection, **18**: 217–224. doi:10.1016/S0261-2194(99)00019-8.

Eckroth, E.G., and McNeal, F.H. 1953. Association of plant characters in spring wheat with resistance to the wheat stem sawfly. Agronomy Journal, **45**: 400–404. doi:10.2134/agronj1953.00021962004500090002x.

Faris, D.G., and DePauw, R.M. 1981. Effect of seeding rate on growth and yield of three spring wheat cultivars. Field Crops Research, **3**: 289–301. doi:10.1016/0378-4290(80)90036-2.

Farstad, C.W., King, K.M., Glen, R., and Jacobson, L.A. 1945. Control of the wheat stem sawfly in the prairie provinces. War-time Production series – Agricultural Supplies Board Special Publication No. 59. pp. 1–7.

Farstad, C.W., and Platt, A.W. 1946. The reaction of barley varieties to wheat stem sawfly attack. Scientific Agriculture, **26**: 216–224.

Fletcher, J. 1896. ddThe western wheat stem sawfly (*Cephus pygmaeus* L.). Dominion of Canada, Department of Agriculture, Report of the Dominion Entomologist: 147–149.

Fletcher, J. 1904. Experimental farms reports – Report of the Entomologist and Botanist. Appendix to the Report of the Minister of Agriculture, Sessional Paper No. 16. pp. 172–173.

Goosey, H.B. 1999. In field distributions of the wheat stem sawfly, (Hymenoptera: Cephidae), and evaluation of selected tactics for an integrated management program. M.Sc. thesis, Montana State University, Bozeman, Montana.

Goosey, H.B., Lenssen, A.W., Johnson, G.D., Blodgett, S.L., Carlson, G.R., and Kephart, K.D. 2007. Durum spring wheat susceptibility to wheat stem sawfly (Hymenoptera: Cephidae). Journal of Entomological Science, **42**: 133–138.

Hardin, B. 2001. Cutting through wheat stem sawfly dilemmas [online]. Available from http://www.ars.usda.gov/is/AR/archive/jul01/sawfly0701.pdf [accessed 1 August 2010].

Hayat, M.A., Martin, J.M., Lanning, S.P., McGuire, C.F., and Talbert, L.E. 1995. Variation for stem solidness and its association with agronomic traits in spring wheat. Canadian Journal of Plant Science, **75**: 775–780.

Holmes, N.D. 1977. The effect of the wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), on the yield and quality of wheat. The Canadian Entomologist, **109**: 1591–1598. doi:10.4039/Ent1091591-12.

Holmes, N.D. 1979. The wheat stem sawfly. *In* Proceedings of the Twenty-sixth Annual Meeting of the Entomological Society of Alberta, **26**: 2–13.

Holmes, N.D. 1982. Population dynamics of the wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), in wheat. The Canadian Entomologist, **114**: 775–788. doi:10.4039/Ent114775-9.

Holmes, N.D. 1984. The effect of light on the resistance of hard red spring wheats to the wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae). The Canadian Entomologist, **116**: 677–684. doi:10.4039/Ent116677-5.

Holmes, N.D., and Farstad, C.W. 1956. Effects of field exposure on immature stages of the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae). Canadian Journal of Agricultural Sciences, **36**: 196–202.

Holmes, N.D., and Peterson, L.K. 1957. Effect of continuous rearing in Rescue wheat on the survival of the wheat stem sawfly *Cephus cinctus* Nort. (Hymenoptera: Cephidae). The Canadian Entomologist, **89**: 363–364. doi:10.4039/Ent89363-8.

Holmes, N.D., and Peterson, L.K. 1960. The influence of the host on oviposition by the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae). Canadian Journal of Plant Science, **40**: 29–40. doi:10.4141/cjps60-004.

Holmes, N.D., and Peterson, L.K. 1961. Resistance of spring wheats to the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae) I. Resistance to the egg. The Canadian Entomologist, **93**: 250–260. doi:10.4039/Ent93250-4.

Holmes, N.D., and Peterson, L.K. 1962. Resistance of spring wheats to the wheat stem sawfly *Cephus cinctus* Nort. (Hymenoptera: Cephidae) II. Resistance to the larva. The Canadian Entomologist, **94**: 348–365. doi:10.4039/Ent94348-4.

Holmes, N.D., and Peterson, L.K. 1963*a*. Effects of variety and date of seeding spring wheats and location in the field on sex ratio of the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae). Canadian Journal of Zoology, **41**: 1217–1222. doi:10.1139/z63-101.

Holmes, N.D., and Peterson, L.K. 1963*b*. Heptachlor as a systemic insecticide against the wheat stem sawfly, *Cephus cinctus* Nort. The Canadian Entomologist, **95**: 792–796. doi:10.4039/Ent95792-8.

Holmes, N.D., and Peterson, L.K. 1965. Swathing wheat and survival of wheat stem sawfly. Canadian Journal of Plant Science, **45**: 579–581. doi:10.4141/cjps65-109.

Holmes, N.D., Nelson, W.A., Peterson, L.K., and Farstad, C.W. 1963. Causes of variations in effectiveness of *Bracon cephi* (Gahan) (Hymenoptera: Braconidae) as a parasite of the wheat stem sawfly. The Canadian Entomologist, **95**: 113–126. doi:10.4039/Ent95113-2.

Ivie, M.A. 2001. On the geographic origin of the wheat stem sawfly (Hymenoptera: Cephidae): a new hypothesis of introduction from northeastern Asia. American Entomologist, **47**: 84–97.

Ivie, M.A., and Zinovjev, A.G. 1996. Discovery of the wheat stem sawfly (*Cephus cinctus* Norton) (Hymenoptera: Cephidae) in Asia, with the proposal of a new synonymy. The Canadian Entomologist, **128**: 347–348. doi:10.4039/Ent128347-2.

Jacobson, L.A., and Farstad, C.W. 1952. Effect of time of seeding Apex wheat on infestation and sex ratio of the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenotpera: Cephidae). The Canadian Entomologist, **84**: 90–92. doi:10.4039/Ent8490-3.

Kemp, H.J. 1934. Studies of solid stem wheat varieties in relation to wheat stem sawfly control. Scientific Agriculture, **15**: 30–38.

Lacey, L.A., Frutos, R., Kaya, H.K., and Vail, P. 2001. Insect pathogens as biological control agents: Do they have a future? Biological Control, **21**: 230–248. doi:10.1006/bcon.2001.0938.

Lafond, G.P., Boyetchko, S.M., Brandt, S.A., Clayton, G.W., and Entz, M.H. 1996. Influence of changing tillage practices on crop production. Canadian Journal of Plant Science, **76**: 641–649.

Lal, R. 1997. Residue management, conservation tillage and soil restoration for mitigating greenhouse effect by CO_2-enrichment. Soil and Tillage Research, **43**: 81–107. doi:10.1016/S0167-1987(97)00036-6.

Lanning, S.P., Fox, P., Elser, J., Martin, J.M., Blake, N.K., and Talbert, L.E. 2006. Microsatellite markers associated with a secondary stem solidness locus in wheat. Crop Science, **46**: 1701–1703. doi:10.2135/cropsci2005.10-0379.

Lindwall, C.W., and Anderson, D.T. 1981. Agronomic evaluation of minimum tillage systems for summer fallow in southern Alberta. Canadian Journal of Plant Science, **61**: 247–253. doi:10.4141/cjps81-037.

Luginbill, P., Jr., McNeal, F.H. 1954. Effect of fertilizers on the resistance of certain winter and spring wheat varieties to the wheat stem sawfly. Agronomy Journal, **46**: 570–573. doi:10.2134/agronj1954.00021962004600120010x.

Luginbill, P., and McNeal, F.H. 1958. Influence of seeding density and row spacings on the resistance of spring wheats to the wheat stem sawfly. Journal of Economic Entomology, **51**: 804–808.

Macedo, T.B., Peterson, R.K.D., Weaver, D.K., and Morrill, W.L. 2005. Wheat stem sawfly, *Cephus cinctus* Norton, impact on wheat primary metabolism: an ecophysiological approach. Environmental Entomology, **34**: 719–726. doi:10.1603/0046-225X-34.3.719.

Macedo, T.B., Weaver, D.K., and Peterson, R.K.D. 2007. Photosynthesis in wheat at the grain filling stage is altered by larval wheat stem sawfly (Hymenoptera: Cephidae) injury and reduced water availability. Journal of Entomological Science, **42**: 228–238.

Mathews, O.R. 1945. Crop residue management in dry-land crop production. Agronomy Journal, **37**: 297–306. doi:10.2134/agronj1945.00021962003700040007x.

Mawdsley, J.R. 2002. Ecological notes on species of Cleridae (Insecta: Coleoptera) associated with the prairie flora of central North America. The Great Lakes Entomologist, **35**: 15–22.

McGinnis, A.J. 1950. Sex ratio studies on the wheat stem sawfly, *Cephus cinctus* Nort. M.Sc. thesis, Montana State College, Bozeman, Montana.

McKenzie, H. 1965. Inheritance of sawfly reaction and stem solidness in spring wheat crosses: stem solidness. Canadian Journal of Plant Science, **45**: 591–600. doi:10.4141/cjps65-111.

McNeal, F.H., Berg, M.A., and Luginbill, P., Jr. 1955. Wheat stem sawfly damage in four spring wheat varieties as influenced by date of seeding. Agronomy Journal, **47**: 522–525. doi:10.2134/agronj1955.00021962004700110008x.

Meers, S.B. 2005. Impact of harvest operations on parasitism of the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae). M.Sc. thesis, Montana State University, Bozeman, Montana.

Miller, P.R., Waddington, J., McDonald, C.L., and Derksen, D.A. 2002. Cropping sequence affects wheat productivity on the semiarid northern Great Plains. Canadian Journal of Plant Science, **82**: 307–318.

Miller, R.H., El Masri, S., and Al Jundi, K. 1993. Plant density and wheat stem sawfly (Hymenoptera: Cephidae) resistance in Syrian wheats. Bulletin of Entomological Research, **83**: 95–102. doi:10.1017/S0007485300041821.

Molberg, E.S. 1963. Yield and quality of Selkirk wheat swathed at different stages of maturity. Canadian Journal of Plant Science, **43**: 338–343. doi:10.4141/cjps63-063.

Morrill, W.L. 1983. Early history of cereal grain insect pests in Montana. Bulletin of the Entomological Society of America, **29**: 24–28.

Morrill, W.L., and Kushnak, G.D. 1996. Wheat stem sawfly (Hymenoptera: Cephidae) adaptation to winter wheat. Environmental Entomology, **25**: 1128–1132.

Morrill, W.L., and Kushnak, G.D. 1999. Planting date influence on the wheat stem sawfly (Hymenoptera: Cephidae) in spring wheat. Journal of Agricultural and Urban Entomology, **16**: 123–128.

Morrill, W.L., Gabor, J.W., Hockett, E.A., and Kushnak, G.D. 1992. Wheat stem sawfly (Hymenoptera: Cephidae) resistance in winter wheat. Journal of Economic Entomology, **85**: 2008–2011.

Morrill, W.L., Gabor, J.W., Weaver, D.K., Kushnak, G.D., and Irish, N.J. 2000. Effect of host plant quality on the sex ratio and fitness of female wheat stem sawflies (Hymenoptera: Cephidae). Environmental Entomology, **29**: 195–199. doi:10.1603/0046-225X(2000)029[0195:EOHPQO]2.0.CO;2.

Morrill, W.L., Gabor, J.W., and Wichman, D. 1993. Mortality of the wheat stem sawfly (Hymenoptera: Cephidae) at low temperatures. Environmental Entomology, **22**: 1358–1361.

Morrill, W.L., Kushnak, G.D., and Gabor, J.W. 1998. Parasitism of the wheat stem sawfly (Hymenoptera: Cephidae) in Montana. Biological Control, **12**: 159–163. doi:10.1006/bcon.1998.0629.

Morrill, W.L., Weaver, D.K., Irish, N.J., and Barr, W.F. 2001*a*. *Phyllobaenus dubius* (Wolcott) (Coleoptera: Cleridae), a new record of a predator of the wheat stem sawfly (Hymenoptera: Cephidae). Journal of the Kansas Entomological Society, **74**: 181–183.

Morrill, W.L., Weaver, D.K., and Johnson, G.D. 2001*b*. Trap strip and field border modification for management of the wheat stem sawfly (Hymenoptera: Cephidae). Journal of Entomological Science, **36**: 34–45.

Nansen, C., Macedo, T.B., Weaver, D.K., and Peterson, R.K.D. 2005*a*. Spatiotemporal distributions of wheat stem sawfly eggs and larvae in dryland wheat fields. The Canadian Entomologist, **137**: 428–440. doi:10.4039/N04-094.

Nansen, C., Payton, M.E., Runyon, J.B., Weaver, D.K., Morrill, W.L., and Sing, S.E. 2005*b*. Preharvest sampling plan for larvae of the wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), in winter wheat fields. The Canadian Entomologist, **137**: 602–614. doi:10.4039/N04-087.

Nansen, C., Weaver, D.K., Sing, S.E., Runyon, J.B., Morrill, W.L., Grieshop, M.J., *et al.* 2005*c*. Within-field spatial distribution of *Cephus cinctus* (Hymenoptera: Cephidae) larvae in Montana wheat fields. The Canadian Entomologist, **137**: 202–214. doi:10.4039/N04-036.

Nelson, W.A., and Farstad, C.W. 1953. Biology of *Bracon cephi* (Gahan) (Hymenoptera: Braconidae), an important native parasite of the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae), in Western Canada. The Canadian Entomologist, **85**: 103–107. doi:10.4039/Ent85103-3.

Norton, E. 1872. Notes on North American Tenthredinidae with descriptions of new species. Transactions of the American Entomological Society, **4**: 77–86.

O'Keeffe, L.E., Callenbach, J.A., and Lebsock, K.L. 1960. Effect of culm solidness on the survival of the wheat stem sawfly. Journal of Economic Entomology, **53**: 244–246.

Ozberk, I., Atl, A., Yucel, A., Ozberk, F., and Coskun, Y. 2005. Wheat stem sawfly (*Cephus pygmaeus* L.) damage; impacts on grain yield, quality and marketing prices in Anatolia. Crop Protection, **24**: 1054–1060. doi:10.1016/j.cropro.2005.03.006.

Perez-Mendoza, J., and Weaver, D.K. 2006. Temperature and relative humidity effects on postdiapause larval development and adult emergence in three populations of wheat stem sawfly (Hymenoptera: Cephidae). Environmental Entomology, **35**: 1222–1231. doi:10.1603/0046-225X(2006)35[1222:TARHEO]2.0.CO;2.

Perez-Mendoza, J., Weaver, D.K., and Morrill, W.L. 2006. Infestation of wheat and downy brome grass by wheat stem sawfly and subsequent larval performance. Environmental Entomology, **35**: 1279–1285. doi:10.1603/0046-225X(2006)35[1279:IOWADB]2.0.CO;2.

Piesik, D., Weaver, D., Runyon, J.B., Buteler, M., Peck, G.E., and Morill, W. 2008. Behavioral responses of wheat stem sawflies to wheat volatiles. Agricultural and Forest Entomology, **10**: 245–253. doi:10.1111/j.1461-9563.2008.00380.x.

Piesik, D., Wenda-Piesik, A., Weaver, D.K., Macedo, T.B., and Morrill, W.L. 2009. Influence of *Fusarium* infection and wheat stem sawfly infestation on volatile metabolites collected from wheat plants. Journal of Plant Protection Research, **49**: 167–174. doi:10.2478/v10045-009-0024-2.

Platt, A.W., and Farstad, C.W. 1946. The reaction of wheat varieties to wheat stem sawfly attack. Scientific Agriculture, **26**: 231–247.

Platt, A., and Farstad, C.W. 1949. Breeding spring wheats for resistance to wheat stem sawfly attack. *In* Proceedings of the 7th Pacific Science Congress, **4**: 215–220.

Platt, A.W., and Larson, R.I. 1944. An attempt to transfer solid-stem from *Triticum durum* to *T. vulgare* by hybridization. Scientific Agriculture, **24**: 214–220.

Platt, A.W., Farstad, C.W., and Callenbach, J.A. 1948. The reaction of Rescue wheat to sawfly damage. Scientific Agriculture, **28**: 154–161.

Runyon, J.B., Hurley, R.L., Morrill, W.L., and Weaver, D.K. 2001. Distinguishing adults of *Bracon cephi* and *Bracon lissogaster* (Hymenoptera: Braconidae), parasitoids of the wheat stem sawfly (Hymenoptera: Cephidae). The Canadian Entomologist, **133**: 215–217. doi:10.4039/Ent133215-2.

Runyon, J.B., Morrill, W.L., Weaver, D.K., and Miller, P.R. 2002. Parasitism of the wheat stem sawfly (Hymenoptera: Cephidae) by *Bracon cephi* and *B. lissogaster* (Hymenoptera: Braconidae) in wheat fields bordering tilled and untilled fallow in Montana. Journal of Economic Entomology, **95**: 1130–1134. PMID:12539822 doi:10.1603/0022-0493-95.6.1130.

Saint Pierre, C., Trethowan, R., and Reynolds, M. 2010. Stem solidness and its relationship to water-soluble carbohydrates: association with wheat yield under water deficit. Functional Plant Biology, **37**: 166–174. doi:10.1071/fp09174.

Salt, R.W. 1947. Some effects of temperature on the production of and elimination of diapause in the wheat stem sawfly, *Cephus cinctus* Nort. Canadian Journal of Research, **25**: 66–86.

Seamans, H.L. 1928. The value of trap crops in the control of the wheat stem sawfly in Alberta. Entomological Society of Ontario Annual Report, 1928. pp. 59–64.

Seamans, H.L. 1945. A preliminary report on the climatology of the wheat stem sawfly (*Cephus cinctus* Nort.) on the Canadian prairies. Scientific Agriculture, **25**: 432–457.

Seamans, H.L., Manson, G.F., and Farstad, C.W. 1944. The effect of wheat stem sawfly (*Cephus cinctus*) on the heads and grain of infested stems. Seventy-fifth Annual Report of the Entomolological Society of Ontario, **75**: 10–15.

Shanower, T.G., and Hoelmer, K.A. 2004. Biological control of wheat stem sawflies: past and future. Journal of Agricultural and Urban Entomology, **21**: 197–221.

Sherman, J.D., Weaver, D.K., Hofland, M.L., Sing, S.E., Buteler, M., Lanning, S.P., *et al.* 2010. Identification of novel QTL for sawfly resistance in wheat. Crop Science, **50**: 73–86. doi:10.2135/cropsci2009.03.0145.

Smith, C.W. 1931. Colonization in Canada of *Collyria calcitrator* (Hymenoptera: Ichneumonidae), a parasite of the wheat stem sawfly. Bulletin of Entomological Research, **22**: 547–550. doi:10.1017/S0007485300035367.

Somsen, H.W., and Luginbill, P. 1956. Bracon lissogaster Mues., a parasite of the wheat stem sawfly. USDA Technical Bulletin No. 1153. pp. 1–7.

Wahl, D.B., Shanower, T.G., and Hoelmer, K.A. 2007. A new species of *Collyria* Schiødte (Hymenoptera: Ichneumonidae: Collyriinae), a parasitoid of *Cephus fumipennis* (Hymenoptera: Cephidae) in China, and potential biological control agent for *Cephus cinctus* in North America. Journal of the Kansas Entomological Society, **80**: 43–50. doi:10.2317/0022-8567(2007)80[43:ANSOCS]2.0.CO;2.

Wall, A. 1952. The diameter of the wheat stem in relation to the length and sex of emerging sawfly (*Cephus cinctus* Nort.). Scientific Agriculture, **32**: 272–277.

Wallace, L.E. 1962. Field-plot tests of chemicals for wheat stem sawfly control. Journal of Economic Entomology, **55**: 908–912.

Wallace, L.E., and Butler, L.I. 1967. Residues of heptachlor and heptachlor epoxide in wheat treated to control the wheat stem sawfly. Journal of Economic Entomology, **60**: 254–256.

Wallace, L.E., and McNeal, F.H. 1966. Stem sawflies of economic importance in grain crops in the United States. Agricultural Research Service, United States Department of Agriculture, Washington, D.C.

Weaver, D.K., Buteler, M., Hofland, M.L., Runyon, J.B., Nansen, C., Talbert, L.E., Lamb, P., and Carlson, G.R. 2009. Cultivar preferences of ovipositing wheat stem sawflies as influenced by the amount of volatile attractant. Journal of Economic Entomology, **102**: 1009–1017. PMID:19610414 doi:10.1603/029.102.0320.

Weaver, D.K., Sing, S.E., Runyon, J.B., and Morrill, W.L. 2004. Potential impact of cultural practices on wheat stem sawfly (Hymenoptera: Cephidae) and associated parasitoids. Journal of Agricultural and Urban Entomology, **21**: 271–287.

Weaver, D.K., Nansen, C., Runyon, J.B., Sing, S.E., and Morrill, W.L. 2005. Spatial distributions of *Cephus cinctus* Norton (Hymenoptera: Cephidae) and its braconid parasitoids in Montana wheat fields. Biological Control, **34**: 1–11. doi:10.1016/j.biocontrol.2005.04.001.

Weiss, M.J., Morrill, W.L., and Reitz, L.L. 1987. Influence of planting date and spring tillage on the wheat stem sawfly. Montana AgResearch Montana Agricultural Experiment Station Montana University, **4**: 2–5.

Weiss, M.J., Riveland, N.R., Reitz, L.L., and Olson, T.C. 1990. Influence of resistant and susceptible cultivar blends of hard red spring wheat on wheat stem sawfly (Hymenoptera: Cephidae) damage and wheat quality parameters. Journal of Economic Entomology, **83**: 255–259.

Wenda-Piesik, A., Morrill, W.L., Grey, W.E., and Weaver, D.K. 2006. Entomopathogenic capacity of fusarium crown rot on wheat stem sawfly larvae. Progress in Plant Protection, **46**: 380–387.

Wenda-Piesik, A., Sun, Z.T., Grey, W.E., Weaver, D.K., and Morrill, W.L. 2009. Mycoses of wheat stem sawfly (Hymenoptera: Cephidae) larvae by *Fusarium* spp. isolates. Environmental Entomology, **38**: 387–394. PMID:19389287 doi:10.1603/022.038.0211.