OXFORD

Plant Resistance

Characterization of Resistance to *Cephus cinctus* (Hymenoptera: Cephidae) in Barley Germplasm

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Abstract

Most barley cultivars have some degree of resistance to the wheat stem sawfly (WSS), *Cephus cinctus* Norton (Hymenoptera: Cephidae). Damage caused by WSS is currently observed in fields of barley grown in the Northern Great Plains, but the impact of WSS damage among cultivars due to genetic differences within the barley germplasm is not known. Specifically, little is known about the mechanisms underlying WSS resistance in barley. We characterized WSS resistance in a subset of the spring barley CAP (Coordinated Agricultural Project) germplasm panel containing 193 current and historically important breeding lines from six North American breeding programs. Panel lines were grown in WSS infested fields for two consecutive years. Lines were characterized for stem solidness, stem cutting, WSS infestation (antixenosis), larval mortality (antibiosis), and parasitism (indirect plant defense). Variation in resistance to WSS in barley was compared to observations made for solid-stemmed resistant and hollow-stemmed susceptible wheat lines. Results indicate that both antibiosis and antixenosis are involved in the resistance of barley to the WSS, but antibiosis seems to be more prevalent. Almost all of the barley lines had greater larval mortality than the hollow-stemmed wheat lines, and only a few barley lines had mortality as low as that observed in the solid-stemmed wheat line. Since barley lines lack solid stems, it is apparent that barley has a different form of antibiosis. Our results provide information for use of barley in rotation to control the WSS and may provide a basis for identification of new approaches for improving WSS resistance in wheat.

Key words: antibiosis, antixenosis, indirect plant defense, wheat stem sawfly

The wheat stem sawfly (WSS), *Cephus cinctus* Norton (Hymenoptera: Cephidae), is an economically important pest of cereal crops in the Northern Great Plains of the United States and southern parts of the Canadian Prairie Provinces (Beres et al. 2011). In the recent years, damaging populations of the WSS have also been reported in Wyoming, Nebraska and Colorado (Lesiuer et al. 2016). The stem-mining larva chews the stem of the host, obstructing the translocation of minerals and reducing photosynthetic rate (Macedo et al. 2005, Delaney et al. 2010). Additionally, once the plant becomes physiologically mature, the WSS larva moves to the base of the plant and makes a v-shaped groove by chewing around the interior of the stem. Cut stems lodge with a gentle breeze or gravity and are difficult to harvest (Beres et al. 2011).

Numerous control strategies have been implemented in an attempt to mitigate WSS-related losses. Insecticides have shown minimal efficacy (Knodel et al. 2009). Cultural control in the form of adjusted seeding date, deep and shallow ploughing, swathing, trap cropping, altered row spacing, and altered sowing densities have resulted in limited control (Beres et al. 2011). Biological control has shown potential to reduce WSS populations (Weaver et al. 2004, Peterson et al. 2011), but parasitism rates have so far been inconsistent across years and locations (Weaver et al. 2005, Peterson et al. 2011, Buteler et al. 2015) . Host plant resistance in the form of solid-stemmed wheat cultivars has been the most successful control strategy used against this insect pest (Beres et al. 2009, 2013). However, stem solidness expression is adversely affected by environmental conditions during stem elongation, which causes otherwise solid stems to become hollow (Platt et al. 1941, Holmes et al. 1959, Beres et al. 2017). Thus, to this date, no single control method has been demonstrated to consistently and reliably reduce WSS-related losses.

Despite the high susceptibility of spring and winter wheat to WSS damage, other species of the grass tribe Triticeae have been reported to be significantly more resistant to this insect pest. Barley, for instance,

has been shown to have average stem cutting less than 10% (Criddle 1923, Farstad and Platt 1946), with cutting never exceeding 30% in the most susceptible variety in field trials evaluated over a number of sites and years. In wheat, stem cutting can be as high as 95% in highly infested fields (Wallace and McNeal, 1966). Although barley is predominantly resistant to the WSS, mechanisms or genes underlying WSS resistance in barley have not been identified and the last report on WSS stem cutting in barley was more than 70 yr ago (Farstad and Platt 1946). The phylogeography of WSS populations confirms that diverse populations in Montana are able to cut both winter and spring wheat, as well as native grasses, while adaptation of this native species to wheat elsewhere is to either winter or spring wheat (Lesiuer et al. 2016). Therefore, barley grown in Montana may be more susceptible to WSS given the potential for adaptation within the diverse populations, as has already occurred for both spring and winter wheat (Morrill and Kushnak 1996). Exploitation of the barley gene pool could result in the identification of new alleles for WSS resistance. Transfer of useful alleles to wheat from related species through the development of wheat-alien translocations has been shown to be successful for disease resistance breeding (Friebe et al. 1996, Oliver et al. 2005, Hurni et al. 2013), thus there might be potential for improving WSS resistance in wheat using the genetic diversity present in barley germplasm. A prior requirement for this strategy to succeed is to build up knowledge on sources and mechanisms of resistance in barley. This relies on variation in susceptibility in barley germplasm and requires populations of WSS that can damage barley in the field at levels greater than historically reported (Farstad and Platt 1946), for which we provide evidence. In addition, knowledge of levels of resistance in crops other than wheat may allow development of rotations that diversify the mechanisms of WSS mortality that are deployed in grower fields.

This research was conducted primarily to assess types of resistance to WSS present in current and historically important barley lines from North America and was driven by an increase in the level of damage in barley fields in the last decade. This allows for comparison of antibiosis, antixenosis, and indirect plant defense due to braconid parasitoids for WSS in barley to the same categories of resistance in solid-stemmed resistant and hollow-stemmed susceptible wheat lines. Identification of phenotypic variation for WSS resistance in barley provides the possibility of determining the underlying genetic basis for WSS in barley through quantitative trait loci (QTL) mapping approaches. In addition, we report on recent levels of WSS damage in Montana barley fields. The use of barley in crop rotations to control WSS and a potential new approach for improving WSS resistance in wheat are discussed.

Material and Methods

Damage in Barley and Wheat Fields

Infrequent rotations to barley by wheat growers provided an opportunity to obtain data on the level of susceptibility of barley to WSS. Samples were taken from seven pairs of barley and wheat fields from Fergus, Gallatin, Glacier, Liberty, and Pondera counties (Montana) in 2005, 2007, 2008, 2009, 2011, 2016, and 2017. Harvest samples were randomly collected using a 6 by 6 grid layout for a total of 36 samples. The distance between two adjacent samples was 35 m. Each sample was 30 cm of row that was dissected to record infestation, survival to stem cutting, and levels of parasitism by *Bracon cephi* Gahan and *B. lissogaster* (Muesebeck) (Hymenoptera: Braconidae). Data on WSS survival to stem cutting were corrected for parasitism of the late-instar larvae by the two species of braconids (Sherman et al. 2010, Talbert et al. 2014)

Barley Germplasm

The two-row spring barley germplasm used in this study consisted of 193 elite breeding lines and cultivars from North American breeding programs of Busch Agricultural Resources Inc. (*n* = 25), Minnesota (*n* = 1), Montana (*n* = 51), North Dakota (*n* = 44), Idaho (*n* = 24), Washington (*n* = 41), and the CAP (Coordinated Agricultural Project) core (*n* = 7) previously described in Blake et al. (2012) (Supp. Table 1 [online only]). This panel is a subset of the spring barley CAP germplasm panel recently exploited for genomic selection of multiple agronomic traits (Pauli et al. 2014). Pedigree information and agronomic data from panel lines are available online at The Triticeae Toolbox (T3) Barley (https://triticeaetoolbox.org/barley/ [verified 3 April. 2017]).

Phenotypic Evaluation

Panel lines were planted in late April of 2015 and 2016 in the midst of stubble from a previous WSS-infested wheat crop, at a site with a history of WSS infestation located near Amsterdam, MT. Plots consisted of 10 seeds per entry planted in individual hills with spacing of 0.8 m between adjacent hills. Trials were conducted using an augmented design in which entries were unreplicated and checks were replicated four times (Wolfinger et al. 1997). Check entries included the barley lines 'Craft' (PI646158), 'Conrad', 'Hockett', and 'Harrington', and the spring wheat lines 'McNeal' (PI574642) (WSS susceptible) and 'Choteau' (PI633974) (WSS resistant). At maturity, plots were visually evaluated for percent cut stems and scored for stem solidness using a 1 (completely hollow) to 5 (completely solid) scale, as described by Varella et al. (2016). Afterward, plots were collected and dissected to determine WSS infestation, larval mortality (due to host plant resistance), and parasitism.

Statistical Analysis

Preliminary data on WSS damage in barley and paired wheat fields were analyzed for significance using a *t*-test. Check lines in the barley panel were subjected to least-square mean comparisons for traits associated with WSS resistance using PROC GLM in SAS version 9.3 (SAS Institute 2012). Results from the augmented design experiment were analyzed using PROC MIXED in SAS version 9.3 (SAS Institute 2012). The blocks and entries were considered random effects. Best linear unbiased predictors (BLUPs) were obtained for all entries in each year. An analysis of variance (ANOVA) was combined over years using the BLUP values for the entries from each year. ANOVA was also used to compare panel lines to the WSS susceptible check McNeal.

Results

Damage in Barley and Wheat Fields

Samples of barley and wheat were both infested in grower fields. Wheat stem sawfly infestation in barley was often significantly (*P* < 0.05) lower than in wheat (years 2005, 2007, 2008, 2009, 2011, and 2017), although similar levels of WSS infestation were observed in 2016 (Fig. 1). Mean WSS infestation in barley reached the highest values in 2017, when 55.8% of stems were infested and 27.92% were cut by mature larvae (Fig. 1). Wheat stem sawfly mortality was greater (*P* < 0.05) in barley in 2009 and 2011, and greater (*P* < 0.05) in wheat in 2008 (Fig. 1).

Phenotypic Variation for Traits Associated with WSS Resistance

Significant (*P* < 0.05) variation for traits associated with WSS resistance was observed among lines used as checks on the barley panel
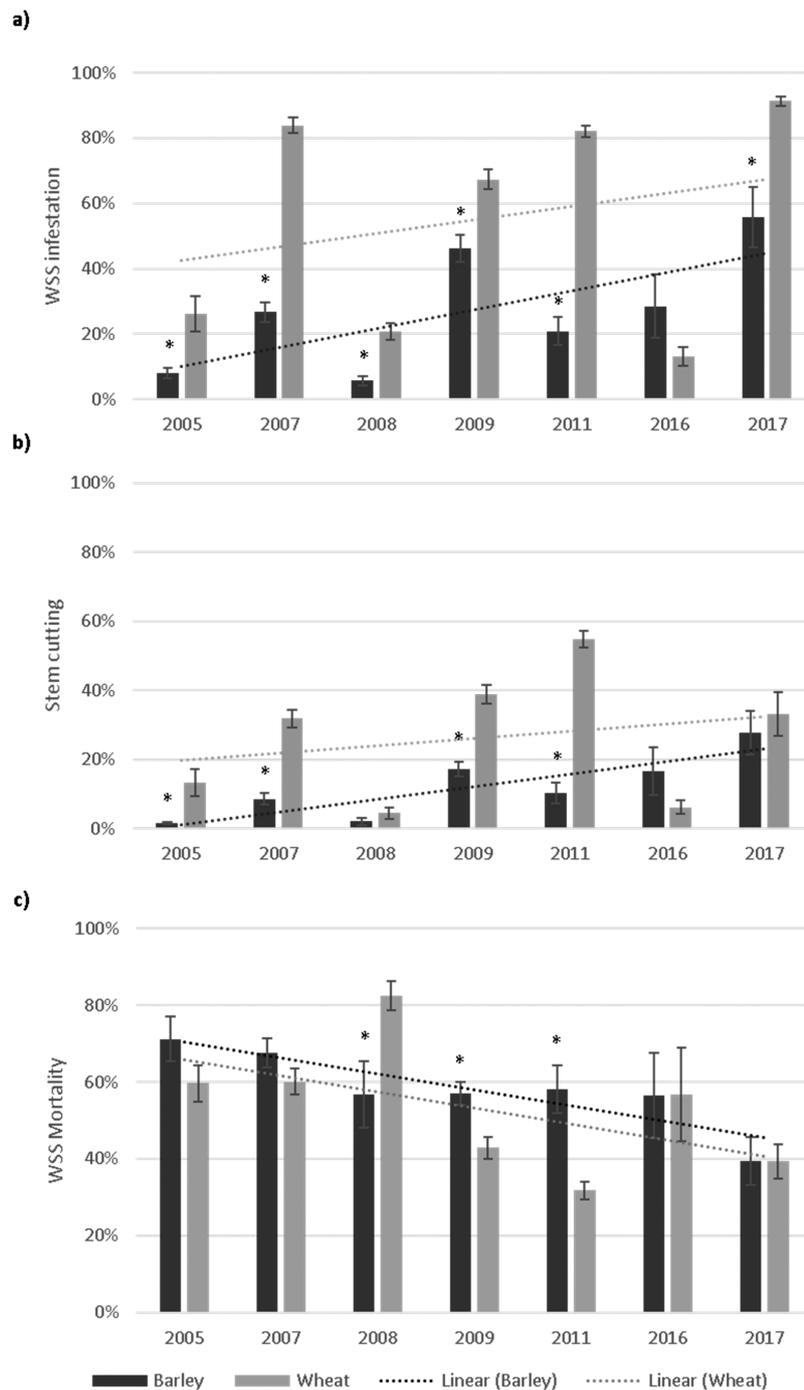
Fig. 1. Damage in barley and paired wheat fields. (a) Wheat stem sawfly infestation (Mean ± SE), (b) stem cutting (Mean ± SE), and (c) WSS mortality (Mean ± SE). Asterisks above error bars indicate significant differences ($P < 0.05$) between paired fields of barley and wheat according to *t*-test (LSD).

(Table 1). Barley checks had hollow stems comparable to the wheat check McNeal, while Choteau displayed solid stems (Table 1). In 2015, ambient WSS pressure was low and mean infestation among checks ranged from 3 to 16%; in 2016, natural infestation rates were above 25% (Table 1). Parasitism rates followed the trends in WSS infestation, with higher values in 2016 (Table 1). The main species of parasitoids found were *B. cephi* and *B. lissogaster* (data not shown).

There was significant differences among the six check lines for infestation in 2015 (Table 1). The two wheat lines and Hockett barley did not differ significantly for percent infestation ($P > 0.05$). Harrington barley had less infestation than the other five lines

($P < 0.05$). No differences in percentage infestation were observed in 2016 ($P > 0.05$). There were significant differences in WSS mortality in both years (Table 1). Mortality in Hockett did not differ significantly from the wheat varieties in 2015 ($P > 0.05$) and was similar to solid stem Choteau in 2016 ($P > 0.05$). Hollow-stemmed McNeal wheat showed reduced levels of WSS mortality compared to Choteau and all barley lines in 2016 ($P < 0.05$). Hockett did not differ significantly for stem cutting relative to McNeal or Choteau in 2015 ($P > 0.05$) and had greater stem cutting than the other barley lines ($P < 0.05$). Stem cutting was greater in McNeal than either Hockett or Choteau in 2016 ($P < 0.05$). Harrington was in the highest group

for WSS mortality and the lowest group for stem cutting based on least significant difference (*P* = 0.05) in both years.

Significant variance was observed for stem solidness, WSS infestation, and heading date among the 193 barley lines (Table 2). Significant variation was also observed between the 2015 and 2016 field seasons for all traits evaluated (Table 2). Stem solidness ranged from 1.15 to 2.54 in 2015 and from 1.00 to 1.10 in 2016 (Table 3). Despite a wider range of variation in 2015, the mean values for stem solidness for that field season was 1.16, indicating that the majority of the lines had stems that were completely hollow (Table 3). In fact, barley lines with stem solidness scores greater than 1 were still within the range that is considered hollow (solid stem score below 3). The range of WSS infestation was from 3.58 to 29.22% in 2015 and from 0 to 74.15% in 2016 (Table 3). Most barley lines had reduced parasitism rates relative to the wheat checks. Exceptions were '08MT-36' (synonym MT080170), from Montana State University, '08BA-25' (synonym Z203U001V), from Busch Agricultural Resources Inc., and '09N2-69' (synonym 2ND27678), from North Dakota, that had more than 69% parasitism in at least 1 yr of experiments (data not shown). Parasitism was not correlated with WSS infestation in either 2015 (cor = 0.03, *P* = 0.54) or 2016 (cor = 0.13, *P* = 0.07) field seasons. Indeed, the three barley lines that had high levels of parasitism had intermediate levels (>13 and <47%) of WSS infestation. Mean values for WSS larval mortality in barley were high (>80%) in both field seasons, while mean values for stem cutting were low (<3%) (Table 3).

Barley panel lines headed within a 10 day period in both field seasons (Table 3).

Figure 2 shows the distribution of barley panel lines for traits associated with WSS resistance (mean values across seasons). The values for the two wheat checks, McNeal and Choteau, and two barley checks, Craft and Hockett, are indicated in the distribution. The overall range of variation for WSS infestation in barley is wide, with the wheat checks falling in the middle of the distribution (Fig. 2a). Values for WSS larval mortality in the barley panel is skewed toward higher values, while wheat checks McNeal and Choteau show low and intermediate levels of mortality, respectively (Fig. 2b). When panel lines were compared to the WSS susceptible wheat check McNeal, '07BA-52' (synonym 2B04-0080) from Busch Agricultural Resources Inc. was the only line shown to be significantly more infested than McNeal (*t* = 2.03, df = 203, *P* = 0.0435), and '06WA-29' (synonym 04WA-114.16) from Washington State University was the only line shown to have similar WSS mortality as McNeal (*t* = 1.74, df = 202, *P* = 0.0836). All other panel lines showed more (*P* < 0.05) WSS mortality than McNeal. Overall, panel lines exhibited a narrow range of variation for both WSS parasitism and stem cutting, with McNeal lying at the higher edge of both distributions (Fig. 2c and d). About half of the lines showed less (*P* < 0.05) WSS parasitism than McNeal and most barley lines had values for stem cutting comparable to Choteau, the solid-stemmed WSS resistant variety (Fig. 2d). In fact, all panel lines showed less (*P* < 0.05) stem cutting than the WSS susceptible check, McNeal.

Table 1. Mean ± SE for wheat stem sawfly parameters on barley and wheat lines used as checks in the barley panel. Trials were conducted in Amsterdam, MT in 2015 and 2016 with four replication in each year

Check IDs	Plant species	Stem solidness[a]	WSS infestation (%)	WSS parasitism (%)	WSS mortality (%)	Stem cut (%)	Heading date
2015 Field season							
Craft	Barley	1.07 ± 0.03b	5.81 ± 1.54bcd	0.00 ± 0.00a	87.50 ± 12.50ab	0.00 ± 0.00c	182.25 ± 0.95bc
Conrad	Barley	1.02 ± 0.02b	3.47 ± 2.44cd	0.00 ± 0.00a	96.67 ± 2.36a	0.00 ± 0.00c	185.00 ± 0.71a
Hockett	Barley	1.22 ± 0.10b	12.87 ± 2.41ab	0.00 ± 0.00a	73.96 ± 8.74abc	8.00 ± 3.39ab	180.25 ± 1.11c
Harrington	Barley	1.00 ± 0.00b	1.13 ± 0.69d	0.00 ± 0.00a	100.00 ± 0.00a	1.25 ± 1.25c	184.25 ± 0.75ab
Choteau	Wheat	2.57 ± 0.64a	16.20 ± 5.55a	16.67 ± 16.67a	61.31 ± 6.21c	3.33 ± 1.67bc	182.33 ± 1.33ab
McNeal	Wheat	1.61 ± 0.16b	11.80 ± 4.14abc	0.00 ± 0.00a	54.55 ± 5.97c	12.50 ± 2.50a	183.50 ± 0.87ab
2016 Field season							
Craft	Barley	1.02 ± 0.02b	26.76 ± 7.13a	4.38 ± 2.38c	95.11 ± 2.10a	1.00 ± 0.58c	181.00 ± 0.58ab
Conrad	Barley	1.00 ± 0.00b	33.98 ± 7.29a	3.72 ± 3.72c	86.40 ± 5.36a	2.50 ± 1.44bc	178.75 ± 1.65b
Hockett	Barley	1.00 ± 0.00b	48.89 ± 10.33a	43.36 ± 14.67ab	51.43 ± 10.31b	13.75 ± 3.75b	180.25 ± 0.85b
Harrington	Barley	1.00 ± 0.00b	30.30 ± 4.36a	2.09 ± 1.22c	94.48 ± 2.25a	1.00 ± 0.58c	183.75 ± 1.03a
Choteau	Wheat	3.03 ± 0.24a	43.13 ± 12.15a	26.44 ± 14.19bc	40.14 ± 4.52b	4.25 ± 0.75bc	183.25 ± 0.48a
McNeal	Wheat	1.34 ± 0.22b	39.43 ± 7.64a	60.76 ± 21.58a	15.63 ± 8.17c	27.50 ± 8.54a	183.75 ± 0.48a

Mean values with different letters are significantly different (*P* < 0.05) according to *t*-test (LSD).

[a]Potential values range from 1.00 (hollow stem) to 5.00 (solid stem).

Table 2. P-values from analysis of variance (ANOVA) for traits associated with wheat stem sawfly resistance in the barley panel with 193 lines grown in Amsterdam, MT in 2015 and 2016. There were two replications per line.

Traits	Lines		Field season	
	F-value	*P*-values	*F*-value	*P*-values
Stem solidness	1.29	0.03	76.05	<.0001
WSS infestation (%)	1.39	0.007	699.04	<.0001
WSS parasitism (%)	0.91	0.76	122.03	<.0001
WSS mortality (%)	0.93	0.69	85.81	<.0001
Stem cut (%)	1.04	0.37	16.05	<.0001
Heading date	4.72	<.0001	29.98	<.0001

Table 3. Range, mean, standard deviation, and coefficient of variance for traits associated with wheat stem sawfly resistance in the barley panel grown in Amsterdam, MT in 2015 and 2016. There were two replications per line.

Traits	Range	Mean	SD	Coefficient of variation
2015 Field season				
Stem solidness	1.15–2.54[a]	1.16	0.31	0.27
WSS infestation (%)	3.58–29.22[b]	8.63	4.00	0.46
WSS parasitism (%)	0.00–14.28[b]	0.11	1.20	10.90
WSS mortality (%)	33.33–100.00[b]	90.67	14.39	0.16
Stem cut (%)	0.00–25.00[b]	1.11	3.09	2.78
Heading date	175.10–185.49	180.82	2.64	0.01
2016 Field season				
Stem solidness	1.00–1.10[a]	1.00	0.01	0.01
WSS infestation (%)	0.00–74.15[b]	37.03	16.48	0.44
WSS parasitism (%)	0.00–77.77[b]	13.25	16.50	1.24
WSS mortality (%)	63.81–87.57[b]	80.60	4.60	0.06
Stem cut (%)	0.00–40.00[b]	2.69	4.92	1.83
Heading date	174.78–184.65	180.07	2.10	0.01

[a]Potential values range from 1.00 (hollow stem) to 5.00 (solid stem).

[b]Potential values range from 0.00 to 100.00.
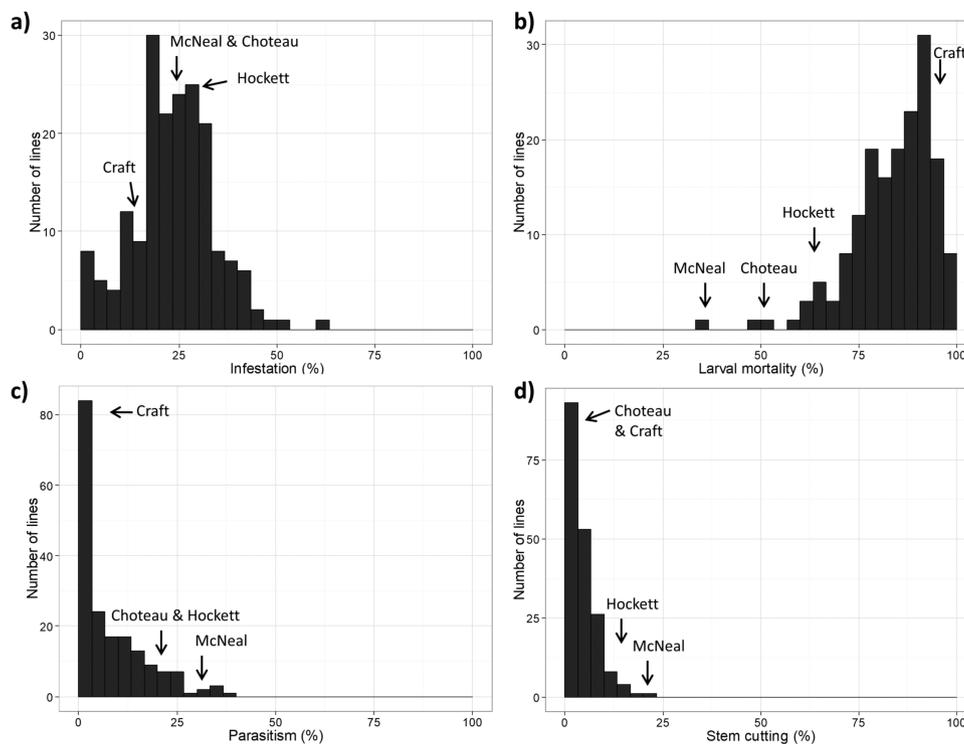
Fig. 2. Distribution of barley lines and wheat checks for (a) wheat stem sawfly infestation, (b) larval mortality, (c) parasitism, and (d) stem cutting (mean values across field seasons). Trials were conducted in Amsterdam, MT, in 2015 and 2016.

Discussion

Barley is often used in rotation with wheat due to its lower susceptibility to damage by the WSS. However, as shown by our preliminary assessment of ongoing WSS damage in paired wheat and barley fields, infestation and stem cutting due to WSS in barley may occur at levels sufficient to cause economic loss. One objective of this study was to determine the genetic variability for WSS resistance in a set of elite barley lines from North American breeding programs. A second objective was to determine types of resistance in barley, especially related to the use of barley as a rotational crop to control the WSS. Insights into the genetics of WSS resistance in barley may also help design strategies for enhancing resistance in wheat.

Both antibiosis as measured by larval mortality and antixenosis as measured by oviposition are involved in the resistance of barley to the WSS, but antibiosis seems to be prevalent (Table 1). These forms of resistance in cereals were first described as 'infestability' as a measure of host choice and acceptance, and 'resistance', which referred to mortality of immatures (Roberts 1954). In cereal crops such as wheat and durum, antibiosis to the WSS has been associated with the solid stem trait, which reduces egg and larval survival (Holmes and Peterson 1962, 1964; Wallace and McNeal 1966; Houshmand et al. 2003, 2007; Varella et al. 2016). Contrary to wheat and durum, antibiosis in barley is not associated with the solid stem trait.

The few susceptible barley lines identified in this study were found to have stem cutting ratings similar to those of resistant wheat lines. For instance, 07BA-52 had high levels of WSS infestation, with mean value across seasons of 60%. However, 94% of WSS larvae died inside the stem, which resulted in a stem cutting rate of only 3.4%. Similarly, lines that had lower larval mortality also had lower infestation rates and, consequently, reduced stem cutting. Thus, in barley lines, susceptibility to WSS infestation was counteracted by high larval mortality and vice versa. This suggests that antibiosis and antixenosis in barley have distinct physiological/genetic bases. This contrasts with the primary mechanism of WSS resistance known in wheat, the solid stem trait, in which a single gene may cause both antixenosis and antibiosis (Varella et al. 2017a).

An important factor to consider while evaluating WSS resistance under natural field infestation is plant heading date. Plants can only be used as a host during stem elongation period and before the emergence of the inflorescence (Holmes and Peterson 1960). Late heading plants may miss the short WSS flight period and thereby escape infestation. Although considerable variation for this trait was observed among barley lines, no correlation was detected between heading date and WSS infestation (cor = −0.051, $P = 0.49$, data not shown), indicating that antixenosis was not an artifact of plant growth stage during WSS flight. Besides plant growth stage, WSS preference for oviposition (infestation) in wheat has been associated with stem height and diameter (Buteler et al. 2009), stem solidness (Holmes and Peterson 1962, Varella et al. 2016), and volatile compounds primarily released by leaves (Weaver et al. 2009). It is likely that gravid females employ the same sensory and behavioral mechanisms to evaluate similar plant traits during host plant selection in barley.

Results shown here suggest that indirect plant defense via parasitoids also plays a role in barley defense against the WSS. Three barley lines had increased parasitism rates despite their intermediate level of WSS infestation. Similar results were recently observed in several wheat landrace accessions from different geographical regions of the world (Varella et al. 2017b). In wheat, WSS infestation is known to cause changes in the pattern of emitted volatiles. Synthetic volatiles matching those produced by WSS-infested plants were also shown to generate a positive behavioral and electrophysiological response from both *B. cephi* and *B. lissogaster* (Peck 2004, Perez 2009). In fact, braconid wasps are the most commonly reported parasitoids to be attracted by volatiles of plants under herbivore attack (Aljbory and Chen 2018). Nevertheless, to date, no genes have been associated with indirect plant defense against the WSS in either wheat or barley germplasm. Thus, the characterization of barley lines with increased parasitism rates may contribute to the identification of genes associated with indirect plant defense in grass species.

In areas of high WSS infestation, crops such as barley and durum (Criddle 1923), or even flax (Farstad 1942) have been recommended as an alternative to wheat because they can break the life cycle of the WSS in the absence of highly suitable hosts and reduce pest pressure in subsequent years (Beres et al. 2011). Our results show that variation of damage due to WSS in barley may be a result of WSS pressure and the suite of varieties being grown in any given area or year. This is true regardless of the broad end use categories of the barley lines. Overall, feed, food, forage, or malt barley lines were similarly infested and experienced similar levels of stem cutting (data not shown). However, Hockett has become a popular variety in Montana over the past few years (Montana Agricultural Statistics 2014) and is more susceptible to WSS damage than most other varieties, including Harrington, which has until recent years been the most widely grown malting barley in Montana. As a consequence, in areas with high WSS pressure, the use of Hockett as an alternative to wheat in crop rotation may not be beneficial. Indeed, the use of susceptible barley varieties in Montana might, in part, explain the recent increase in stem cutting reported by barley growers, which was also shown by our preliminary assessment of WSS damage, particularly reduced mortality in grower fields. Note that although barley has been historically reported as heavily infested, there is relatively limited evidence of significant levels of stem cutting (Criddle 1923, Farstad and Platt 1946). Current commercially grown varieties such as Craft, Conrad, and Harrington should provide better pest control, although this is not entirely consistent because greater levels of stem cutting were evident in the 2011 population of WSS heavily infesting Harrington near the Amsterdam site where the present research was conducted. This ability to adapt and become more successful on new hosts (Morrill and Kushnak 1996) has been a poorly appreciated feature of this native species until recent outbreaks caused by likely local adaptation to winter wheat in Colorado (Lesiuer et al. 2016).

Genotypic variation for WSS resistance in wheat is well documented (Cook et al. 2004, 2017; Sherman et al. 2010; Kalous et al. 2011; Joukhadar et al. 2013; Varella et al. 2015). However, the same is not true for other economically important host species of the grass tribe Triticeae. Such characterization may be of value because several plant traits have been shown to be controlled by orthologous loci in related species (Magalhaes et al. 2004, Bossolini et al. 2006, Myles et al. 2009). Thus, there is potential to identify orthologous genes in barley conferring resistance to the WSS that have not been mapped in wheat due to lack of polymorphism.

In this study, we have successfully characterized phenotypic variation for WSS resistance in barley lines from six North American breeding programs. Previously, we used a similar panel of elite wheat lines from North America to successfully identify QTL associated with WSS resistance in wheat (Varella et al. 2015). The procedure outlined in Varella et al. (2015) for wheat was followed for the barley data presented in this paper (data not shown). However, we have failed to detect QTL for resistance using an association mapping approach in the barley panel. In an association mapping analysis, the power of QTL detection is determined by the effect of a QTL and the frequencies of alleles in the target population (Mackay et al. 2009). The larger the effect of a QTL and the closer the allele frequencies are to 0.5, the greater the power of detection (Myles et al. 2009). Unfortunately, in this barley panel, only a small number of genotypes displayed susceptibility to WSS. Thus, it is likely that alleles associated with WSS susceptibility were poorly represented in the panel. A solution to this issue is bi-parental mapping, where parents are selected to differ for the trait of interest. In this case, alleles at potential QTL are present in 50% of the progeny, providing maximum power for QTL detection. The current identification of WSS susceptible barley lines will allow for the use of a family mapping approach that artificially inflates the frequency of susceptible alleles in biparental populations. This strategy will increase chances of QTL discovery in barley, which in turn will lead to a greater understanding of the genetic basis of WSS resistance in cereals.

In summary, germplasm from two-row barley harbors phenotypic variation for traits associated with WSS resistance. In the North American germplasm, antibiosis seems to be the predominant type of WSS resistance, although antixenosis and indirect plant defense characterized by the recruitment of parasitoids were also observed. Barley damage by the WSS will be impacted by the suite of varieties being grown in any given area or year. Thus, the selection of varieties for crop rotation aimed at WSS management should target lines showing increased antibiosis. Additionally, due to the potential of

using barley germplasm to improve WSS resistance in wheat, both the physiological and the genetic basis of mechanisms conferring antibiosis in barley warrant further investigation.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

Acknowledgments

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