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Review

Host Plants of the Wheat Stem Sawfly (Hymenoptera: Cephidae)

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Abstract

Wheat stem sawfly (*Cephus cinctus* Norton) is a pest of economic importance across much of the wheat (*Triticum aestivum* L.)-growing areas of the western Great Plains of North America as well as an ecologically important insect owing to its wide range of grass hosts. Little research has been published regarding the noncultivated native and invasive grasses attacked by this insect. Knowledge of the complete host range of *C. cinctus* can inform future research about potential new sources of genetic resistance, improve understanding of the biology and spread of natural enemies, and better define this insect's role in grassland and agricultural systems. The aim of this review is to compile a checklist of reported host plants of *C. cinctus* and present data from an extensive survey of noncultivated hosts used by *C. cinctus*.

Key words: survey, pest, *Cephus cinctus*, grass

The wheat stem sawfly, *Cephus cinctus* Norton, is an endemic species originally described in 1872 from Colorado as a grass-boring sawfly (Norton 1872). The wheat stem sawfly is known to be a major pest in spring and winter wheat (*Triticum aestivum* L.) in the northern Great Plains (Bekkerman 2013). Adult wheat stem sawfly oviposit in a host plant stem, where after hatching, the larvae feed on the pith and vascular bundles of the stem. Eventually the larva cuts the stems at the base, causing a large amount of wheat to lodge (Holmes 1954). Larval feeding hinders the plant's ability to transport water and nutrients, thus lowering photosynthetic capacity by as much as 12% (Macedo et al. 2005, Macedo et al. 2007), reduces grain weights by 10–20% (Holmes 1977, Morrill et al. 1992), and causes an estimated 15.5% harvest loss due to lodging before harvest (Ainslie 1920, Holmes 1977, Weiss and Morrill 1992).

Winter wheat and downy brome (*Bromus tectorum* L.) have similar ecologies and growth stages, as both are annual winter grasses (Morrow and Stahlman 1984). In the 19th century, downy brome was accidentally introduced into North America from Mediterranean Europe (Mack 1981). In Montana, wheat stem sawfly infests spring wheat, winter wheat, and downy brome (Perez-Mendoza et al. 2006). In northeastern Colorado, downy brome is often found near winter wheat fields, providing an opportunity to investigate differences in C. *cinctus* infestation rates between downy brome and winter wheat. Additionally, Lesieur et al. (2016) identified the wheat stem sawfly found in Montana to be of a different haplotype than wheat stem sawfly found in Colorado, possibly confounding differences in host preference between the two populations.

The originally described hosts of wheat stem sawfly were noncultivated grasses (Norton 1872; Ainslie 1920, 1929, Capinera 2004). Gaining a better understanding of the range of grass hosts could identify new sources of resistance for breeders, provide insight into plant traits conferring resistance, expand knowledge of parasitoid biology, and provide an improved understanding of the origins and biology of this important pest. In this study, we 1) compile a list of reported cultivated and noncultivated wheat stem sawfly hosts, 2) present new data from an extensive survey of host use of noncultivated wild grasses in Montana, and 3) compare *C. cinctus* infestations in wheat and downy brome (*Bromus tectorum* L.) based on a survey in northeastern Colorado.

Materials and Methods

Literature Review of Grass Hosts of *C. cinctus*

Relevant research concerning wheat stem sawfly hosts were identified through the use of Web of Science (Clarivate Analytics V5.20–V5.22.3), Academic Search Premier (EBSCO Publishing; for older technical reports), and Google Scholar. The bulk of this literature review was done throughout 2015 and early 2016. We used the following search terms: "wheat stem sawfly" and "grass, host, range, or preference" as well as "*Cephus cinctus* Norton" and "grass, host, range, or preference." Secondary searches were made based on cited references to relevant information on specific known hosts to wheat stem sawfly.

Montana Survey

Surveys for wheat stem sawfly in native and introduced grasses were carried out in north-central Montana (Teton, Glacier, Pondera, Toole, Cascade, Choteau, Liberty, and Hill Counties), which consistently experiences the highest populations of *C. cinctus* in wheat in the state. Grassland sites bordering wheat stem sawfly-infested wheat fields were selected for sampling. In 2010, eight rangelands and 12 Conservation Reserve Program (CRP) grasslands were sampled in late July. In 2012, an additional eight rangelands and eight CRP fields were sampled in both late July and September. Grass stems were collected individually using a serrated shovel to cut the stem at the soil surface. At each site, we aimed to collect 100 stems of each grass species present, starting from the field edge and extending ≥100 m into the field, collecting haphazardly along a 50-m wide transect. This target was not always attained, as some grasses were uncommon at some sites. However, in most cases, at least 100 total grass stems were examined for each species present in Table 1. Exceptions were *Achnatherum hymenoides* (Roem. & Shult.), *Bouteloua gracilis* (Willd. ex Kunth), *Calamovilfa longifolia* (Hook.) Scribn., and *Festuca idahoensis* Elmer, for which only 50 stems were sampled for each species. Edges were identified by changes in habitat cover and evidence of changes in landuse, usually delineated by a fenceline, road, or a transition from planted edges or crops. Collected grass stems were returned to the Northern Plains Agricultural Research Laboratory in Sidney, MT, and dissected to determine wheat stem sawfly host use, which was indicated by the presence of larvae, whether alive or dead, within the stems. As such, the data indicate ovipositional acceptance of a particular grass host species by *C. cinctus*, but do not indicate whether larvae successfully complete their development within the host. Sawfly larvae were identified based on descriptions in Criddle (1915) and Wallace and McNeal (1966), and assumed to be *C. cinctus* based on distribution records. Of the four known North American species in the grass-mining tribe Cephini, only *Cephus cinctus* has been recorded from the Great Plains, including Montana, with the other three species confined to the eastern (*Cephus pygmaeus* (L.) and *Trachelus tabidus* (F.)) or western (*Calameuta clavata* (Norton)) United States (Smith 1979).

Colorado Case Study

The objectives of this survey were 1) to study infestation by wheat stem sawfly on winter wheat and downy brome in northeastern Colorado and 2) to compare wheat stem sawfly presence and survivorship (overwintering) in cultivated winter wheat and in nearby downy brome. These data will expand our knowledge base of the interaction between wheat, downy brome, and *C. cinctus*, first described by Perez-Mendoza et al. (2006), using wheat fields with co-occurring downy brome in Montana. Contrary to Perez-Mendoza et al., the data presented here are from surveys in areas with either downy brome or winter wheat, but not both (nor spring wheat). These methods can be used as a model for other experiments investigating *C. cinctus* infestation in other noncultivated grasses.

Seven commercial wheat fields and eight nearby downy brome sites in northeastern Colorado along CO Hwy 14 east of Fort Collins were selected in 2013 and 2014 (Table 2). The wheat fields chosen contain susceptible hollow-stemmed winter wheat cultivars, including 'Byrd' and 'Hatcher'. Wheat was grown mostly using no-till practices. Winter wheat field sizes were approximated using Google Earth (Table 2), while downy brome field sizes were not approximated owing to grass fields being of mixed species. Downy brome sites were adjacent to the wheat sites, and were generally much smaller in size than the wheat fields. Stem samples ($n = 50$) were randomly collected from each site (wheat and brome sites sampled identically) by digging crowns up in bunches within 20 m of the field edge, weekly beginning in spring (mid-May) through the summer. Samples were taken without concern for distance between them, but generally were all within 50 m of each other. Stubble samples ($n = 50$) were collected from each site monthly in fall and winter. Sweep samples (100 sweeps per site) were taken weekly during the wheat stem sawfly flight period from late May through early June. Mature stems or stubble were dissected and examined for the presence of wheat stem sawfly larvae. Larvae were identified as *C. cinctus* using descriptions given by Wallace and McNeal (1966). The number of eggs, larvae, and pupae were recorded in each stem. Stems containing frass (evidence of larval wheat stem sawfly feeding) but no larvae, as well as stems containing one of the wheat stem sawfly developmental stages, were considered to be infested. Larval establishment was defined by feeding within the stem, even if the larvae died before reaching maturity. A stem containing frass but no dead larvae as well as stems containing dead larvae were recorded as instances of larval mortality. Larval survival was defined as the presence of a living larva within the stem at the time of sampling. Overall presence of wheat stem sawfly was compared in winter wheat and grasses.

The effects of each factor (sample date, collection site, and host plant) on the infestation rate of the wheat stem sawfly were analyzed using separate one-way ANOVAs for each year (2013 and 2014) after logit transformations of the infestation rates. Larval mortality on wheat and downy brome were logit transformed and assessed across dates for sites in each year. Separate *t*-tests were used to compare the wheat stem sawfly infestation in wheat fields and downy brome across sites for each year of the survey. Adult sweep counts collected in May were square-root transformed. The effect of each factor (sample date, collection site, and host plant) on the number of wheat stem sawfly adults collected in May by sweep samples was analyzed using separate one-way ANOVAs for 2013 and 2014. All statistics were completed using R software version 3.2.5 (R Core Team 2016).

Results and Discussion

Literature Review

Wheat stem sawfly has been observed injuring a number of cereal crops over the past 100 yr. The wheat stem sawfly is most common in bread wheat, *T. aestivum*, but has been found in other *Triticum* spp., as well as cultivated barley (*Hordeum vulgare* L.) and rye (*Secale cereale* L.) (Wallace and McNeal 1966; Table 3).

There are several species of cereal grains that were identified as showing some resistance to larval wheat stem sawfly development. The modes of resistance were not specified by the authors. These include three species of tetraploid wheat: *Triticum durum* (Ainslie 1929, Wallace and McNeal 1966), *Triticum polonicum* L. (Wallace and McNeal 1966), and *Triticum timopheevii* (Zhuk.) Zhuk.

Table 1. Noncultivated grasses found to be infested by wheat stem sawfly larvae in north-central Montana

Species	Common name	No. of sites sampled	No. of sites with *C. cinctus*
Achnatherum hymenoides	Indian ricegrass	2	1
Agropyron cristatum	Crested wheatgrass	32	21
Bouteloua gracilis	Blue grama	11	1
Bromus inermis	Smooth brome	12	12
Bromus arvensis	Field brome (Japanese brome)	25	3
Bromus tectorm	Downy brome; cheatgrass	14	5
Calamovilfa longifolia	Prairie sandreed	1	1
Elymus trachycaulus	Slender wheatgrass	12	12
Festuca idahoensis	Idaho fescue	1	1
Koeleria macrantha	Prairie junegrass	15	2
Leymus cinereus	Basin wildrye	1	1
Pascopyrum smithii	Western wheatgrass	30	29
Poa compressa	Canada bluegrass	15	1
Poa pratensis	Kentucky bluegrass	7	4
Poa secunda	Sandberg bluegrass	5	1
Pseudoroegneria spicata	Bluebunch wheatgrass	9	7
Hesperostipa comata	Needle and thread	16	6
Nassella viridula	Green needlegrass	26	21
Thinopyrum intermedium	Intermediate wheatgrass	11	11

The number of sites sampled for each potential grass host species, and the number of those sites at which wheat stem sawfly were present in that host species are indicated.

Table 2. Commercial wheat fields and nearby downy brome sites selected for the survey of wheat stem sawfly in northeastern Colorado in 2013 and 2014.

Host plants	Year	Sites[a]	Latitude	Longitude	Field size (acres)	Elevation (m)
Winter	2013 and 2014	Merten1	40° 35′37.05″ N	103° 53′4.17″ W	73.18	1,455
		Merten2	40° 34′22.35″ N	103° 53′52.65″ W	101.15	1,471
		Dan1	40° 47′22.74″ N	103° 29′49.92″ W	236.56	1,346
		Dan2	40° 47′23.64″ N	103° 29′23.09″ W	82.40	1,352
		Scott1	40° 59′15.54″ N	104° 21′17.17″ W	88.17	1,636
		Wickstrom1	40° 30′49.79″ N	104° 4′14.95″ W	132.42	1,492
		Wickstrom2	40° 30′51.90″ N	104° 4′13.32″ W	162.49	1,494
Wheat	2013 and 2014	Merten1	40° 35′39.05″ N	103° 52′49.51″ W	78.25	1,457
		Merten2	40° 34′15.89″ N	103° 53′50.28″ W	111.56	1,471
		Dan1	40° 47′21.59″ N	103° 29′48.59″ W	214.82	1,346
		Dan2	40° 47′20.43″ N	103° 29′28.79″ W	92.36	1,350
		Scott1	40° 59′16.52″ N	104° 21′14.59″ W	78.92	1,635
		Wickstrom1	40° 31′29.21″ N	104° 4′20.14″ W	145.08	1,495
		Wickstrom2	40° 34′3.58″ N	104° 4′5.33″ W	164.32	1,486
Downy brome	2013 and 2014	Merten3	40° 35′44.29″ N	103° 52′49.86″ W	–	1,458
		Merten4	40° 34′15.31″ N	103° 53′52.62″ W	–	1,471
		Dan3	40° 45′37.37″ N	103° 31′1.34″ W	–	1,339
		Dan4	40° 47′21.48″ N	103° 29′51.00″ W	–	1,346
		Dan5	40° 47′25.14″ N	103° 29′14.86″ W	–	1,350
		Scott2	40° 58′24.49″ N	104° 19′30.74″ W	–	625
		Scott3	40°59’15.27″ N	104°21′10.98″ W	–	1,635
		Wickstrom3	40°30’49.36″ N	104° 4′13.41″ W	–	1,493

[a] Different numbers refer to different sites within the grower’s field.

(Wallace and McNeal 1966). Both oats (*Avena sativa*) and flax (*Linum usitatissimum*; a broadleaf oilseed crop) are accepted for oviposition but apparently do not support larval development (Holmes and Peterson 1962; Farstad 1944).

Many noncultivated grasses have been identified as suitable hosts for wheat stem sawfly larval development (Table 4). Many are economically important as forage for livestock. *Agropyron* and *Elymus* species are the most frequently used by wheat stem sawfly, likely owing to their robust stems (Ainslie 1920, Criddle 1917, Painter 1953). Morrill et al. (2000) found that host stem diameter is a major factor for female oviposition preference. Additionally, the phenology of many noncultivated grasses matches the needs of the developing larvae. Most have the C3 pathway of photosynthesis similar to wheat and are thus active early in the growing season. C3 grasses dominate, in terms of plant production, cooler regions of the Great Plains, which may have contributed to the relative abundance of this pest in Montana (Epstein et al. 1997). The genus *Agropyron* currently contains a total of 24 species of wheatgrasses (Watson and Dallwitz 1992), and many current and former members of this genus were most commonly cited as suitable hosts, summarized in Table 4.

Table 3. Cultivated species known to be infested by wheat stem sawfly, as reported by Wallace and McNeal (1966)

Species	Common name
Triticum aestivum ssp. *aestivum* L.	Common bread wheat
Triticum carthlicum Neveski	Persian wheat
Triticum monococcum L.	Eikorn wheat
Triticum polonicum L.	Spelt wheat
Triticum durum	Durum wheat
Triticum timopheevii (Zhuk.) Zhuk	Timopheev wheat
Triticum aestivum ssp. *compactum* (Host) MacKey	Club wheat
Triticum dicoccum Schübl.	Emmer wheat
Triticum turanicum Jakubz.	Khorasan wheat
Secale cereale L.	Common rye
Hordeum vulgare L.	Common barley

Table 4. Noncultivated grass species cited as harboring wheat stem sawfly—species are listed by their most current nomenclature, followed by synonyms used in citations in parenthesis

Species	Cited by
Pascopyrum smithii (*Agropyron occidentale*; *Agropyron smithii*)[a]	(Ainslie 1920, 1929; Criddle 1917; Davis 1955; Painter 1953; Table 1)
Elymus caninus (*Agropyron caninum*)	(Ainslie 1920, 1929; Perez-Mendoza et al. 2006)
Elymus trachycaulus[b] (*Agropyron trachycaulum*)	(Davis 1955, Post 1945, Wallace and McNeal 1966; Table 1)
Elymus trachycaulus (*Agropyron tenerum*)	(Ainslie 1920, 1929; Table 1)
Elymus caninus (*Agropyron richardsoni*)	(Ainslie 1920, 1929)
Elymus repens (*Agropyron repens*)	(Ainslie 1920, 1929; Luginbill and McNeal 1954; Morrill and Kushnak 1996; Morrill et al. 1998; Wallace and McNeal 1966)
Thinpyrum intermedium (*Agropyron intermedium*)	(Davis 1955, Wallace and McNeal 1966; Table 1)
Agropyron cristatum	(Farstad 1940, Wallace and McNeal 1966; Table 1)
Thinopyrum ponticum (*Agropyron elongatum*)[c]	(Farstad 1940, Wallace and McNeal 1966)
Elymus albicans (Agropyron griffithsii)	(Farstad 1940)
Bromus inermis[d]	(Ainslie 1920, 1929; Criddle 1924; Luginbill and McNeal 1954; Wallace and McNeal 1966; Table 1)
Bromus tectorum	(Perez-Mendoza et al. 2006; Table 1)
Bromus arvensis	(Table 1)
Elymus canadensis	(Ainslie 1920, 1929)
Leymus cinereus (*Elymus cinereus*)	(Youtie and Johnson 1988; Table 1)
Elymus dahuricus	(Farstad 1940)
Calamovilfa longifoli	(Davis 1955; Table 1)
Elyhordeum montanense (*Hordeum montanense*)	(Wallace and McNeal 1966)
Hordeum jubatum	(Wallace and McNeal 1966)
Festuca idahoensis	(Table 1)
Koeleria macrantha	(Table 1)
Phleum pretense[e]	(Ainslie 1920, 1929; Farstad 1940)
Poa compressa	(Table 1)
Poa pranesis	(Table 1)
Poa secunda	(Table 1)
Psuedoroegneria spicata	(Table 1)
Hesperostipa comata (*Stipa comata*)	(Table 1)
Nassella viridula (*Stipa viridula*)[f]	(Farstad 1940; Table 1)
Calamagrostis spp.	(Ainslie 1920, 1929)
Deschampsia sp.	(Ainslie 1920, 1929)

[a] Found infested in good growing conditions.
[b] Found with high rate of parasitism.
[c] Solidness of stem is often deleterious to larvae.
[d] Found with high rate of parasitism by Criddle (1917).
[e] Found to have high larvae mortality by Farstad (1940).
[f] Found to have little to no lodging owing to cutting because of solid stems by Farstad (1940).

Additional, but unspecified, *Agropyron* species are also likely hosts (Ainslie 1920, 1929; Criddle 1917; Luginbill and McNeal 1954; Wallace and McNeal 1966). *Bromus* and *Elymus*, the latter commonly called wild rye or wild wheatgrasses, also have been cited as suitable hosts for wheat stem sawfly; however, the prevalence of infestation is less than that of *Agropyron* (Ainslie 1920; Table 4). Other grasses have been associated with wheat stem sawfly adults or larvae but have not been confirmed as important hosts.

This host list is a resource for future research on the ecology of wheat stem sawfly and how it interacts with its native and introduced hosts and parasites. Additionally, there is unexplored genetic diversity within the species listed here, which could further our understanding of the genetic basis for resistance to this pest in crops. Grasslands provide an ideal laboratory to study potential resistance, as the native grasses that occur within them have coevolved with the wheat stem sawfly for much longer than the century it has been considered a pest on wheat. Although stem solidness is often shown to confer resistance in wheat, most of the grass hosts mentioned above have hollow stems yet tend to show higher rates of resistance than wheat. This may be owing to the often variable environmental conditions common to grasslands (i.e., soil moisture deficit, high or plant diversity, etc.) rather than heritable resistance. By investigating how these species interact with the wheat stem sawfly, we may be able to determine other plant traits conferring resistance that might also occur in wheat.

Montana Survey

In total, 19 grass species across 15 genera were found to contain *C. cinctus* larvae (instars not differentiated), indicating a very broad range of grass host species accepted by ovipositing *C. cinctus* females. Host use of a number of common species including *Bromus inermis*, *Elymus trachycaulus*, and *Thinopyrum intermedium* was ubiquitous, with larvae found within stems sampled at every site where the grass species occurred. Host use of the most common wheatgrass species, *Pascopyrum smithii* (which occurred at 30 of the sampled sites), was similarly high, with site occupancy at 96%. These patterns are consistent with the literature survey above, in which wheatgrass and brome species have been recorded to be highly suitable hosts (Table 4). On the contrary, a number of relatively common grasses had low occupancy by *C. cinctus* (*Bouteloua gracilis*: 9% occupancy; *Bromus arvensis*: 12% occupancy; *Koeleria macrantha*: 33% occupancy; Table 1), suggesting that they may be less preferred. These species tend to be smaller, both in terms of height and stem diameter, compared with the species with higher occupancy listed above. Additionally, the phenology of *B. gracilis*, a late-season C4 grass, may not have matched well with the active period of *C. cinctus*.

The few grass species collected in our survey in which *C. cinctus* larvae were not found (*Aristida purpurea*, *Deschampsia cespitosa*, *Elymus glaucus*, *Sporobolus heterolepis*, and *Vulpia octoflora*) were relatively rarely encountered, such that limited sample sizes precluded any definitive conclusions regarding their lack of acceptance as hosts. One exception was *Hordeum jubatum*. No *C. cinctus* larvae were found in stems of this species despite the dissection of 450 stems collected across seven sites. Thus, although previous work suggests that this grass is within the *C. cinctus* host range (Table 4), our work suggests that it is not generally preferred.

The apparent preference of wheat stem sawfly for C3 grasses is of interest, especially considering predicted trends in climate change. The Great Plains are expected to experience increased temperatures as well as an increased frequency of drought (Intergovernmental Panel on Climate Change 2013). A warmer climate (increase of only 2 °C) will force C3 grasses to recede northward, reducing their dominance in a large portion of the Great Plains (Epstein et al. 1997). The influence of climate change on the abundance and phenology of C3 hosts for wheat stem sawfly may impact the ability of this pest to remain in natural populations. Although wheat stem sawfly populations are rapidly increasing to the south, it is possible that this pest's host range will also expand north to align with future noncultivated host species distributions.

Table 5. Wheat stem sawfly infestation (mean number ± SE of wheat stem sawfly per 50 stems) on wheat and downy brome in northeastern Colorado in 2013 and 2014

Year	Wheat crop			Downy brome		
	Mean ± SE	*t*-test	*P*-value	Mean ± SE	*t*-test	*P*-value
2013	10.03 ± 0.41	24.38	0.0001	0.74 ± 0.38	1.93	0.0543
2014	11.04 ± 0.46	24.01	0.0001	0.94 ± 0.43	2.18	0.0302

P-values indicate significant differences between sites for each species.

Colorado Survey

Overall, wheat stem sawfly infestation rates were higher in wheat than in downy brome across all sites over the 2 yr of survey. Wheat fields had 13.5 and 11.8 times more wheat stem sawfly than downy brome in 2013 and 2014, respectively (Table 5).

Collection date was not correlated with wheat stem sawfly infestation in the 2 yr of the survey. However, wheat stem sawfly infestation rates differed significantly across study sites in both years of the survey (2013: $F_{16,\ 231} = 51.614$, $P < 0.0001$; 2014: $F_{16,\ 227} = 66.101$, $P < 0.0001$). Merten1 had the highest level of wheat stem sawfly infestation among all wheat fields in 2013, while Wickstrom1 had the highest infestation on wheat in 2014. Downy brome had the highest wheat stem sawfly infestation at Wickstrom3 in 2013, while Merten4 had the highest infestation in 2014.

Larval mortality varied significantly as a function of host plant species and collection site in 2013 ($F_{1,\ 246} = 247.872$, $P < 0.0001$ and $F_{14,233} = 167.086$, $P < 0.0001$, respectively). In 2014, host plant affected larval mortality ($F_{1,\ 242} = 267.064$, $P < 0.0001$), with an overall decrease from 2013 to 2014. In 2014, collection site was significant in relation to larval mortality ($F_{1,\ 242} = 267.064$, $P < 0.0001$) Mean mortality of overwintering wheat stem sawfly in downy brome was higher than in winter wheat across dates in 2013 and 2014, suggesting wheat to be a more suitable host than downy brome (Fig. 1).

Host plant species had a minor effect on the number of adults collected by sweep sampling during May of 2013 ($F_{1,13} = 8.1965$, $P = 0.01$) and 2014 ($F_{1,13} = 4.1715$, $P = 0.06$). The number of adults collected during the early season sweep was 4.9–5.2 times higher in the wheat fields compared with the downy brome locations in 2013 and 2014 (Fig. 2). The mean numbers of adults collected in the flight period of the 2 yr were not significantly different: $F_{1,26} = 1.39$, $P = 0.25$.

Across both years, adult abundance and larval numbers were generally higher on winter wheat than on downy brome. Additionally, the adults collected from winter wheat in May during emergence were approximately five times more abundant than wheat stem sawfly adults collected from downy brome. Nevertheless, wheat stem sawfly still use downy brome as an alternate host. The clear differences in host preference seen in this 2-yr survey suggest that there are plant traits and characteristics of downy brome yet to be investigated that may reduce wheat stem sawfly success or preference for egg laying. The quality and availability (i.e., proximity to newly emerged adult wheat stem sawfly) of downy brome were likely important cues in female preference and host selection. Wheat stem sawfly preferred to lay more eggs on downy brome plants that were taller and had thicker stems. Furthermore, downy brome plants located in sites with higher soil moisture were more likely to be attacked.

Perez-Mendoza et al. (2006) reported higher infestation by the wheat stem sawfly on downy brome than on spring wheat in

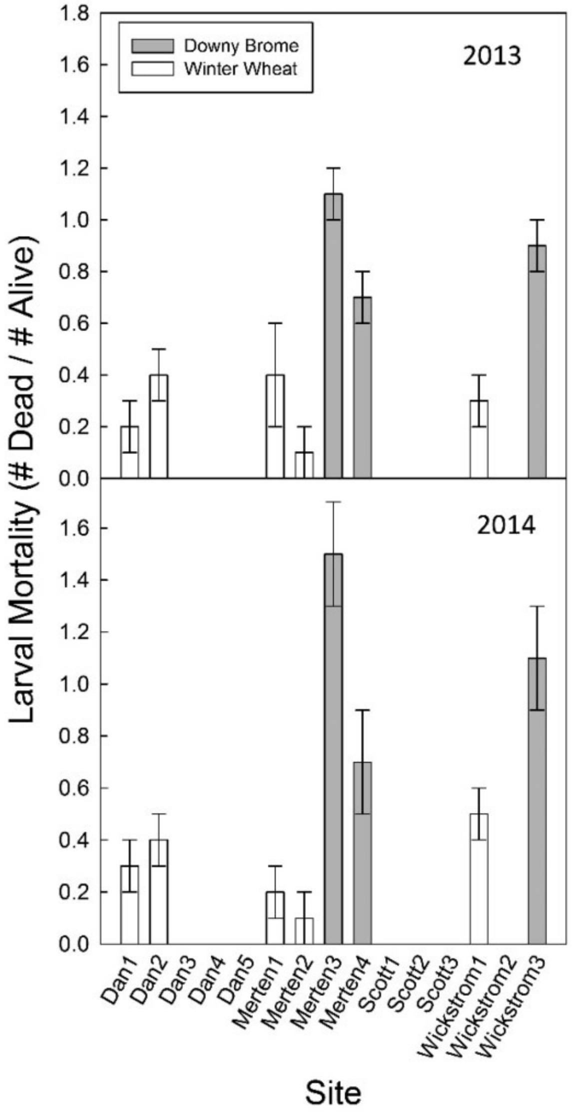

Fig. 1. Mean of wheat stem sawfly larval mortality in winter wheat and downy brome across northeastern Colorado sites in 2013 and 2014.

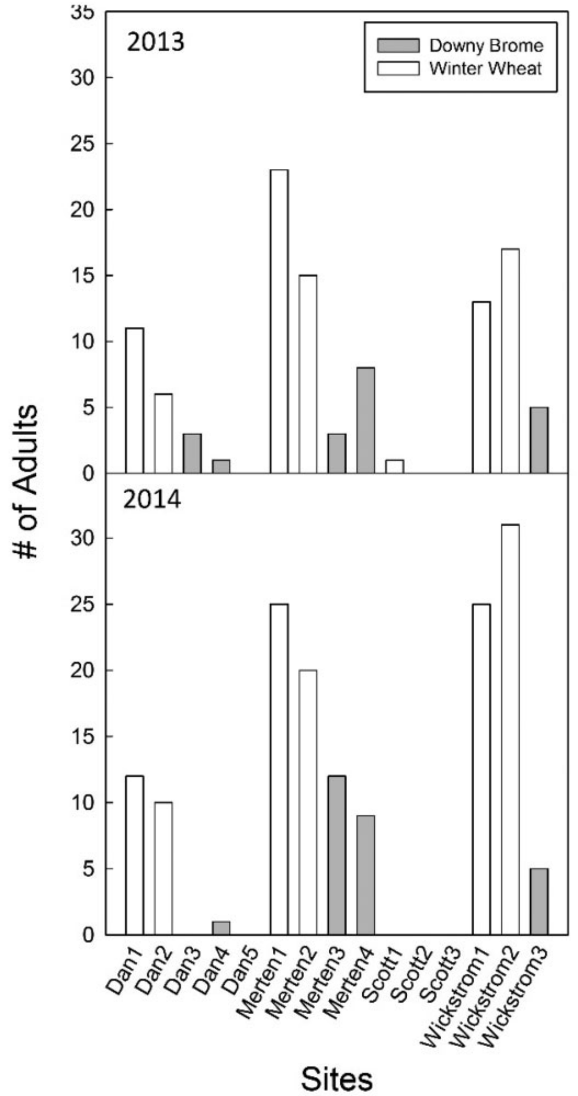

Fig. 2. Mean number of wheat stem sawfly adults on winter wheat and downy brome across sites in May of 2013 and 2014.

Montana, though to a lesser degree (twofold difference vs. 11.8–13.5× greater infestation). They also found a significant correlation between stem height and diameter of downy brome and wheat stem sawfly oviposition preference. Results from Perez-Mendoza et al. (2006) show a comparison of tall and sparse downy brome plants with shorter spring wheat, while in this system, the downy brome was short and thin-stemmed, making the two systems only distantly comparable. It is also possible that the differences in infestation rates seen between our survey and that of Perez-Mendoza et al. (2006) are the result of facilitation of wheat infestation by downy brome when growing in proximity to winter wheat. Perez-Mendoza et al. (2006) surveyed fields with co-occurring spring wheat and downy brome, while data presented here are from surveys in which each species was geographically isolated from the another. There is clearly an ecological interaction between downy brome, winter wheat, and *C. cinctus* that warrants further research, especially because co-occurrence seems to reduce infestation in downy brome and may facilitate infestation in wheat. Perez-Mendoza et al. (2006) also report higher larval survivorship in wheat than in downy brome. Furthermore, larvae that developed in wheat were heavier than those in downy brome. Similarly, our results suggest that larvae of the wheat stem sawfly may survive in downy brome stems but suffer much higher rates of mortality relative to winter wheat. Wheat stems are larger than those of most grass species, particularly in drought seasons, whereas stems of noncultivated species may be too small to support larval development (Morrill et al. 2000). The higher larval mortality rates seen in downy brome may also be owing to higher parasitism rates, although parasitism was not quantified in this study. Although downy brome is considered a weed in wheat fields and may even facilitate *C. cinctus* infestation in wheat (Perez-Mendoza et al. 2006), high mortality in downy brome may lower the relative success of wheat stem sawfly in wheat fields over multiple growing seasons.

The intensive survey described here comparing downy brome infestation with that in wheat can be used as a framework for pursuing many of these questions in noncultivated grasses. It is clear that there are differences in *C. cinctus* host preference. A suite of plant traits in noncultivated grasses potentially alter host preference or confer resistance to *C. cinctus*. Here, we show that the presence of all growth stages of *C. cinctus* is reduced and mortality rates are higher in downy brome compared with nearby winter wheat plants. This is a highly valuable information, especially if the plant traits and ecological adaptations that are responsible for these observations have a genetic basis capable of being bred into wheat cultivars.

Future Research

Our list of host plant species (both from literature reviews and the Montana survey) may be used as a reference for future research on wheat stem sawfly infestation in noncultivated grasses. The Colorado survey indicates that there are clear differences between infestation in wheat and noncultivated grasses, the mechanisms for which need to be investigated. We recognize several avenues of future research involving noncultivated plant hosts of *C. cinctus*, including plant traits and parasitism variability.

There are several traits in addition to stem height and diameter that should be investigated in the grass species listed here. For example, heading date has been correlated to wheat stem sawfly resistance in bread wheat and a quantitative trait loci describing its variability has been found (Varella et al. 2015). Late-season heading reduces *C. cinctus* infestation by altering stem characteristic during the oviposition period of wheat stem sawfly (Varella et al. 2015). The high diversity of flowering phenology observed in noncultivated grasses provides an excellent opportunity to study how heading date may confer resistance in a diversity of species (Sherry et al. 2007). Maturity date has been shown to affect parasitism levels, such that lower parasitism occurs when wheat ripens earlier in the season (Holmes et al. 1963, Runyon et al. 2002). Multitrophic responses have been shown involving spring wheat, downy brome, and wheat stem sawfly, where infestation levels in wheat decreased as the density of downy brome increased (Keren et al. 2015). This interaction further exemplifies that wheat stem sawfly host preference may be tied closely to the local agroecosystem. Plant phenology and its interaction with environmental conditions, such as temperature and soil moisture, may play an important role in the success of wheat stem sawfly and its parasitoids (Holmes et al. 1963). By studying grassland communities while monitoring environmental variability, there is the potential to gather insight into how plant characteristics influence wheat stem sawfly egg-laying preference. For instance, volatile compounds have been shown to influence female wheat stem sawfly flight behavior and preference for egg-laying (Piesik et al. 2008, Weaver et al. 2009). A better understanding of plant volatile chemistry in noncultivated grasses and how this might influence wheat stem sawfly behavior among native hosts may be useful for wheat breeders especially if the genetic basis for volatile production can be determined.

The high degree of parasitism of the wheat stem sawfly seen in noncultivated grasses is of clear importance. Large-scale surveys reveal that parasitism levels in wheat can reach high levels, but are spatially variable across its range (mean parasitism = 20%; range 0–88%; Rand et al. 2014). Although high parasitism levels can occur in wheat, they tend to be lower than in many noncultivated native grasses where parasitism can reach 100% (Criddle 1922; reviewed in Morrill et al. 1998), warranting further research into the ecology of these parasitoids in noncultivated grasses. This is partially owing to the fact that only two species of *Bracon* have successfully parasitized the wheat stem sawfly in wheat (Morrill et al. 1998), but more likely owing to *Bracon cephi*'s second generation being disturbed by wheat harvest (Nelson and Farstad 1953, Holmes et al. 1963). The potential diversity of stem morphology among the noncultivated grasses mentioned here provides an excellent opportunity to search for relationships between the degree of parasitism and stem characteristics. It is well known that parasitoids have low survivorship in plants with solid stems (Holmes and Peterson 1962, Rand et al. 2012), yet there are likely other plant characteristics that impact parasitoid performance.

Lastly, an understanding of wheat stem sawfly infestation in noncultivated grasses is potentially important for rangeland managers concerned about grazing potential of their managed lands. Wheat stem sawfly infestation of basin wild rye in Idaho has the potential to reduce seed yield (as it does in wheat), but has little to no impact on forage production that would be used by livestock (Youtie and Johnson 1988). This suggests that rangeland managers have little to worry about in terms of wheat stem sawfly reducing yield in tallgrass prairies where >99% of established tillers originate from belowground bud banks and not seeds (Benson and Hartnett 2006). In rangelands where seed banks are of higher economic importance, the role of *C. cinctus* as a pest should be addressed.

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