

A Multiple Decrement Life Table Reveals That Host Plant Resistance and Parasitism Are Major Causes of Mortality for the Wheat Stem Sawfly

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ABSTRACT This study investigated the dynamics of parasitism, host plant resistance, pathogens, and predation on the demography of wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), developing in susceptible (hollow stem) and resistant (solid stem) wheat hosts. This study is also the first to investigate the prevalence and impact of cannibalism on wheat stem sawfly mortality. Wheat stem sawflies were sampled in two commercial wheat fields over 4 yr from the egg stage through adult emergence, and multiple decrement life tables were constructed and analyzed. Cannibalism, host plant resistance, or unknown factors were the most prevalent factors causing egg mortality. Summer mortality of pre-diapause larvae ranged from 28 to 84%, mainly due to parasitism by *Bracon cephi* (Gahan) and *Bracon lisogaster* Muesebeck, cannibalism, and host plant resistance. Winter mortality ranged from 6 to 54% of the overwintering larvae, mainly due to unknown factors or pathogens. Cannibalism is a major cause of irreplaceable mortality because it is absolute, with only a single survivor in every multiple infested stem. Subsequent to obligate cannibalism, mortality of feeding larvae due to host plant resistance was lower in hollow stem wheat than in solid stem wheat. Mortality from host plant resistance was largely irreplaceable. Irreplaceable mortality due to parasitoids was greater in hollow stem wheat than in solid stem wheat. Host plant resistance due to stem solidness and parasitism in hollow stems cause substantial mortality in populations of actively feeding larvae responsible for all crop losses. Therefore, enhancing these mortality factors is vital to effective integrated pest management of wheat stem sawfly.

KEY WORDS multiple decrement life table, mortality risk, mortality dynamics, parasitoid, wheat stem sawfly

The wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), is a stem-mining insect whose univoltine life cycle is synchronized with the physiological development of its host plants (Morrill and Kushnak 1996). It is a major pest of wheat, *Triticum aestivum* L., in the northern Great Plains of the United States and southern parts of the Canadian Prairie Provinces, with combined annual losses estimated at US\$350 million (Beres et al. 2011a). There are currently no effective insecticides available to manage this insect. In addition, resistant wheat cultivars are only partially effective and the efficacy of other pest management practices like cultural controls is marginal. Therefore, understanding the biology and population dynamics of this pest is crucial to devise new integrated pest management tools to manage it (Beres et al. 2011b).

Peterson et al. (2011) described the biology of the wheat stem sawfly developing in wheat in detail. Briefly, adults emerge from stubble after metamorphosis of larvae that overwinter in diapause inside the cut stems. Adults do not feed and their average life span is 7 d, although this is greatly influenced by climatic conditions (Criddle 1923). Females may lay as many as 50

eggs during their brief life span. The eggs take ~5–8 d to hatch and the larvae develop within the wheat stems feeding on parenchyma and vascular tissues (Ainslie 1929). As the host plant starts to senesce, the larva moves down the stem, cuts a notch around the stem interior, and creates a hibernaculum where it overwinters in obligate diapause (Holmes 1975). Pupal development starts the following spring and adults emerge from the stubble ~1–2 wk afterward (Church 1955, Holmes 1975). Crop damage is caused by larval feeding and cutting of the stem, which leads to stem lodging.

Several females may lay eggs in the same stem (Buteler et al. 2009), although only one larva will survive because of cannibalism within the stem (Wallace and McNeal 1966). Thus, cannibalism can have important implications for the population dynamics of this insect. However, it has never been studied directly, in part, because development of eggs and larvae of the wheat stem sawfly occur while protected within the plant stems. These insects are most likely to cannibalize smaller conspecifics or those that are defenseless such as eggs (Wallace and McNeal 1966). Similarly, conspecifics that are infected with pathogens, parasitized, or injured are also more vulnerable (Polis 1984). In concealed herbivores such as the wheat stem sawfly, cannibalism is a density-dependent factor and could

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reduce population size, thereby minimizing competition for limited resources and improving the fitness of the cannibal (Richardson et al. 2010).

Wheat stem sawflies are susceptible to two congeneric parasitoids in Montana, the larval idiobionts *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae) (Morrill 1998, Runyon et al. 2002, Weaver et al. 2005). These ectoparasitoids attack wheat stem sawfly late-instar larvae by inserting their ovipositor through the stem wall and paralyzing them (Muesebeck 1953). Parasitism by *B. cephi* and *B. lissogaster* can reach up to 98% (Morrill 1998), but varies greatly between fields owing to environmental conditions, date of crop harvest, and wheat stem sawfly abundance (Holmes et al. 1963). Other natural enemies occur sporadically and seem to be restricted to small areas in wheat fields, although intensive studies have yet to be conducted to characterize their effect on wheat stem sawfly populations. These include filamentous fungi *Fusarium* spp. that infect the wheat stem sawfly inside wheat stems as facultative entomopathogens (Wenda-Piesik et al. 2009) and a predatory clerid beetle, *Phyllobaenus dubius* (Wolcott) (Morrill et al. 2001).

Demographic analytical techniques to estimate mortality within multiple decrement life tables were used for the first time for wheat stem sawfly by Peterson et al. (2011). These techniques, which permit estimating the risks of insect death in the presence or absence of multiple causes, are important tools for population and applied ecology (Carey 1989, 1993). The multiple decrement life table and its associated demographic techniques emerged from reliability and competing risk theory in operations research (Carey 1993).

Peterson et al. (2011) conducted a life table study of pre-diapause wheat stem sawfly larvae in hollow stem wheat, the injurious stage causing plant injury during the summer growing season while protected within the stem. These authors showed that parasitism is an important, irreplaceable contributor to mortality when the larva is protected in the developing stem, and that it has the potential to be quite effective in reducing populations of the injurious stage of wheat stem sawfly.

The present study compared mortality rates and mortality factors between individuals developing in susceptible hollow and resistant solid stem spring wheat to investigate the interaction of host plant resistance and parasitism and how it translates into total mortality. This study is also the first to investigate the prevalence and impact of cannibalism on wheat stem sawfly mortality. As a result, we have created the most complete partial life tables for wheat stem sawfly (i.e., from the egg stage in the spring until adult emergence the following spring). Thus, this study adds to the understanding of population dynamics of wheat stem sawfly because it now includes the egg stage and also quantifies mortality factors occurring in overwintering larvae (in diapause) and through metamorphosis to adult emergence in different types of wheat hosts.

Materials and Methods

Study Site and Biomaterial Used. Wheat stems and larvae were sampled from designated plot areas maintained within commercial wheat fields at two locations between 2008 and 2011. One field was located between Pendroy and Conrad in Pondera County in north-central Montana (48° 05' 083"N; 112° 04' 006"W; Conrad location). The other field was north of Havre in Hill County, MT (48° 49' 951"N; 110° 05' 730"W; Havre location).

Both locations have a history of large wheat stem sawfly infestations with varying degrees of parasitism. Both locations were conventional rain-fed monocultures of hollow-stem ('Reeder') and solid-stem ('Choateau') spring wheat in which the growers practiced alternate year herbicide fallowing of cropland to minimize erosion and replenish soil moisture. These two cultivars were well suited for the experiment because they are both attractive to wheat stem sawfly females (Lanning et al. 2014).

At each location, two 24- by 30-m plots for each type of wheat were established within a strip of crop that was ~200 by 1,000 m. Plant samples containing wheat stem sawfly larvae were collected weekly from the time ovipositing females were first observed in the field through harvest. To accomplish this, two 3- by 30-m sampling areas were established weekly along the length of each plot. Two samples were collected in an area near the field margin and two more samples were collected from an area at least 15 m into the field. Samples were 10 random plants and each plant had two to five stems. Postharvest sampling was first conducted in September and subsequently in February, April, and July the following calendar year to collect overwintering wheat stem sawfly larvae through metamorphosis to adult emergence. To accomplish this, two samples of 25 larvae were collected in each plot by collecting infested plant stubble. So, each cohort study ran for two consecutive years, 2008–2009, 2009–2010, and 2010–2011. The samples were taken to the laboratory and processed by dissecting each stem to characterize the stage of the immature and to determine whether it was alive or dead. Mortality was categorized following procedures described by Peterson et al. (2011). To estimate wheat stem sawfly density, percentages of wheat stem sawfly in the sample consisting of 10 plants were also calculated after the peak oviposition period was over, typically the first week in July for each year of the study.

Determination of Wheat Stem Sawfly Presence and Mortality Factors. Variables used in the analysis consisted of six mortality categories: parasitism, pathogens, predation, intraspecific mortality due to cannibalism, mortality attributed to host plant resistance during wheat development and maturation, and unknown factors during overwintering and metamorphosis. Given that there are no characters available to distinguish between the two species of congeneric parasitoids as immatures (Runyon et al. 2002, Weaver et al. 2005), the level of parasitism reported was pooled for the two braconid species for all analyses. The designation

“pathogens” refers to observation of a dead larva with signs of hyphae from *Fusarium* spp. The designation “predator” refers to the clerid beetle, *P. dubius*, and was used when larvae of the developing beetles were found next to a dead wheat stem sawfly larva.

Cannibalism was estimated by counting the number of eggs and larvae present in a given stem at each sampling event. There are frequently two or more immature wheat stem sawfly per stem because females fail to recognize stems that already contain conspecific eggs or larvae during an oviposition event (Buteler et al. 2009). Only one larva will survive and typically the larger one will consume unhatched eggs or smaller larvae (Holmes 1954, Weiss and Morrill 1992, Weaver et al. 2005). Thus, we assumed that any additional egg or small larva in an infested stem was going to die due to cannibalism. The designation “plant response” refers to death due to host plant resistance, and is most likely due to antibiosis, given that the cadavers were usually associated with a discoloration or darkening of the plant stem (Morrill et al. 1992), and was considered typical of hypersensitive plant response, or necrosis leading to drying of eggs or newly hatched larvae (Shapiro and DeVay 1987, Petzold-Maxwell et al. 2011).

Multiple Decrement Life Tables. Multiple decrement tables were created for each type of wheat, location, and year. A broad mathematical assumption of the multiple decrement life table is that an individual surviving to a certain age is the product of all independent risk of death probabilities. More specific assumptions are that 1) each death is due to a single cause; 2) each individual in a population has the same probability of dying from any of the causes operating in the population; and 3) the probability of dying from any given cause is independent of the probability of dying from any other source (Carey 1993). Calculation techniques for multiple decrement life tables used the methods described by Carey (1993), Peterson et al. (2009, 2011), and Davis et al. (2011). We used an elimination-of-cause method as part of the program MDEC (Davis et al. 2011) to examine combinations of causes of death in relationship to the absence of other causes and to characterize each factor in terms of irreplaceable mortality. Irreplaceable mortality is the mortality rate from a specific factor that cannot be replaced by another factor in the system being studied at that particular time (Southwood 1978, Carey 1993).

Following the same methodology described by Peterson et al. (2011), variables were defined as: x = the life stage index; l_x = the number of individuals alive at each x ; k_x = the number at the beginning of each x ; d_x = the total number of deaths in each stage; al_x = the fraction of the cohort living at the beginning of the stage (starting at 1.0 for the first stage and calculated by $al_{x-1} - ad_{x-1}$); ad_{i_x} = fraction of the original cohort dying in stage x due to cause i ; ad_x = fractions of all deaths from all causes ($ad_{1x} + ad_{2x} + \dots + ad_{5x}$), and; aq_x = stage-specific probability of death within that stage calculated by the sum of the probability of dying from all listed causes (d_x/k_x).

To estimate irreplaceable mortality, an algorithm represented by a quadratic formula was used to generate

mortality solutions for independent mortality factors in the absence of all other factors. Elimination-of-cause analysis relies on the probability of surviving each source of mortality (p_x) and its complement ($1 - q_x$) where $(1 - q_1) \times \dots \times (1 - q_n)$ is the chance of jointly surviving a set of mortality factors and its complement, $1 - [(1 - q_1) \times \dots \times (1 - q_n)]$, is the chance of jointly dying from a set of mortality factors. To estimate mortality in the absence of one or more factors, two simultaneous equations with two unknowns are used. For example, by expressing q_1 (e.g., parasitism) in terms of q_2 (e.g., all other mortality factors), D_1 and D_2 (the fraction of all individuals observed that died of cause 1 and 2), this yields the quadratic equation:

$$aq_2^2 + bq_2 + c = 0$$

where $a = D_1$, $b = -(D_1 + D_2)$ and $c = D_2(D_1 + D_2)$. The value of q_2 can be found by substituting a , b , and c into the quadratic formula (Davis et al. 2011, Peterson et al. 2011).

Data Analyses. Analysis of variance was used to compare percentage of infested stems and number of immatures found in solid and hollow wheat stem samples at each location and year. The data were analyzed using the Mixed Procedure of version 9.3 of the SAS system (SAS Institute 2012, Cary, NC), with infestation percentage per sample as the response variable and type of wheat, location, and their interaction as main fixed effects. Year and plant samples were considered random factors.

Analysis of variance was used to compare mortality in the presence of other causes and irreplaceable mortalities caused by each mortality factor and in each wheat type. The data were analyzed using the Mixed Procedure of version 9.3 of the SAS System (SAS Institute 2012), with percent mortality attributed to each factor as the response variable and type of wheat, location, and their interaction as main fixed effects. Year and replicate samples were assumed to be random factors in the analysis because random effects are used for making broad inferences about an entire population, including levels of the population that are not included in the experiment, such as the population of years and plants. Parasitism and pathogen mortalities were square root-transformed to better meet assumptions of homogeneity of variance. Untransformed means and SEs are presented.

Results

Presence of Wheat Stem Sawfly Immatures in Wheat Stems. In total, 7,300 larvae were collected over all locations and years. At Havre, 1,237, 1,014, and 1,128 larvae were collected in 2008, 2009, and 2010, respectively. At Conrad, 1,216, 710, and 1,895 larvae were collected in 2008, 2009, and 2010, respectively (Fig. 1). In total, 206, 137, and 171 eggs were collected at Havre in 2008, 2009, and 2010, respectively. At Conrad, 165, 184, and 237 eggs were collected in 2008, 2009, and 2010, respectively (Fig. 1).

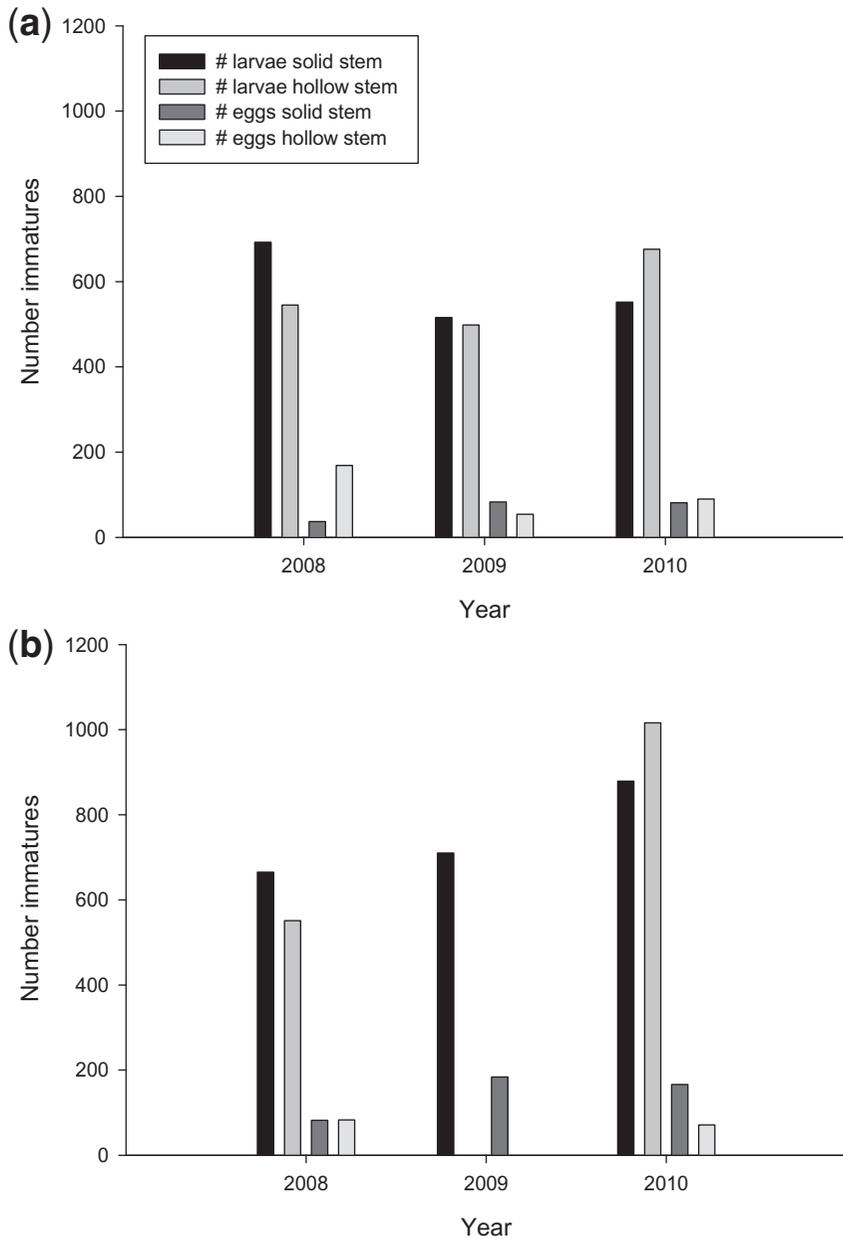


Fig. 1. Total numbers of immature wheat stem sawfly, *C. cinctus*, larvae sampled per location and type of wheat at (a) Havre and (b) Conrad. Data not available for hollow stem at Conrad in 2009 due to crop failure.

Both hollow and solid stem wheat were readily infested (Fig. 2). At Havre, infestation in solid stem ranged from 59% in 2010 to 77.2% in 2008, while infestation in hollow stem wheat ranged from 11.5% in 2009 to 52.4% in 2008. At Conrad, infestation in solid stem ranged from 59% in 2010 to 77.2% in 2008, while infestation in hollow stem wheat ranged from 39.5% in 2010 to 62.7% in 2008 (Fig. 2). Infestation percentage varied by cultivar ($F = 30.12$; $df = 1, 35$; $P < 0.001$) and location ($F = 5.03$; $df = 1, 35$; $P = 0.03$), with no significant interaction between cultivar and location ($F = 0.3$; $df = 1, 35$; $P = 0.6$). Number of immatures per stem

also varied by cultivar ($F = 39.63$; $df = 1, 35$; $P < 0.001$) and location ($F = 5.69$; $df = 1, 35$; $P = 0.02$), with no significant interaction between cultivar and location ($F = 0.49$; $df = 1, 35$; $P = 0.5$). Solid stem wheat had greater infestation percentages and number of immatures per stem than hollow stem wheat.

Multiple Decrement Life Tables. Multiple decrement life tables for each location are presented in Table 1. Unhatched eggs succumbed to only two categories of mortality, either unknown mortality or cannibalism. Wheat stem sawfly larvae succumbed to six mortality categories: parasitism, predation, pathogens,

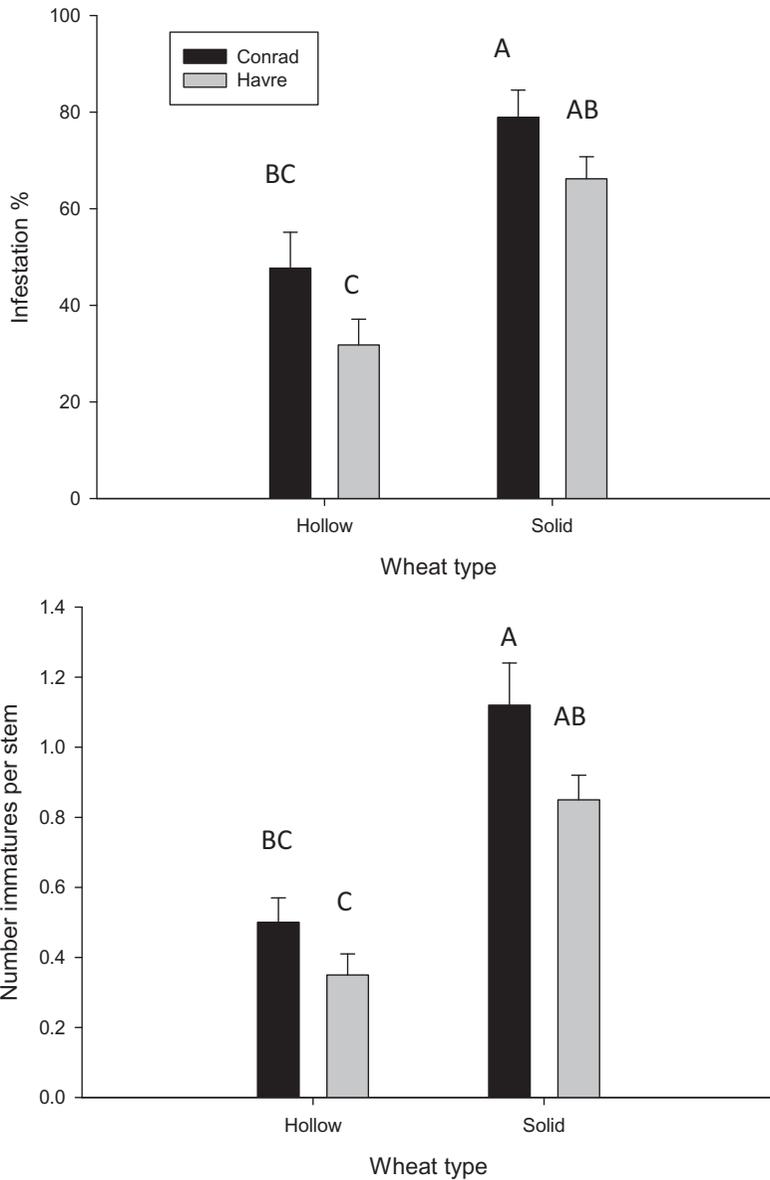


Fig. 2. Percentage of infested stems and number of immature wheat stem sawflies per stem in solid and hollow stem wheat collected at Conrad and Havre, MT, in 2008, 2009, and 2010.

cannibalism, plant response, and unknown factors. The greatest larval mortality occurred during the summer, although as much as 50% mortality occurred during the winter for the overwintering larvae. Plant response mortality occurred only during the summer on feeding larvae. This factor did not cause any mortality after larvae had girdled the stems to overwinter.

Mortality in the Presence of Other Causes. Data in Table 2 represent the probability of death from the specified causes in the presence of all observed causes over all stages. For mortality due to parasitoids in the presence of other causes, there was a significant interaction between location and type of wheat ($F = 9.06$; $df = 1,14$; $P = 0.009$). At Conrad,

mortality due to parasitoids was greater in hollow stem wheat than in solid stem wheat, but no differences were observed between types of wheat at Havre. Unknown mortality was typically low, ranging from 1.37 to 7.01%. Mortality due to unknown factors varied with location ($F = 15.04$; $df = 1,14$; $P = 0.002$) where larvae in hollow stems at Conrad had a greater mortality due to unknown factors than larvae developing in hollow stems at Havre. Mortality due to parasitoids ranged from 5 to 34%. There was an expected effect of the type of wheat for mortality due to host plant resistance ($F = 30.94$; $df = 1,2$; $P = 0.03$), with no location effect or significant interactions between location and type. Mortality due to host plant resistance was lower

Table 1. Multiple decrement life table for wheat stem sawfly, *C. cinctus*, in hollow or solid stem spring wheat at Conrad and Havre, MT, including egg and larval stages through development and metamorphosis to adult emergence for 2008, 2009, and 2010

Location	Wheat type	Year	Category, x	Fraction Dying, aq_x	Fraction Living, al_x	Fraction of total dying, ad_x	Unknown, aq_{1x}	Parasitism, aq_{2x}	Predation, aq_{3x}	Pathogen, aq_{4x}	Cannibalism, aq_{5x}	Plant response, aq_{6x}
Conrad	Hollow	2008	Egg	0.4	1.0	0.4	0.0	0.0	0.0	0.0	0.4	0.04
			Summer	0.5	0.6	0.3	0.0	0.2	0.0	0.0	0.0	0.1
			Winter	0.3	0.3	0.3	0.1	0.0	0.0	0.0	0.0	0.0
			Total			1.0	0.1	0.2	0.0	0.0	0.4	0.1
Conrad	Solid	2008	Egg	0.7	1.0	0.7	0.0	0.0	0.0	0.0	0.4	0.3
			Summer	0.6	0.4	0.2	0.0	0.1	0.0	0.0	0.0	0.1
			Winter	0.2	0.2	0.2	0.02	0.0	0.0	0.0	0.0	0.0
			Total			1.0	0.02	0.1	0.0	0.0	0.4	0.4
Havre	Hollow	2008	Egg	0.4	1.0	0.4	0.0	0.0	0.0	0.0	0.3	0.1
			Summer	0.3	0.6	0.2	0.0	0.03	0.0	0.0	0.0	0.1
			Winter	0.1	0.3	0.4	0.0	0.0	0.0	0.0	0.0	0.0
			Total			1.0	0.0	0.03	0.0	0.0	0.3	0.3
Havre	Solid	2008	Egg	0.6	1.0	0.6	0.0	0.0	0.0	0.0	0.3	0.3
			Summer	0.5	0.4	0.2	0.0	0.02	0.0	0.0	0.0	0.2
			Winter	0.1	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0
			Total			1.0	0.0	0.02	0.0	0.0	0.3	0.4
Conrad	Solid	2009	Egg	0.6	1.0	0.6	0.0	0.0	0.0	0.0	0.4	0.1
			Summer	0.7	0.5	0.3	0.0	0.0	0.0	0.0	0.0	0.3
			Winter	0.4	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0
			Total			1.0	0.0	0.0	0.0	0.0	0.4	0.4
Havre	Hollow	2009	Egg	0.2	1.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0
			Summer	0.7	0.8	0.5	0.0	0.2	0.0	0.0	0.0	0.3
			Winter	0.4	0.3	0.3	0.1	0.0	0.0	0.0	0.0	0.0
			Total			1.0	0.1	0.2	0.0	0.0	0.2	0.3
Havre	Solid	2009	Egg	0.4	1.0	0.4	0.0	0.0	0.0	0.0	0.3	0.1
			Summer	0.7	0.6	0.4	0.0	0.0	0.0	0.0	0.0	0.3
			Winter	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0
			Total			1.0	0.0	0.0	0.0	0.0	0.3	0.4
Conrad	Hollow	2010	Egg	0.5	1.0	0.0	0.1	0.0	0.0	0.0	0.4	0.0
			Summer	0.5	1.0	0.5	0.0	0.3	0.0	0.0	0.04	0.0
			Winter	0.5	0.5	0.5	0.1	0.0	0.0	0.1	0.0	0.0
			Total			1.0	0.2	0.3	0.0	0.1	0.5	0.0
Conrad	Solid	2010	Egg	0.5	1.0	0.5	0.0	0.0	0.0	0.0	0.3	0.2
			Summer	0.5	0.5	0.2	0.0	0.1	0.0	0.0	0.0	0.1
			Winter	0.4	0.3	0.3	0.1	0.0	0.0	0.1	0.0	0.0
			Total			1.0	0.1	0.1	0.0	0.1	0.3	0.3
Havre	Hollow	2010	Egg	0.6	1.0	0.6	0.0	0.0	0.0	0.0	0.6	0.0
			Summer	0.4	0.4	0.2	0.0	0.1	0.0	0.0	0.0	0.04
			Winter	0.3	0.3	0.3	0.1	0.0	0.0	0.0	0.0	0.0
			Total			1.00	0.1	0.1	0.0	0.0	0.6	0.04
Havre	Solid	2010	Egg	0.5	1.0	0.5	0.0	0.0	0.0	0.0	0.2	0.2
			Summer	0.8	0.5	0.5	0.0	0.1	0.0	0.0	0.0	0.3
			Winter	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
			Total			1.0	0.0	0.1	0.0	0.2	0.5	

aq_x , fraction of deaths from all causes in stage x given that the individual is alive at the beginning of stage x ; al_x , fraction of survivors at stage x out of original cohort of al_1 ; ad_x , fraction of deaths in stage x from all causes; aq_{ix} , fraction of deaths from cause i in stage x in the presence of all other causes given that the individual is alive at the beginning of stage x .

Table 2. Mortality in the presence of the other factors by location, year, and type of wheat for wheat stem sawfly, *C. cinctus*, eggs, and larvae through development, overwintering diapause and metamorphosis to adult emergence

Location	Type of wheat	Total mortality	Percentage mortality in the presence of other factors					
			Cannibalism	Plant response	Pathogen	Predation	Parasitism	Unknown
Conrad	Hollow	45.9 ± 4.3	22.3 ± 4.6a	13.5 ± 1.2a	7.5 ± 2.4a	0.3 ± 0.3a	26.8 ± 7.9a	7.0 ± 0.0a
Conrad	Solid	63.3 ± 9.1	37.5 ± 3.9a	36.9 ± 3.0b	2.5 ± 0.1b	0.2 ± 0.2a	6.7 ± 1.3b	4.0 ± 1.0ab
Havre	Hollow	35.2 ± 8.3	43.5 ± 9.3a	12.8 ± 7.6a	1.7 ± 0.6b	0.0 ± 0.0a	8.0 ± 2.6b	2.6 ± 1.2b
Havre	Solid	41.0 ± 4.8	25.3 ± 3.1a	45.4 ± 4.9b	1.2 ± 0.2b	1.1 ± 0.0a	10.0 ± 3.0ab	3.0 ± 0.9b

Data are presented as mean ± SEM. ($n = 12$ for each treatment). Rows within columns followed by different letters are significantly different ($\alpha = 0.05$).

in hollow stem wheat than in solid stem wheat, ranging from 5 to 14% in hollow stem wheat and from 34 to 50% in solid stem wheat. The incidence of predation was very low overall, ranging from 0 to ~1.5%, with no differences between locations ($F = 0.43$;

$df = 1,14$; $P = 0.52$) or types of wheat ($F = 0$; $df = 1,2$; $P = 0.9$).

Mortality due to pathogens varied across locations ($F = 10.67$; $df = 1,12$; $P = 0.006$), but there was also a significant interaction between location and type of

Table 3. Irreplaceable mortality by location, year, and type of wheat for wheat stem sawfly, *C. cinctus*, eggs, and larvae through development, overwintering diapause, and metamorphosis to adult emergence

Location and year	Type of wheat	Percentage irreplaceable mortality					
		Cannibalism	Plant response	Pathogen	Predation	Parasitism	Unknown
Conrad	Hollow	8.9 ± 3.3a	4.9 ± 0.7c	5.8 ± 1.6a	0.1 ± 0.1a	11.0 ± 1.8a	8.2 ± 1.8a
Conrad	Solid	10.2 ± 1.0a	18.6 ± 2.5b	1.5 ± 0.5b	0.1 ± 0.1a	2.3 ± 0.8b	3.7 ± 0.8ab
Havre	Hollow	15.5 ± 4.5a	10.8 ± 3.7b	3.0 ± 1.1ab	0.5 ± 0.4a	7.4 ± 1.8a	4.4 ± 1.5b
Havre	Solid	7.8 ± 1.8a	31.2 ± 3.6a	0.9 ± 0.1b	0.3 ± 0.2a	1.9 ± 0.6b	1.7 ± 0.5b

Data were pooled across years and are presented as mean ± SEM. ($n = 12$ for each treatment). Rows within columns followed by different letters are significantly different ($\alpha = 0.05$).

wheat ($F = 5.41$; $df = 1,14$; $P = 0.03$). Pathogen mortality was greater at Conrad in hollow stems than in solid stems, but there were no differences between wheat types at Havre. Cannibalism mortality ranged from 18 to 52% with no significant differences between locations ($F = 0.17$; $df = 1,14$; $P = 0.68$) or type of wheat ($F = 0.45$; $df = 1,2$; $P = 0.57$).

Irreplaceable Mortality. Data in Table 3 represent the mortality from the specified causes, which cannot be replaced by the other causes that were observed (irreplaceable). There was a significant effect of type of wheat ($F = 27.61$; $df = 1,2$; $P = 0.03$) and location ($F = 8.32$; $df = 1,14$; $P = 0.01$) on the irreplaceable mortality due to host plant resistance. Mortality attributed to host plant resistance was greater at Havre than at Conrad and was greater in solid stem wheat than in hollow stem wheat.

There was a location effect on unknown mortality, where wheat stem sawfly from Conrad typically had a greater unknown mortality, particularly in hollow stem wheat ($F = 10.17$; $df = 1,14$; $P < 0.01$). No significant differences were observed between locations ($F = 3.97$; $df = 1,14$; $P = 0.07$), types of wheat ($F = 11.9$; $df = 1,2$; $P = 0.07$), or their interaction ($F = 1.66$; $df = 1,14$; $P = 0.22$) in the irreplaceable mortality due to pathogens. No significant differences were observed between locations ($F = 0.68$; $df = 1,14$; $P = 0.42$), types of wheat ($F = 0.78$; $df = 1,2$; $P = 0.47$), or their interaction ($F = 2.72$; $df = 1,14$; $P = 0.12$) in the irreplaceable mortality due to cannibalism. Mean mortality due to cannibalism ranged from ~6 to 20%.

Irreplaceable mortality due to predation was very low and no differences were observed between locations ($F = 0.93$; $df = 1,14$; $P = 0.35$), types of wheat ($F = 0.23$; $df = 1,2$; $P = 0.68$), or their interaction ($F = 0.04$; $df = 1,14$; $P = 0.85$).

There was a significant effect of type of wheat on the irreplaceable mortality due to parasitism ($F = 30.77$; $df = 1,2$; $P = 0.03$) with no effect of location ($F = 2.44$; $df = 1,14$; $P = 0.14$) or of the interactions between both factors ($F = 1.49$; $df = 1,14$; $P = 0.24$). Irreplaceable mortality due to parasitism was greater in hollow stem wheat than in solid stem wheat, where it was reduced significantly compared with the parasitoid mortality, considering the presence of other factors.

Discussion

The most significant sources of wheat stem sawfly mortality were parasitism, host plant resistance,

pathogens, and unknown mortality factors. The multiple decrement life tables show that for eggs, cannibalism and host plant resistance or unknown factors were the most prevalent mortality factors. Egg parasitoids were not detected. Summer mortality of injurious larvae ranged from 29 to 84% mainly due to parasitism by *B. cephi* and *B. lissogaster* and host plant resistance. Winter mortality factors varied greatly by location and year, ranging from 6 to 52% of the overwintering larvae, mainly due to unknown factors or pathogens.

Parasitism in the presence of other factors caused a mean mortality of as much as 34%. Irreplaceable mortality due to parasitism in this study reached a mean maximum of 12%, surpassed only by the host plant resistance factor selected for in solid-stem wheat, at ~34% mortality. These results agree with those obtained by Peterson et al. (2011), who found that parasitism represents an important mortality factor for wheat stem sawfly larvae developing in the stems during the summer, and that when parasitism occurs, it is largely not replaced by other factors. Irreplaceable mortalities from parasitism are lower in the present study than those reported by Peterson et al. (2001), which ranged from 22 to 35%. This difference is most likely because overall parasitism in the presence of other factors was also lower in this study and because we have also accounted for mortality factors occurring during the winter and through adult emergence. However, winter mortality occurs after the prediapause larvae have already injured the plants. Therefore, the impact of prediapause larvae mortality, during the summer growing season, is much greater than that of winter mortality.

Mortality by parasitism in hollow stem wheat was more irreplaceable than in solid stem wheat, where it is most likely replaced to some degree by host plant resistance. Interestingly, larval mortality from parasitism was lower in solid stem wheat than in hollow stem wheat. This could be explained because parasitoids may not find as many suitable hosts in solid stems because host plant resistance causes greater mortality in eggs and young larvae than hollow stem wheat, reducing the availability of individuals that can grow large enough to be injurious to the crop and potentially parasitized. Mean mortality in solid stem wheat due to host plant resistance for eggs and larvae ranged from 12 to 50% in the presence of other factors, but these life stages are not viable as hosts for endemic braconid parasitoids. Infestation in solid stem wheat was

significantly greater than in hollow stem wheat, which could explain the lower number of parasitoids in this type of wheat given that parasitism rates can decline at very high levels of infestation, due to increased cannibalism and host location inefficiency at greater host numbers (Weaver et al. 2005).

As expected, eggs and larvae developing in solid stem wheat had a greater risk of dying within the stems during the summer because of host plant responses. Mortality of eggs and larvae from plant responses in the presence of other factors was greater in solid stem (means from 34 to 50%) than in hollow stem wheat (means from 12 to 15%). On the contrary, mortality due to unknown factors occurring in the winter was similar across wheat types and ranged from 3 to 13%. These results clearly demonstrate that mortality due to solid stem wheat occurs during the egg and prediapause larval stages within the stem. Our results agree with Cárcamo et al. (2011), who showed that overwintering mortality was not related to the type of wheat cultivar.

There was significant variability in the percentage mortality due to host plant resistance across locations and this is expected based on the consistency of stem solidness, where the amount and density of pith varies with climatic conditions during wheat development. Stem solidness in wheat relates to the degree of solid pith (undifferentiated parenchyma cells) development within the stem, which can vary from 0 to 100%, depending on plant genotype and environmental conditions (Berzonsky et al. 2003, Beres et al. 2012). Moreover, the timing of the wheat stem sawfly flight may also affect the efficacy of solid stem wheat at killing larvae, especially when a dense plant stand causes canopy shading that limits pith expression (Luginbill and McNeal 1958). However, host plant resistance represents a significant source of larval mortality, with a mean maximum of 34% irreplaceable mortality in solid stem wheat in this study. Moreover, the negative effects of solid-stem host plants have also been shown to extend to lower fecundity as smaller larvae generally produce smaller female adults with lower egg loads (Morrill et al. 1994, Cárcamo et al. 2005). Over time, this could have an impact on the potential overall infestation in wheat stem sawfly populations repeatedly exposed to solid stem wheat.

The occurrence of obligate cannibalism within a protective stem allows for a substantial analysis of this phenomenon. No significant differences were observed in cannibalism among locations or wheat types. Mortality due to cannibalism, in the presence of other factors, ranged from ~18 to 52%. Mean irreplaceable mortality due to cannibalism had a maximum of ~20% with no significant differences between locations or types of wheat. Cannibalism is most readily detected in the egg stage and was negligible in larvae (with an observed maximum mean of 3.5%). For wheat stem sawfly, the presence of conspecifics in a stem will be influenced by a combination of factors related to ovipositing decisions, as well as biotic factors related to the host. First, females do not avoid infested stems (Buteler et al. 2009) and stems with more than one egg will result in obligate cannibalism given that only one larva can

survive in any infested stem. Second, wheat stem sawfly will infest different hosts at different rates, depending on oviposition preference (Perez-Mendoza et al. 2006, Weaver et al. 2009), and this will also have an effect on the number of eggs per stem. Finally, oviposition decisions may not be associated with larval performance, given that, as seen in this study, wheat stem sawfly females prefer to lay eggs in plants where larvae will have a lower chance of survival (solid stem wheat). Perez-Mendoza et al. (2006) also observed an oviposition preference for downy brome grass, *Bromus tectorum* L., when compared with adjacent wheat, although mortality of late instars at plant maturity was significantly greater in the ripening grass weed than in ripening wheat stems. Also, in this cropping system, eggs are weakly aggregated along a field, while larvae tend to be more aggregated, overall, within a wheat field (Nansen et al. 2005a, b). Aggregations of eggs decreased later during the oviposition window because females utilized plants further in the growing fields, while larval aggregation became more exaggerated, reflecting the spatial variability in optimal wheat hosts and the higher rates of oviposition and subsequent cannibalism in these more suitable hosts, both along the field periphery and further into the field (Nansen et al. 2005a, b).

Our results suggest that the impact of host plant resistance on early developmental stages in solid stem wheat and the greater parasitism of larger, more mature larvae in hollow stem wheat are the most significant mortality factors, even when mortality factors occurring throughout the year are taken into account. Further, estimates of irreplaceable mortality indicate that these factors cause significant, appreciable reductions in populations at different stages of development when they are operating. Therefore, attention should be focused on enhancing these mortality factors within an integrated pest management program for wheat stem sawfly, primarily by planting solid stem wheat in heavily infested fields (Beres et al. 2012b) and by post-harvest conservation of parasitoids in wheat stubble (Runyon et al. 2002) that serves as the primary reservoir of overwintering parasitoid populations. More broadly, the multiple decrement life table analysis allowed for estimation of mortality risks, competing risks, and irreplaceable mortality, further demonstrating the utility of biodemographic analytical approaches for insects. This is clearly important for all phytophagous insects, but is essential when dealing with a cryptic pest with all injurious stages concealed inside the stem.

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