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The causes of wheat stem sawfly (Hymenoptera: Cephidae) larval mortality in the Canadian prairies

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Abstract

Cephus cinctus Norton (Hymenoptera: Cephidae), the wheat stem sawfly, is a well-established and important pest of wheat, *Triticum aestivum* Linnaeus (Poaceae), and its relatives in North America. Crop losses are caused directly by *C. cinctus* feeding inside wheat stems during larval development and indirectly when weakened plants lodge before being harvested. Understanding the factors that affect population dynamics of *C. cinctus* can help farmers to better manage it. Our study therefore explored how *C. cinctus* and natural enemy densities vary in space (southern Alberta, Canada) and over time. Five fields were sampled using an established protocol in fall 2019 and resampled in spring 2020; six additional fields were sampled in fall 2020 and resampled in spring 2021. Wheat stubs were dissected to record numbers of cut stems, *C. cinctus* larvae, and sources of larval mortality (*i.e.*, parasitism, fungal infection). Densities of wheat stem sawfly and the impact of natural enemies varied between the sampled fields. No *C. cinctus* mortality was observed during the winter, indicating that *C. cinctus* population dynamics are not susceptible to mortality (abiotic or biotic) between years. Results of our study will be incorporated into new models to predict wheat stem sawfly phenology and risk to crop production.

Introduction

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), is native to North America and was first described in Colorado, United States of America in 1872 (Norton 1872). Since the 1920s, severe *C. cinctus* infestations have occurred in many cultivated cereal (Poaceae) crops, including common wheat (*Triticum aestivum* Linnaeus), durum wheat (*T. durum* Desfontaines), barley (*Hordeum vulgare* Linnaeus), and triticale (× *Triticosecale* Wittmer ex A. Camus; Wallace and McNeal 1966; Cockrell *et al.* 2017; Varella *et al.* 2018; Cárcamo *et al.* 2023). *Cephus cinctus* populations impact cereal crop producers in the northwestern provinces (Alberta, Saskatchewan, and Manitoba, Canada) and states (Montana, North Dakota, South Dakota, Nebraska, Colorado, and Wyoming, United States of America) of the North American Great Plains region (Criddle 1923; Holmes 1982; Morrill *et al.* 1993; McCullough *et al.* 2020; Cockrell *et al.* 2021). Adult wheat stem sawflies emerge from wheat stubble in late spring, and females oviposit individual eggs into their host plants from June to July (Holmes 1977). Larvae develop within the plant stem and feed on parenchymal tissue and vascular bundles throughout the summer (Holmes 1977). Larval feeding decreases kernel head weight, protein content, and photosynthetic capacity of the host plant (Macedo *et al.* 2005, 2007).

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From August to mid-September, as plant moisture begins to decrease, mature larvae travel to the base of the stem and cut the stem to create their overwintering hibernaculum (Holmes 1979). The cereal stems that host *C. cinctus* larvae are susceptible to lodging as the result of winds or other incidental contact, making it difficult for producers to harvest their crops. Using modern commodity prices, economic losses in years with high *C. cinctus* population densities (*i.e.,* when 50% or more of wheat stems in a field have been cut) can be upwards of $CAD 400M annually (Beres *et al.* 2007, 2017).

Sowing of resistant solid-stem cultivars and implementing methods that enhance local established populations of natural enemies are the primary tactics used to manage *C. cinctus*. Solid-stem plants develop greater amounts of pith within the stem that increases juvenile wheat stem sawfly mortality (Holmes and Peterson 1961, 1962) and reduces adult fitness (Morrill *et al.* 2000; Cárcamo *et al.* 2005). Several wheat and durum solid-stem cultivars like "AC Lillian" (DePauw *et al.* 2005), "AAC Stronghold" (Ruan *et al.* 2019), and "CDC Fortitude" (Pozniak *et al.* 2015) are registered for use in Canada to mitigate wheat stem sawfly damage but are not widely selected as preferred cultivars by producers for seeding (Agriculture Financial Services Corporation 2021).

Two idiobiont ectoparasitoids, *Bracon cephi* Gahan and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae), are the most common natural enemies of *C. cinctus* in North America (Nelson and Farstad 1953; Somsen and Luginbill 1956). *Bracon cephi* is the predominant parasitoid species in Canada; however, *B. lissogaster* has been reported in small numbers southeast of Lethbridge, Alberta (Cárcamo *et al.* 2012). First-generation adult *B. cephi* parasitoids attack wheat stem sawfly larvae in early summer (*e.g.,* in July in the southern Canadian prairies), before they cut the host plant stem (Nelson and Farstad 1953). The success of the second generation of parasitoids depends on abiotic factors (*i.e.,* cold, wet conditions) that prolong the growing season and delay host plant senescence (Holmes *et al.* 1963). Parasitism rates vary substantially by geographic region, with some areas having over 90% of *C. cinctus* attacked (Morrill *et al.* 1998). Within the stem, *C. cinctus* larvae are susceptible to infection and subsequent death by a complex of *Fusarium* (Nectriaceae), including *F. acuminatum* Ellis and Everh *sensu* Gordon, *F. avenaceum* (Fr.) Sacc., *F. culmorum* (W.G. Smith) Sacc., *F. equiseti* (Corda) Sacc. *sensu* Gordon, and *F. graminearum* (Schwabe) (Sun 2008; Wenda-Piesik *et al.* 2009). Wheat stem sawfly larvae are also susceptible to predation by the clerid beetle *Phyllobaenus dubius* Wolcott (Coleoptera: Cleridae) (Morrill *et al.* 2001; Meers 2005). Despite extensive research over the last 100 years on *C. cinctus* and its natural enemies, it is not always clear how these larval mortality factors are influenced across time and space or how abiotic factors affect larval mortality. Regional data on biotic and abiotic factors need to be augmented.

Insect populations are dynamic and constantly fluctuate over time and geographic area in response to biotic and abiotic factors. Availability of suitable hosts (Sétamou *et al.* 2000; Opedal *et al.* 2020), abiotic conditions (*e.g.,* temperature, precipitation; Kingsolver 1989; Crozier 2004; Khokhar *et al.* 2019), natural enemy populations (Alyokhin *et al.* 2011; Bouchard *et al.* 2018), and anthropogenic activities (*e.g.,* habitat destruction and chemical pesticide use; Ciesla 2015; Wagner *et al.* 2021) can heavily influence population densities. To better understand the population ecology of an insect, researchers and integrated pest management practitioners use species-specific biological parameters and climatic factors to create complex population models (Nietschke *et al.* 2007). For example, mechanistic or process-based population models (*i.e.,* phenology models) and distribution models have been developed for a number of insect pests of Canadian agriculture, including *Melanoplus sanguinipes* Fabricius (Orthoptera: Acrididae) (Olfert and Weiss 2006; Olfert *et al.* 2021), *Plutella xylostella* Linnaeus (Lepidoptera: Plutellidae) (Li *et al.* 2016), *Aphis glycines* Matsumura (Hemiptera: Aphididae) (Bahlai *et al.* 2013), and *Sitodiplosis mosellana* Géhin (Diptera: Cecidomyiidae) (Olfert *et al.* 2020). These models are excellent integrated pest management tools for researchers. In addition, output from these models provides important information to producers and helps them to make appropriate agronomic and pest management decisions to protect their crop yields. To date, a phenology model with predictive capacity within and between growing seasons has not been developed for *C. cinctus*.

The present study aimed to explore how *C. cinctus* larval mortality and the associated causes of mortality change between crop growing seasons and across a regional scale because these two pieces of information will be required for the development of a forthcoming phenology model for *C. cinctus*. Previously developed multiple decrement life tables (Peterson *et al.* 2011; Buteler *et al.* 2015; Achhami *et al.* 2020) and population matrix models (Rand *et al.* 2017, 2020) have demonstrated the influence of parasitism and fungal infection on larval morality during the summer and that the impact of parasitism and fungal infection drops during the overwintering period. However, Rand *et al.* (2017) and Olfert *et al.* (2019) have pointed out that additional information is required to better understand the potential effect of these mortality factors on *C. cinctus* during the early spring growing period when postdiapause larvae are completing their development. The present study's sampling strategy was designed to address the impact of parasitism and fungal infection during the understudied portions of the *C. cinctus* life cycle. Within *C. cinctus*–infested regions, past studies have shown that populations vary spatiotemporally (Sing 2002; Nansen *et al.* 2005b) and that *C. cinctus* mortality is not uniform from field to field (Holmes *et al.* 1957; Perez-Mendoza and Weaver 2006); however, these studies did not specifically question if larval mortality factors were also variable across spatial scales. The recent increase in *C. cinctus* population densities in areas of southern Alberta (Prairie Pest Monitoring Network 2023) provided an excellent opportunity to examine the impacts of parasitism and fungal infection on *C. cinctus* population dynamics across a large portion of the prairie agroecosystem.

Methods

Experimental locations and sampling protocol

Commercial wheat fields in southern Alberta, Canada with reported wheat stem sawfly damage were sampled. Fields were initially sampled as part of the annual wheat stem sawfly survey conducted by Alberta Agriculture, Forestry, and Rural Economic Development (now Alberta Agriculture and Irrigation) in late summer–early fall of 2019 and 2020. Permission to resample the fields for the present study was granted by the farmers. All fields were seeded with a hollow stem wheat variety in both years of the study. In fall 2019, six harvested wheat fields in Alberta with known *C. cinctus* infestations were visited and sampled for stems cut by wheat stem sawfly (Table 1). The sampling procedure followed the survey protocol provided by the Prairie Pest Monitoring Network (https://prairiepest.ca/monitoring-protocols/) but was modified to focus on field edges where wheat stem sawfly larval densities are typically highest (Nansen *et al.* 2005a). Using this protocol, the total number of wheat stems, including the number of wheat stubs (cut by wheat stem sawfly larvae) and long stems (cut mechanically during harvest), was counted along 1-m transects at four locations in each field, with each location separated from the others by 50 m. The protocol ensured that more than 200 wheat stems were collected from each of the fields surveyed, giving confidence in our estimations of overall field population densities (Cárcamo *et al.* 2007).

All wheat stub samples were transported to Agriculture and Agri-Food Canada's Saskatoon Research and Development Centre (Saskatoon, Saskatchewan), where we determined the number of *C. cinctus*–cut stems and presence of *C. cinctus* larvae in the cut stems, and we dissected the stems to assess the condition of the wheat stem sawfly larvae inside the stubs. Wheat stem sawfly larval presence was tallied when *C. cinctus* larvae (regardless of condition) or parasitoid pupae were recovered from a dissected stem. The number of live *C. cinctus* larvae, dead *C. cinctus* larvae, and probable causes of mortality (*e.g.*, parasitism, fungal pathogen, and unknown) were recorded. Unknown mortality may have been due to malnutrition, diseases not detectable using our methods, abiotic conditions including heat or cold stress (over the winter), or other factors. The average percentage of wheat stems cut was calculated for each field. In April 2020, the sites

Table 1. Field locations in southern Alberta, Canada and sampling dates for the survey of *Cephus cinctus*; due to logistical constraints, fields sampled in fall 2019 could be sampled only once in spring 2020.

Fall 2019–spring 2020				
Field site	Location (latitude, longitude)	Fall sample date	Spring 1 sample date	Spring 2 sample date
Special Area #3	51.29, –110.14	22 Oct	27 Apr	–
Acadia	51.06, –110.20	22 Oct	27 Apr	–
Vulcan	50.20, –113.24	23 Oct	–	–
Willow Creek	49.94, –113.31	23 Oct	27 Apr	–
Warner	49.24, –111.65	23 Oct	28 Apr	–
Forty Mile	49.29, –111.60	23 Oct	28 Apr	–
Fall 2020–spring 2021				
Field site	Location (latitude, longitude)	Fall sample date	Spring 1 sample date	Spring 2 sample date
Willow Creek	49.93, –113.30	21 Sep	19 Apr	17 May
Lethbridge	50.01, –113.19	21 Sep	19 Apr	17 May
Vulcan	50.57, –112.98	21 Sep	19 Apr	17 May
Warner	49.26, –111.69	08 Sep	20 Apr	18 May
Forty Mile	49.30, –111.60	08 Sep	20 Apr	18 May
Special Area #3	51.21, –110.74	28 Sep	19 Apr	17 May

(excluding the Vulcan site, where sawfly larval populations were very low in fall 2019) were resampled, using the process described above.

In fall 2020, six new fields were selected for the wheat stem sawfly mortality survey (Table 1). Samples were collected between 8 and 21 September from each site to determine the infestation pressure and larval state before winter. In spring 2021, the fields were resampled twice, first in April and then in May. Sampling and stem dissections were conducted using the same protocol as that described for fall 2019. Voucher specimens from the field collections are stored in the Ecological Entomology Lab at the Agriculture and Agri-Food Canada, Saskatoon Research and Development Centre.

Statistical analysis

Data analyses were performed with R, using RStudio, version 3.6.1 (R Core Team 2019). All data were tested and successfully met the analysis of variance testing assumptions of normal distribution and homogeneity of variance as confirmed by nonsignificant ($P > 0.05$) Kolmogorov–Smirnov and Levene tests, respectively (model residual testing completed using the R package "DHARMa", version 0.4.6). Generalised linear mixed-effects models with binomial discrete probability distributions were used to test for the effect on field site on the presence *versus* absence of live *C. cinctus* larvae using the R package "lme4", version 1.1-27.1, with separate analyses for each sampling year where $\alpha = 0.05$. For these models, field site was treated as the fixed factor, and sampling period nested within site was the random factor. Differences between field sites were determined using a Type II analysis of variance with Wald Chi-square test statistics. Within each sampling year, individual fields were further analysed using generalised linear models with binomial discrete probability distributions to determine the effect of sampling period

Table 2. Total number of stems dissected, percentage of *Cephus cinctus*–cut stems, and percentage of cut stems with *C. cinctus* larvae present (± standard error) when fields were sampled in September 2019 and again in April 2020.

Fall 2019			
Site	# Stems dissected	Stems cut % (± standard error)	Larvae present % (± standard error)
Special Area #3	278	31.2 ± 2.8	29.6 ± 2.7
Acadia	401	5.4 ± 1.2	4.7 ± 1.1
Vulcan	657	0 ± 0	0 ± 0
Willow Creek	279	19.5 ± 4.4	23.2 ± 5.0
Warner	374	68.6 ± 4.8	50.6 ± 5.1
Forty Mile	375	67.0 ± 4.3	66.2 ± 4.5
Spring 2020			
Site	# Stems dissected	Stems cut % (± standard error)	Larvae present % (± standard error)
Special Area #3	320	22.5 ± 4.7	23.2 ± 4.7
Acadia	447	9.0 ± 1.9	3.3 ± 1.3
Vulcan	n/a	n/a	n/a
Willow Creek	220	14.8 ± 0.3	23.9 ± 0.4
Warner	403	53.6 ± 5.0	48.3 ± 5.1
Forty Mile	483	41.0 ± 3.8	50.9 ± 4.4

(*e.g.*, fall 2019 *versus* spring 2020) on the presence *versus* absence of live *C. cinctus* larvae, α = 0.05 for the comparison of sampling period for each site.

Results

From September 2019 to April 2020, 4237 stems were collected and dissected from six wheat fields (Table 2). The Vulcan site was the only field that did not have any measurable *C. cinctus* damage or larvae in September 2019, so it was not resampled in April 2020. The remaining five fields had stem cutting, with the percentage of stems that were cut and that contained *C. cinctus* larvae ranging from 5.4 to 68.6% and from 3.3 to 66.2%, respectively, in September 2019 (Table 2). Field was a significant factor that influenced the percentage of live *C. cinctus* larvae recovered, regardless of when the fields were surveyed ($x^2_5 = 65.678$, $P < 0.0001$). Within each field, mortality did not change significantly from September 2019 to April 2020 (Table 3). Larval mortality factors were not uniform across the five fields (Fig. 1B–D). If parasitoids were present, then parasitoid-associated mortality contributed most to *C. cinctus* larval mortality (Fig. 1C). Mortality in April 2020 resulting from pathogen infection and unknown causes ranged from 1.1 to 14.2% and from 1.6 to 5.2%, respectively (Fig. 1B and D).

A total of 7342 stems were collected from six new wheat fields sampled in September 2020 and resampled in April 2021 and May 2021 (Table 4). All fields in each sampling period had measurable *C. cinctus* damage or *C. cinctus* larvae, but numbers ranged widely, based on where the samples were taken. Stem cutting was lowest at the Willow Creek site and highest at the Forty Mile site during all sampling periods (Table 4). At Forty Mile, the proportion of cut stems with larvae was highest, whereas the Lethbridge field site had the lowest proportion of stems with

Table 3. Analysis of variance results for the effect of sampling time on larval *Cephus cinctus* mortality observed at five wheat fields surveyed between September 2019 and April 2020 and at six wheat fields surveyed in September 2020, April 2021, and May 2021. Statistically significant results (α < 0.05) are denoted with an asterisk (*).

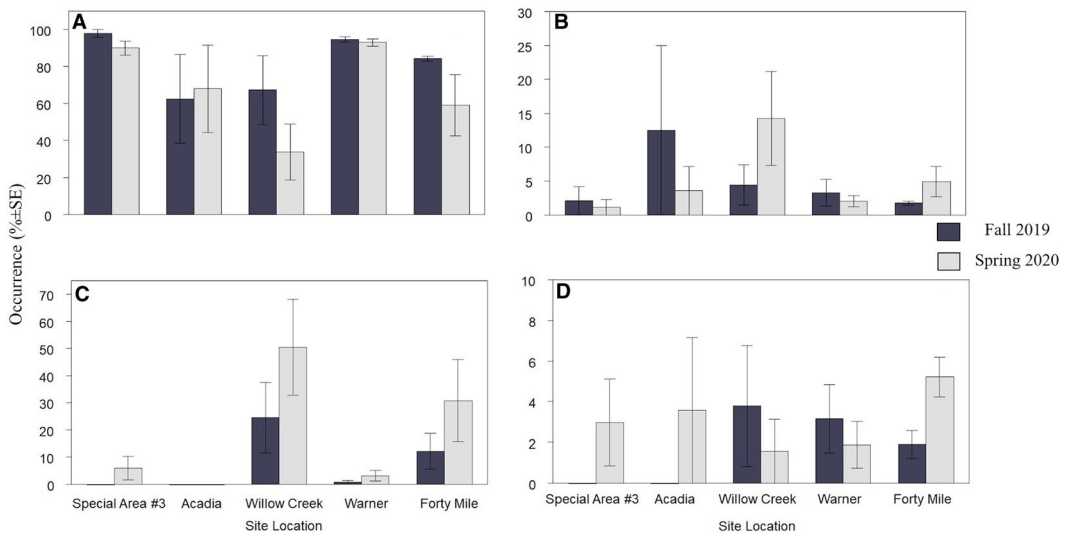| Fall 2019–spring 2020		
Site	$F_{(df)}$	*P*-value
Special Area #3	$3.7332_{(1,6)}$	0.1015
Acadia	$0.0030_{(1,4)}$	0.9590
Willow Creek	$1.8356_{(1,6)}$	0.2243
Warner	$0.2907_{(1,6)}$	0.6092
Forty Mile	$2.1272_{(1,6)}$	0.1950
Fall 2020–spring 2021		
Site	$F_{(df)}$	*P*-value
Willow Creek	$0.6727_{(2,8)}$	0.5370
Lethbridge	$0.3197_{(2,9)}$	0.7343
Vulcan	$0.8103_{(2,7)}$	0.4825
Warner	$0.2163_{(2,9)}$	0.8096
Forty Mile	$0.5288_{(2,9)}$	0.6066
Special Area #3	$4.5533_{(2,9)}$	0.04303*

Figure 1. Observations (% ± standard error) of **A**, live *Cephus cinctus* larvae; **B**, fungal-associated larval mortality; **C**, parasitism-associated larval mortality; and **D**, unknown larval mortality from fall 2019 and spring 2020 larval mortality surveys.

larvae (Table 4). Larval mortality varied based on field ($x^2_5 = 177.25$, $P < 0.0001$) but was not affected by sampling period at any field except the field site in Special Area #3 (a rural municipality in southeastern Alberta; Table 3). At this field, mortality was lower in fall 2020 compared to the

Table 4. Total number of stems dissected, percentage of *Cephus cinctus*–cut stems, and percentage of cut stems with *C. cinctus* larvae present (± standard error) when fields were sampled in September 2020 and again in April and May 2021.

Site	# Stems dissected	Stems cut % (± standard error)	Larvae present % (± standard error)
Fall 2020			
Willow Creek	599	1.3 ± 0.7	52.4 ± 4.0
Lethbridge	525	13.7 ± 2.9	22.7 ± 3.6
Vulcan	489	34.3 ± 4.4	49.4 ± 4.5
Warner	398	45.5 ± 5.0	48.3 ± 5.2
Forty Mile	399	72.2 ± 4.3	71.1 ± 4.4
Special Area #3	493	33.7 ± 4.2	58.0 ± 4.7
Spring: April 2021			
Willow Creek	530	1.8 ± 0.7	9.5 ± 2.1
Lethbridge	488	2.7 ± 1.5	4.2 ± 1.8
Vulcan	634	3.3 ± 1.0	3.7 ± 1.3
Warner	365	79.5 ± 4.3	71.1 ± 4.9
Forty Mile	513	82.3 ± 3.3	80.1 ± 3.4
Special Area #3	320	43.6 ± 5.6	39.1 ± 5.5
Spring: May 2021			
Willow Creek	361	2.0 ± 1.2	17.1 ± 2.7
Lethbridge	505	3.0 ± 1.3	4.0 ± 1.7
Vulcan	322	4.4 ± 1.5	5.3 ± 1.9
Warner	343	73.3 ± 4.7	53.4 ± 5.3
Forty Mile	356	76.1 ± 4.1	68.0 ± 5.0
Special Area #3	302	45.1 ± 5.5	45.4 ± 5.5

two sampling periods in spring 2021 (Fig. 2A). Fungus-associated and unknown mortality were irregular in the second year of the study, ranging from 0 to 27.6% and from 0 to 9.0%, respectively (Fig. 2B and D). Notably, the rate of fungal infection at the Willow Creek field site was nearly double that of the other fields during the May 2021 sampling period (Fig. 2B and D).

Discussion

Sequential sampling of harvested wheat fields in the fall and following spring yielded two key observations. First, in the majority of the wheat fields, *C. cinctus* mortality was not affected by time, and the proportion of the larval population alive in the preoverwintering larval phase was approximately equal to that observed during the spring postoverwintering phase of larval development. In addition, mortality due to unknown factors, which could have included abiotic stress, was minimal in all sampling periods in both years of the study (*i.e.*, < 10%), which provides
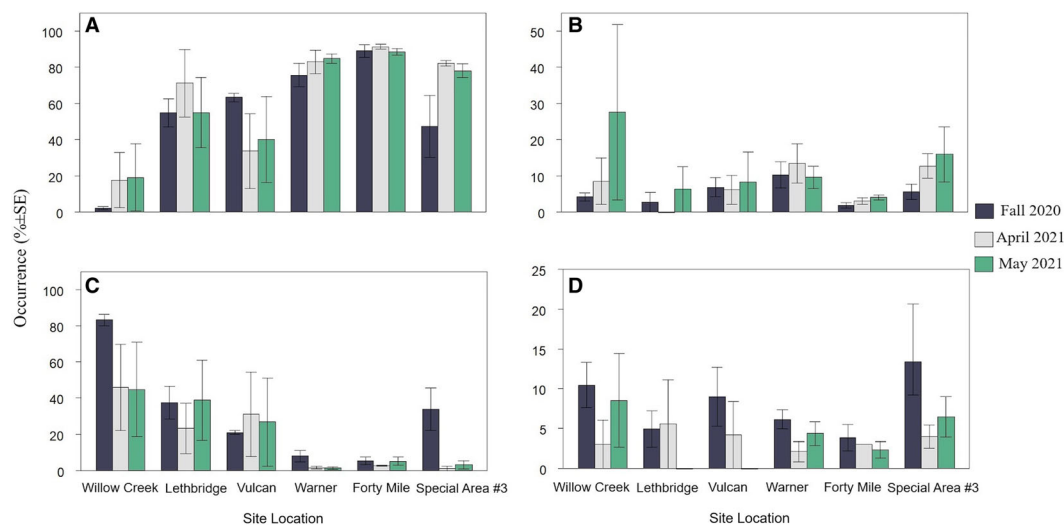
Figure 2. Observations (% ± standard error) of **A**, live *Cephus cinctus* larvae; **B**, fungal-associated larval mortality; **C**, parasitism-associated larval mortality; and **D**, unknown mortality from the fall 2020 and spring 2021 larval mortality surveys.

indirect evidence that it is unlikely that winter weather, even extreme conditions, impacts *C. cinctus* populations. These results agree with past studies, which also concluded that overwintering abiotic conditions do not affect *C. cinctus* mortality (Morrill *et al.* 1993; Cárcamo *et al.* 2011). Second, the present study highlighted the field-level variability of *C. cinctus* larval mortality in wheat fields in southern Alberta. Both of these key observations have implications for management of *C. cinctus.* Specifically, scouting and surveying as many individual fields as possible is needed in the fall of one year to provide the highest level of resolution for accurate predictions of potential *C. cinctus* densities in the upcoming growing season. Sampling many fields is needed because of the variability between field locations that we observed in this study. However, because there was very little unexplained mortality between the fall and spring sampling periods, sampling once in the fall and accounting for parasitism of *C. cinctus* can provide a putative forecast of *C. cinctus* risk between years. Insect population forecasting, coupled with in-season scouting, helps to ensure that appropriate actions (*e.g.,* planting solid-stem wheat or planting an alternative crop) can be taken to avoid yield losses.

In addition, both of our key observations provide important information that will contribute to the future development of phenology models and forecasting systems for *C. cinctus* in Canadian agroecosystems. For example, phenology models are initiated in the spring with an estimate of larval density (see Olfert *et al.* 2020). In the case of *C. cinctus*, the density of viable larvae observed in the fall can be used as an estimate of the viable larval density in the spring with confidence. This is because we observed that abiotic conditions have minimal, if any, impact on overwintering survival and that the proportion of viable larvae in the fall is approximately equal to the number of viable larvae found in the spring. Phenology models can also incorporate the impact of natural enemies and other mortality factors (see Olfert *et al.* 2020); because mortality factors varied spatially, it could be difficult to accurately incorporate the effects of mortality due to natural enemies on *C. cinctus* into models for wide geographic areas.

The present study aimed to sample fields in southern Alberta with known *C. cinctus* populations, but logistical constraints prevented us from obtaining detailed information about field histories for all of the fields (*e.g.*, previous crop rotations, products applied, etc.). Therefore, that information could not be accounted for in our analyses. Despite this, our results allude to the

potential effect of field-scale differences in pest management, agronomic practices, and overall landscape ecology on *C. cinctus* larval mortality. Several past studies have highlighted the effect of field configuration on the survivorship and overall population densities of *C. cinctus*. For example, cultural methods that influence *C. cinctus* infestation rates and female oviposition behaviour, such as changing wheat row spacing and seeding rates (Luginbill and McNeal 1958; Beres *et al.* 2012), delaying seeding date (Morrill and Kushnak 1999; Sing 2002), and managing soil nitrogen and phosphorus levels (Luginbill and McNeal 1954; Delaney *et al.* 2010), decreased wheat stem sawfly densities within fields or in greenhouse experiments. Crop rotation can also affect *C. cinctus* population densities because adults are regarded as poor fliers (Ainslie 1929). Although these studies focused on understanding field-level *C. cinctus* population densities, cultural control tactics may also influence larval mortality and *C. cinctus* natural enemies. Currently, agronomic practices relating to *C. cinctus* larval enemies have primarily focused on parasitoid conservation. For example, overwintering *B. cephi* larvae can be preserved in a field by leaving the bottom one-third of wheat stems standing after harvest (Meers 2005). Parasitoid populations can also be protected from cannibalism by nonparasitised *C. cinctus* larvae when other suitable *C. cinctus* host plants (*i.e.,* wild oats, *Avena fatua* Linnaeus (Poaceae)) are present to act as population sinks (Weaver *et al.* 2004). Future studies could explore how other agronomic practices influence populations of both *C. cinctus* and their natural enemies to further improve integrated pest management strategies for Canadian wheat producers.

Larval mortality of *C. cinctus* did not change significantly between the sampling periods in either study year except for one field, located in Special Area #3, between fall 2020 and spring 2021. In this field, the proportion of larvae that were alive in the fall 2020 sampling period was much lower than in the two spring 2021 sampling periods. In the same samples, parasitism rates decreased from about 39% in fall 2020 to less than 5% in spring 2021. Although these differences were statistically significant, the difference is likely a sampling artefact, arising from the destructive nature of the sampling protocol that did not permit the same wheat stems sampled in fall to be examined again in the spring. By chance, the samples collected in the fall simply had more dead *C. cinctus* larvae and more parasitoid larvae than the samples collected in the spring did. Overall, the minimal difference in *C. cinctus* larval mortality over time at the majority of the study fields agrees with past research that found the overwintering larval mortality was low and had little influence on wheat stem sawfly population dynamics (Morrill *et al.* 1993; Cárcamo *et al.* 2011).

The lack of difference in *C. cinctus* larval mortality between fall and spring sampling periods was unlikely the result of cold stress or other abiotic factors associated with winter weather because mortality due to "other" or unknown factors did not change between fall and spring. *Cephus cinctus* larvae overwinter in hibernacula inside wheat stems near the soil surface, where they are protected from harsh winter weather; several authors have previously observed that mortality associated with the overwintering period is negligible (Morrill *et al.* 1993; Cárcamo *et al.* 2011). Our results agree with their observations.

Cephus cinctus larval mortality was also effectively static between fall and spring sampling periods because we observed no real change in mortality attributed to parasitism or fungal pathogens between sampling periods. From our samples, we observed two biotic sources of mortality: parasitism and disease related to fungal pathogens. There was no evidence of predation on *C. cinctus* larvae by clerid beetles in our study, although predation has been documented by others (Morrill *et al.* 2001; Meers 2005). To our knowledge, all of the fields sampled grew conventional hollow stem wheat, so we do not expect that any wheat stem sawfly larval mortality occurred in this study due to host plant resistance. Parasitism by both parasitoids, *Bracon cephi* and *B. lissogaster*, was grouped together for our analyses because differentiating between the parasitoids in their larval stage is not possible (Runyon *et al.* 2001). The majority of parasitism was likely caused by *B. cephi* because it is the predominant parasitoid species in Alberta (Cárcamo *et al.* 2012). Parasitoids overwinter as larvae within the lower internodes of wheat stubble and resume their development the following spring (Nelson and Farstad 1953). Therefore, although

parasitoids are an important larval mortality factor for the summer *C. cinctus* larval phase, they are not expected to influence mortality between growing seasons. The next most common mortality factor, fungal infection, was observed in every field but never at levels above 30%. This result matches the conclusions from Sun's (2008) postharvest survey, which was conducted in Montana winter wheat fields and reported that fungal infection could cause 10–30% mean overwintering larval mortality. Similar to parasitism, fungal infection levels are unlikely to have changed between growing seasons because dormant fungal pathogens overwinter within remaining wheat stubble and other crop residues and only become active again under warm and moist conditions (Sutton 1982). Although fungal pathogens may become active again in the early spring months under ideal environmental conditions, the fungus may still not infect the postdiapause *C. cinctus* larvae because the fungal hyphae still need to break through the larva's protective hibernaculum. In scenarios where fungal infection did seem to increase in the spring, such as was seen at the Willow Creek field in 2021, fungal infection did not contribute to additional *C. cinctus* larval mortality in that sampling period. Similar conclusions from a *C. cinctus* multiple decrement life table study from Montana, wherein the authors used barley cultivars, corroborate the findings of the current study (Achhami *et al.* 2020). Overall, *C. cinctus* larval survivorship from the fall into the early spring months did not significantly change, probably because the major mortality factors were inactive in the winter and early spring and because *C. cinctus* are well adapted to survive winter weather.

Conclusion

Here, we demonstrate that *C. cinctus* infestation levels vary between fields in southern Alberta, Canada, including in years where the overall population density is observed to increase. The causes of *C. cinctus* larval mortality also varied in terms of their impact between fields during our study. Although not tested explicitly here, the degree of variation we observed between fields could arise from differences in landscape dynamics and agronomic practices (*i.e.,* conservation of wheat stubble at harvest) that influence *C. cinctus* (and *B. cephi*) field population dynamics. Future research is needed to further elucidate the factors driving variation in *C. cinctus* population dynamics across western Canadian landscapes.

The present study also highlighted that *C. cinctus* population dynamics are not susceptible to measurably increased mortality due to abiotic conditions or biotic mortality factors between growing seasons as larvae undergo their overwintering phase and subsequent spring development. This information will contribute to the future development of phenology models and *C. cinctus* population forecasting tools. Recently constructed Leslie matrix population models have emphasised that winter larval mortality should have the greatest impact on the growth rate of wheat stem sawfly because individuals are in this life stage the longest (Rand *et al.* 2017, 2020). However, in the absence of consistent and wide-reaching mortality pressure on late-stage *C. cinctus* larvae, as we observed, it is unlikely that overwintering and early-season larval mortality is an important factor in the overall population dynamics of wheat stem sawfly in western Canadian agroecosystems.

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