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Integrating Spring Wheat Sowing Density with Variety Selection to Manage Wheat Stem Sawfly

Brian L. Beres,* Héctor A. Cárcamo, Rong-Cai Yang, and Dean M. Spaner

ABSTRACT

The wheat stem sawfly [*Cephus cinctus* Norton (Hymenoptera: Cephidae)] (WSS) has been a serious pest of wheat (*Triticum aestivum* L.) since the late 19th century. Adoption of solid-stemmed cultivars, which are available only in the spring bread wheat class in Canada, can mitigate damage but the trait that confers resistance tends to be variable. Five other classes of wheat are grown within the geographical range of *C. cinctus* and are vulnerable to WSS infestation, and the entire production area for durum (*T. turgidum* L.) in western Canada, Montana, and western North Dakota lies within the geographic range of *C. cinctus*. Our objective was to test the hypothesis that the response of hollow- and solid-stemmed cultivars to sowing density (150, 250, 350, or 450 seeds m^{-2}) would differ and subsequently affect infestation patterns of WSS and an endemic parasitoids. The lowest rates of infestation occurred in the hollow-stemmed durum cultivar AC Avonlea and declined with increased sowing density. Wheat pith expression was optimized at the lowest sowing density but the same level produced low and variable grain yield. In the solid-stemmed cultivar Lillian, pith expression was most stable at 250 or 350 seeds m^{-2}. For all cultivars, grain yield was optimized at the higher seeding rates of 350 and 450 seeds m^{-2}. Solid-stemmed wheat should be seeded at low to moderate density to maximize resistance to WSS, but hollow-stemmed cultivars should be seeded at higher seeding rates to optimize yield, lower WSS infestation, and to increase overall crop competitiveness.

The WSS has been a serious pest of wheat in the northern Great Plains since widespread production of the crop began in the late 19th century (Comstock, 1889). In the southern prairies of Canada, and in Montana, North and South Dakota, and western Minnesota it remains one of the most economically important insect pests of wheat (Beres et al., 2007; Weiss and Morrill, 1992). A comprehensive review of WSS biology and management can be found in Beres et al. (2011b). Briefly, adults emerge from the previous year's crop stubble in late spring through early summer and, following mating, the female seeks out a suitable oviposition host plant, which is usually in an adjacent wheat field (Criddle, 1922). A healthy female can carry up to 50 eggs, therefore, the population can increase exponentially in a single generation (Ainslie, 1920). A larva will hatch in approximately 7 d and begin to bore the culm of the stem (Criddle, 1923). The stem boring activity continues throughout the growing season up to physiological maturity of the plant. Chlorosis associated with plant ripening and the reduction of whole plant moisture cues the larva to begin preparation to overwinter (Holmes, 1979). The larva moves to the base of the stem, notches a v-shaped groove around the stem, fills the region with frass (excrement), and encases itself in a thin cocoon below the groove. The groove weakens the stem and causes it to easily topple to the ground, which proves difficult to recover at harvest (Ainslie, 1929). The injury caused by the stem boring reduces photosynthetic rates (Macedo et al., 2007) and results in losses of spike weight that range from 10 to 17% (Holmes, 1977; Morrill et al., 1992; Seamans et al., 1944). An additional loss in yield potential occurs when toppled stems are not recovered at harvest (Ainslie, 1920; Beres et al., 2007). Thus, overall yield potential in wheat infested by WSS can be reduced by 25% or more, and the loss of anchored residue results in greater vulnerability to soil erosion and lower snow retention potential.

The use of solid-stemmed cultivars can mitigate crop losses and reduce survivorship of *C. cinctus*. The mechanical pressure of developing pith in a solid stem confers on the plant a level of "resistance" through mortality of the egg (Holmes and Peterson, 1961), and hindering the boring activity of larvae. Thus, solid-stemmed wheat cause negative effects to health, fitness, and survivorship of WSS (Cárcamo et al., 2005; O'Keeffe et al., 1960). The plant's ability to develop pith in the culm of the stem, however, is influenced greatly by interactions between the genotype and the environment in which it is grown. All solid-stemmed spring and winter wheat cultivars developed to date are derived from the line S-615 (Kemp, 1934; Platt and Farstad, 1946), but two other sources exist (Clarke et al., 2005). The recessive nature of the genes controlling resistance derived from S-615 leads to inconsistent pith expression in the field (Hayat et al., 1995). This was acknowledged shortly after the

B.L. Beres and H.A. Cárcamo, Agriculture and Agri-Food Canada, Lethbridge Research Centre, 5403 1st Ave. South, Lethbridge, AB, Canada T1J 4B1; B.L. Beres, R.-C. Yang, and D.M. Spaner, Univ. of Alberta, Dep. of Agricultural, Food, and Nutritional Science, 410 Ag/Forestry Bldg., Edmonton, AB, Canada T6G 2P5. Received 14 June 2011. *Corresponding author (brian.beres@agr.gc.ca).

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Abbreviations: IPM, integrated pest management; WSS, wheat stem sawfly.

solid-stemmed spring wheat cultivar Rescue was released, when observations of high susceptibility to stem cutting were noted at Regina, SK (Platt and Farstad, 1949). It was later determined that genes conferring pith development in the culm of a stem are influenced by photoperiod. Intense sunlight results in maximum expression and pith development, whereas shading or cloudy conditions inhibit pith development (Eckroth and McNeal, 1953; Holmes, 1984).

Solid-stemmed cultivars currently available in the Canada Red Western Spring class are AC Eatonia (DePauw et al., 1994), AC Abbey (DePauw et al., 2000), and Lillian (DePauw et al., 2005). Solid-stemmed spring wheat cultivars available in Montana include Fortuna and Choteau. Resistance in winter wheat is also important as Montana has a biotype of WSS that has gradually adapted to become synchronous to winter wheat growth phenology by emerging 10 to 20 d earlier than normal. The adaptation seems to have occurred as a response to a shift away from spring to winter wheat production (Morrill and Kushnak, 1996). Solid-stemmed winter wheat cultivars available to Montana producers include Vanguard (Carlson et al., 1997), Rampart and Genou (Bruckner et al., 1997, 2006). Solid-stemmed cultivars are available only in the bread wheat class in Canada. Five other classes of wheat are grown within the geographical range of *C. cinctus*; including amber durum spring wheat, soft white spring wheat, hard red winter wheat, Canada prairie spring wheat, and general purpose wheat. Furthermore, the entire production area for durum in western Canada, Montana, and western North Dakota lies within the geographic range of *C. cinctus*.

Wheat row spacing and seeding rates can influence *C. cinctus* infestation rates, and the response varies between solid- and hollow-stemmed cultivars. Luginbill and McNeal (1958) reported that narrow row spacing and high seeding rates reduced stem cutting in Thatcher, a hollow-stemmed cultivar, but the same treatments reduced pith expression and led to increased levels of cutting damage in Rescue, a solid-stemmed cultivar. Cultivar development and genetic gain has advanced considerably in recent decades and a review of seeding rates for modern hollow- and solid-stemmed cultivars is warranted. Thus, research is needed to better define target plant populations so that an appropriate balance between yield potential, wheat stem sawfly management, and overall crop competitiveness is achieved.

Blending two cultivars (one hollow-, one solid-stemmed) with compatible maturity, market class attributes, and complementary strengths (Bowden et al., 2001) may be a feasible approach for management of WSS (Beres et al., 2011b). This practice is commonly used in Kansas to achieve yield stability because abiotic and biotic stresses can be inconsistent and unpredictable. Montana studies report that the strategy can be successful at minimizing damage at low to moderate levels of sawfly pressure, but not at high levels (Weiss et al., 1990). Similarly, a 1:1 blend of solid-stemmed AC Eatonia and hollow-stemmed AC Barrie resulted in an 11% increase in yield potential in comparison to a monoculture of AC Barrie in Alberta (Beres et al., 2009).

Thus, cultivar selection should be considered a management tool that provides the foundation on which an integrated pest management (IPM) strategy is built, and which contributes to the higher goal of optimizing an integrated crop management (ICM) strategy. Our objective was to test the hypothesis that the response of hollow- and solid-stemmed cultivars to sowing density would differ and subsequently affect infestation patterns of WSS and endemic parasitoids of WSS.

MATERIALS AND METHODS

Two study locations in the traditional distribution area of the WSS were selected near Coalhurst (49°44' N, 112°57' W), and Nobleford, AB, Canada (49°54'N, 112°58'W). Both sites are an Orthic Dark Brown Chernozem clay loam soil (Typic Boroll). A new area at these locations was selected each year of the study, which was initiated in 2006 and completed in 2008 at Nobleford and 2009 at Coalhurst. The Coalhurst site was divided into wheat-fallow and continuous wheat cropping systems; the crop rotation at the Nobleford site was a diverse cropping system that alternated wheat with peas (*Pisum sativum* L.), canola (*Brassica napus* L.), barley (*Hordeum vulgare* L.), and flax (*Linum usitatissimum* L.). Experiments at each site were planted into a field of spring wheat stubble that was naturally infested the previous growing season with wheat stem sawfly. A total of 7 site-years of data were collected for agronomic and insect-related variables.

Soil nutrient status was determined from soil samples collected in fall and submitted to a commercial soil testing laboratory. Nitrogen and P_2O_5 fertilizer were side-banded at seeding or banded in the previous fall at rates according to recommendations for dryland wheat production (Beres et al., 2008; Selles et al., 2006).

A split-plot, 4x4 factorial, arranged in a randomized complete block design was used each year. To study effects of cultivar, four commercially grown varieties were selected and assigned to the main plot (i) monoculture hollow-stemmed durum spring wheat (cultivar AC Avonlea) susceptible to WSS (Clarke et al., 1998), (ii) monoculture solid-stemmed spring wheat (cultivar Lillian) with resistance to WSS (DePauw et al., 2005), (iii) hollow-stemmed hard red spring wheat (cultivar CDC Go) susceptible to WSS, and (iv) a 1:1 blend of Lillian and CDC Go, achieved by using an air drill with separate grain compartments calibrated to meter out seed in equivalent rates to common seed tubes/openers. To study effects of planting density, four levels of seeding rate were selected and assigned to the subplot 1, 150 seeds m^{-2}; 2, 250 seeds m^{-2}; 3, 350 seeds m^{-2}; and 4, 450 seed m^{-2}.

Plots were seeded at Coalhurst and in 2006 at Nobleford with a modified commercial zero tillage air drill manufactured by Vale Farms (Conserva Pak Model CP 129A, Indian Head, SK, Canada) and equipped with a Valmar air delivery system (Valmar Airflo Inc., Elie, MB, Canada). In all other years plots at Nobleford were seeded with a 13 m wide Morris air drill configured with single-shoot knife openers spaced 26 cm apart (Morris Industries, Saskatoon, SK, Canada). Treatment combinations were replicated four times with subplot experimental unit dimensions that measured 3.3 m wide by 5 m long at Coalhurst and 13 m wide by 50 m long at Nobleford. Each study area was treated with glyphosate (RoundUp, Monsanto, St. Louis, MO) a few days before seeding at a rate of 900 g a.i. ha^{-1} using a motorized sprayer calibrated to deliver a carrier volume of 45 L water ha^{-1} at 275 kPa pressure. In-crop herbicides were chosen based on the weed spectrum present at each site-year, and applied in early June at label rates. No insecticides were used at any site during the study period.

Temperature and light intensity data collection was initiated in 2007 at each site using Hobo Pendant temperature and light loggers (Onset Computer Corporation, Bourne, MA; part no. UA-002-XX). The data loggers were attached near the top of 1m fiberglass whisker stakes (Imagine That Signs and Designs, Saskatoon, AB, Canada) and positioned at the center of each of the three ranges.

Plant counts were performed in mid- to late-May by staking a 1-m section in two randomly selected areas of the plot. The staked sections were counted again in mid- to late-July to assess spike density. To ensure an adequate estimate of stem solidness (Cárcamo et al., 2007), a 0.50 m section of row was collected 2 to 10 d before harvest in two random locations in each plot to determine stem diameter and pith expression or degree of stem solidness in the culm of the main stem. Mean stem diameter was determined by measuring the outside diameter of the first three internodes using a digital caliper. To determine mean pith expression, each stem was then split lengthwise from crown to neck, and starting from the crown, each internode was assessed visually for pith development. Ratings were as follows: 1-Hollow stem-no pith development; 2-Some degree of pith development-may appear cotton like; 3-Large hollow tunnel in the stem, or, a huge cavity at a particular point in the internode; 4-Size of hollow equivalent to a pencil lead, or, some cavitation has occurred at a particular point in the internode; and 5-Solid stem (DePauw and Read, 1982). The samples were also used to determine infestation rates by WSS (live/dead larva, frass, or evidence of stem boring) and parasitism of WSS (parasitized WSS larva, parasitoid, parasitoid cocoon, or exit holes) by *Bracon cephi* (Gahan) (Hymenoptera: Braconidae).

Plots were harvested at crop maturity using a Wintersteiger Expert (Wintersteiger AG, Salt Lake City, UT) plot combine equipped with a straight-cut header, pickup reel, and crop lifters. Grain yield was calculated from the entire plot area at Coalhurst and from a 1.5 by 50 m subsample of the plot in Nobleford. All grain collected from plots at Coalhurst and a 5-kg subsample from Nobleford were retained postharvest to characterize seed weight (g 1000^{-1}), grain bulk density (kg hL^{-1}) and grain protein. Grain protein concentration was determined from whole grain using near infrared reflectance spectroscopy technology (Foss Decater GrainSpec, Foss Food Technology Inc, Eden Prairie, MN).

Data were analyzed with the MIXED procedure of SAS (Littell et al., 2006). Homogeneity of error variances was tested using the UNIVARIATE procedure of SAS; and any outlier observations were removed before a combined analysis over years and environments (site-year) was performed. Normality assumptions were also tested on the categorical data "pith expression" and observational "Infestation by WSS (%)" and "Parasitism of WSS (%)" data as multiple categories were used for rating pith expression; and infestation and parasitism were expressed as percentages with a value distribution that was generally not extreme (Cochran, 1954). For analyses by environments, replicate was considered random and treatment effects were considered fixed; and significant if $P \leq 0.05$. Results by environment indicated similar treatment response patterns among environments; therefore, a combined analysis was performed with replicate, years, environments and their interactions considered random effects and treatment effects fixed and significant if $P \leq 0.05$. Pearson partial correlation coefficients were performed using the CORR procedure of SAS on raw data to determine the contribution of each yield component to overall yield performance. Response variable least square means generated for each site-year were used to create a Pearson correlation coefficient matrix of insect-related variables, stem diameter, stem solidness, grain yield, yield components, and grain protein data using the CORR procedure of SAS.

A grouping methodology previously described by Francis and Kannenberg (1978) and later adapted to agronomy studies (Beres et al., 2010a; Gan et al., 2009; May et al., 2010) was used to further explore treatment responses. The mean and coefficient of variation (CV) were estimated for each level of the treatment and plotted against each other. The overall mean of the treatment means and CVs was included in the plot to categorize the biplot ordination area into four quadrats/categories: Group I: High mean, low variability (optimal); Group II: High mean, high variability; Group III: Low mean, high variability (poor); and Group IV: Low mean, low variability.

RESULTS AND DISCUSSION

Average annual and growing season precipitation during the study period was below average in 2 of 5 yr at Coalhurst and 2 of 3 yr at Nobleford (Table 1). However, the 2006 season at both sites benefitted from above average rainfall and subsequent soil moisture reserves experienced in 2005. The 2007 sites were most adversely affected by low rainfall during critical periods of crop growth. Nobleford received above average precipitation in 2008, and the final 2 yr at Coalhurst received average to above-average precipitation. The precipitation patterns for 2008 are also evident in the temperature and light intensity data summarized in Table 1. Temperatures and light intensity generally peaked in July except in 2008 when it declined sharply after June. Trends in light intensity and temperature were similar at both sites, with the notable exceptions of greater decline of light intensity at Nobleford in 2007, and higher overall temperature and light intensity in Nobleford in 2008 (Table 1). Temperature peaked in 2007 at both sites, which was the hottest month of the entire study period and corresponds to the arid conditions experienced at both sites; however, light intensity was lower in 2007 than in other years (Table 1).

Infestation rates by WSS on wheat cultivars differed between the hard red spring wheat class and the durum cultivar AC Avonlea, but did not differ between hard red spring wheat cultivars within the hard red spring wheat class (Table 2). The use of AC Avonlea durum reduced infestation rates by around 40% compared to CDC Go or the blend of CDC Go and Lillian. The relationship between infestation rates by WSS and the rate of parasitism on WSS by the parasitoid *Bracon cephi* (Gahan) (Hymenoptera: Braconidae) is apparent as both variables displayed similar trends among the cultivar treatments. However, the downward linear trend for WSS infestation with increased seeding rates ($P = 0.02$) was not evident in the rate of WSS parasitism (Table 2).

Table 1. Description of test sites at Coalhurst and Nobleford, AB, Canada, and summary of agronomic practices performed during the study period 2006 to 2009.

Variable												
Location	**Coalhurst, AB, Canada**							**Nobleford, AB, Canada**				
Latitude and longitude	**49°44' N, 112°57 W**							**49°54'N, 112°58' W**				
Soil zone/series/texture	**Orthic Dark Brown Chernozemic Clay Loam (Typic Boroll)**							**Orthic Dark Brown Chernozemic Clay Loam (Typic Boroll)**				
Crop year	2006	2007		2008		2009		2006	2007		2008	
Sowing date	6 May	25 Apr.		30 Apr.		4 May		17 May	17 Apr.		30 May	
Harvest date	1 Sept.	5 Sept.		9 Sept.		11 Sept.		12 Sept.	28 Aug.		30 Sept.	
Mean temperature and light intensity (Lm m^{-2}) × 1000	–	**°C**	**Lux**	**°C**	**Lux**	**°C**	**Lux**	–	**°C**	**Lux**	**°C**	**Lux**
June	–	19.3	26.8	21.9	26.4	–	–	–	20.5	28.4	22.1	49.7
July	–	25.2	29.3	20.8	27.2	20.8	30.6	–	26.2	28.8	20.9	42.7
August	–	21.3	28.4	20.8	20.4	19.4	25.0	–	20.7	24.8	20.9	37.1
Precipitation, mm												
1 May to 15 Sept. long-term avg. = 251	150	164		380		241		150	164		380	
Annual long-term avg. = 398	331	342		525		417		331	342		525	

Table 2. Insect data summary of LSmeans for main effects variety and seeding rate, collected from sites near Nobleford and Coalhurst, AB, Canada 2006 to 2009.

Factor	Treatment	WSS† infestation	Parasitism of WSS	Pith rating (1 = hollow; 5 = solid)	Stem diameter
		%			mm
Variety (main plot)	AC Avonlea	30	8	2.4	2.62
	Lillian	43	16	3.0	2.46
	1:1 Blend of Lillian:Go	51	22	2.1	2.52
	CDC Go	52	28	1.4	2.65
	SED‡	5.02	4.58	0.182	0.043
	Pr > *F*	0.002	0.003	<0.0001	0.0011
	LSD (0.05)§	10	9	0.38	0.09
Seed rate (subplot)	150 seeds m^{-2}	49	21	2.4	2.69
	250 seeds m^{-2}	44	18	2.2	2.57
	350 seeds m^{-2}	42	18	2.2	2.51
	450 seeds m^{-2}	41	18	2.2	2.49
	SED	3.62	1.54	0.054	0.026
	Pr > *F*	0.109	0.224	0.006	<0.0001
	LSD (0.05)	–	–	0.12	0.05
Linear trend	Linear equation (*Y*)	$-0.0288x+52.49$	–	$-0.006x+2.43$	$0.0007x+2.763$
	Regression value (R^2)	0.91	–	0.60	0.90
Contrasts	Linear	0.021	0.162	0.002	<0.0001
Pr > *F*	Quadratic	0.449	0.138	0.046	0.026
	Cubic	0.949	0.616	0.811	0.934
Variety × Seed rate	*Pr* > *F*	0.003	0.261	0.391	0.353

† WSS, wheat stem sawfly.

‡ SED, Standard error of the difference.

§ LSD, Fisher's protected least significant difference.

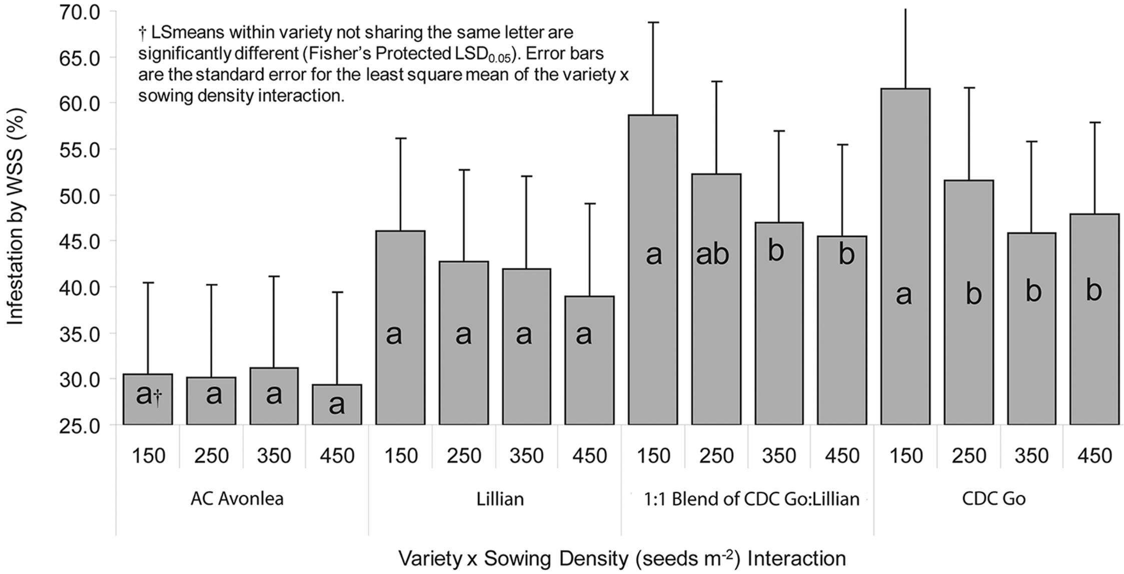

Fig. 1. Response of wheat stem sawfly (WSS) infestation rates to the interaction of variety selection and sowing density.

As expected, pith expression was greatest in the solid-stemmed hard red spring wheat variety Lillian, lowest in the hollow-stemmed CDC Go, and intermediate in the blend treatment (Table 2). Compared to the other hollow treatments, a higher pith rating was recorded for AC Avonlea and is likely due to the thicker stem wall of durum wheat compared to most bread wheat cultivars, which creates a smaller observed cavity in the lumen of the stem (Damania et al., 1997). Reduced pith expression and stem diameter was observed as seeding rates increased over the low rate of 150 seeds m^{-2} (Table 2). Single degree of freedom contrast results indicate that the best fit of the response was linear but the significant quadratic response for both traits may indicate that the downward trend was not strictly linear. Wallace et al. (1973) reported that a mean pith expression of 3.75 would be required to achieve consistent high tolerance to WSS infestations. We did not observe this degree of stem solidness in Lillian (3.0), which indicates that the weather parameters or the genetic potential of Lillian prevented maximum resistance to WSS infestation. The results reinforce the concept that cultivars with tolerant attributes alone do not provide a "magic bullet" for WSS management but need to be integrated with other IPM tactics.

The interaction of variety and seeding rate ($P = 0.003$) was explored further and is summarized in Fig. 1. Increasing seeding rates from 150 to 450 seeds m^{-2} generally reduced rates of infestation by 25% in the bread wheat blend and CDC Go treatments. However, the nonsignificant downward trend for the solid-stemmed variety Lillian and the observed reduction in pith expression at higher seeding rates reinforces recommendations that planting densities for solid-stemmed varieties should not exceed a range of 250 to 300 seeds m^{-2} (Beres et al., 2011a). Host preference by WSS for bread wheat treatments over the durum variety AC Avonlea resulted in low infestation rates in AC Avonlea irrespective of plant density (Fig. 1).

The most attractive host for WSS is a cereal plant that is succulent, in the boot or early anthesis stage, and has a suitable stem diameter that can be readily grasped by an ovipositing female (Holmes and Peterson, 1960). The preference for larger stems was not supported in the cultivar effect as AC Avonlea had the largest stem diameter but lowest infestation rate. However, the preference does correspond to the sowing density results as increased sowing density reduced stem diameter and infestation rates (Fig. 1). The low infestation we report for the durum cultivar has been observed in other studies (Goosey et al., 2007), but the rate of infestation could change if host choice is removed, which would be the case in large monoculture fields of durum wheat (Holmes and Peterson, 1960). Therefore, the adoption of durum cultivars over hard red spring wheat would not necessarily reduce WSS damage.

Average yield, yield component, and grain quality responses were affected by variety selection (Table 3). Grain yield was greatest for the durum variety AC Avonlea (0.2–0.4 Mg ha^{-1} greater than the average of other varieties) and least for the solid-stemmed variety Lillian, with intermediate yields observed for CDC Go and the blend of CDC Go and Lillian (Table 3). Stand establishment response did not differ between varieties but spikes per plant and spike density was low for AC Avonlea compared to the averages of the bread wheat treatments (Table 3). Thus, the large kernel weight and fewer tillers per plant likely accounted for AC Avonlea's greater grain yield.

All yield, yield component, and grain quality variables, except seed mass, responded to the effect of seeding rate (Table 3). High grain yield, stand establishment, spike density, and grain bulk density were associated with the highest seeding rate of 450 seeds m^{-2} (Table 3), but the increase generally diminished after 250 seeds m^{-2} (yield) or 350 seeds m^{-2} (stand establishment, spike density, and bulk density) (Table 3). When averaged over all varieties, plants responded to higher seeding rates and subsequent greater plant density by aborting tillers and partitioning more resources to the main stem (Table 3). This response generally produced more grain (+0.6 Mg ha^{-1} from lowest to highest seeding rate) and suggests that production of more than a single tiller would compromise grain yield optimization. This is apparent in the grain yield results of AC Avonlea where it produced the highest grain yield with the fewest spikes per plant.

Table 3. Agronomic summary of mean responses for main effects of variety and seeding rate, collected from sites near Nobleford and Coalhurst, AB, Canada 2006 to 2009.

Factor	Treatment	Grain yield	Stand establish-ment	Spike density	Seed mass	Grain bulk density	Grain protein	Spikes per plant
		Mg ha^{-1}	plants m^{-2}	heads m^{-2}	g 1000^{-1}	kg hL^{-1}	%	
Variety (main plot)	AC Avonlea	3.15	163	281	39.9	76.7	12.2	2.1
	Lillian	2.75	183	367	30.1	75.7	13.4	2.5
	1:1 Blend of Lillian:Go	2.93	169	344	32.5	76.2	13.4	2.5
	CDC Go	2.90	169	335	34.5	76.7	13.2	2.5
	SED†	0.107	7.57	11.80	0.713	0.392	0.254	0.117
	Pr > *F*	0.0138	0.109	<0.0001	<0.0001	0.044	0.0004	0.011
	LSD (0.05)‡	0.23	–	26	1.50	0.82	0.53	0.26
Seed rate (subplot)	150 seeds m^{-2}	2.56	115	288	34.3	75.3	13.5	2.8
	250 seeds^{-2}	2.98	157	323	34.3	76.4	13.0	2.5
	350 seeds m^{-2}	3.02	196	354	33.9	76.6	12.9	2.2
	450 seeds m^{-2}	3.16	214	362	34.1	76.9	12.8	2.1
	SED	0.118	10.87	10.69	0.226	0.176	0.121	0.097
	Pr > *F*	0.0005	<0.0001	<0.0001	0.207	<0.0001	0.0002	<0.0001
	LSD (0.05)	0.24	24	21	–	0.37	0.25	0.21
Linear trend	Linear equation (*Y*)	0.0018*x*+2.378	0.337*x*+70.15	0.253*x*+255.85	–	0.0046*x*+74.97	–0.0022*x*+13.71	–0.0024*x*+3.12
	Regression (R^2) value	0.85	0.97	0.97	–	0.82	0.84	0.96
Contrasts	Linear	0.0001	<0.0001	<0.0001	0.107	<0.0001	<0.0001	<0.0001
(Pr > F)	Quadratic	0.099	0.133	0.068	0.651	0.003	0.058	0.277
	Cubic	0.205	0.608	0.581	0.179	0.080	0.517	0.506
Var. × seed rate	*Pr* > *F*	0.0003	0.399	0.082	0.011	0.310	0.496	0.183

† SED, Standard error of the difference.

‡ LSD, Fisher's protected least significant difference.

The interaction between variety and sowing density (P = 0.0003) for grain yield indicates a similar positive response by the variety treatments when seeding rates increase from 150 to 450 seeds m^{-2} (Fig. 2). The pattern is most evident with AC Avonlea and confirms that benefits at the highest sowing density level are optimized by selecting cultivars and/or sites with the highest yield potential. The results for the bread wheat variety treatment suggest that the decision to increase seeding rates beyond 250 seeds m^{-2} would need to be based on factors other than just yield performance. In a weed competition study, Beres et al. (2010b) reported high yield response for the durum variety AC Avonlea when planted at 400 seeds m^{-2} (5.3 Mg ha^{-1}). Increased competitive ability with weeds and positive yield response at higher sowing densities has been

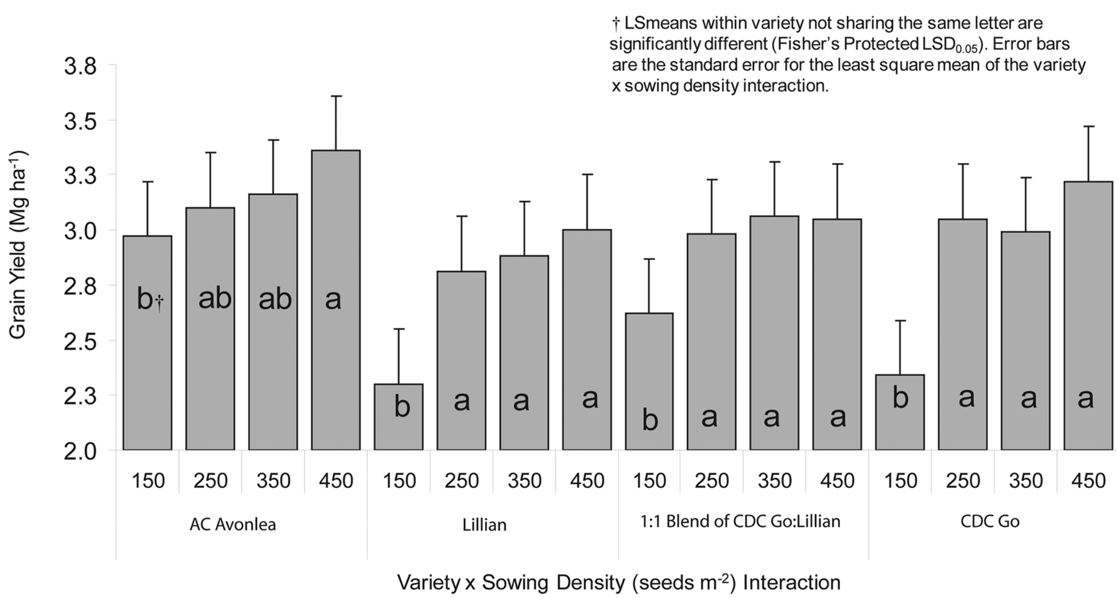

Fig. 2. Grain yield responses of durum and hard red spring wheat cultivars to varying sowing densities.

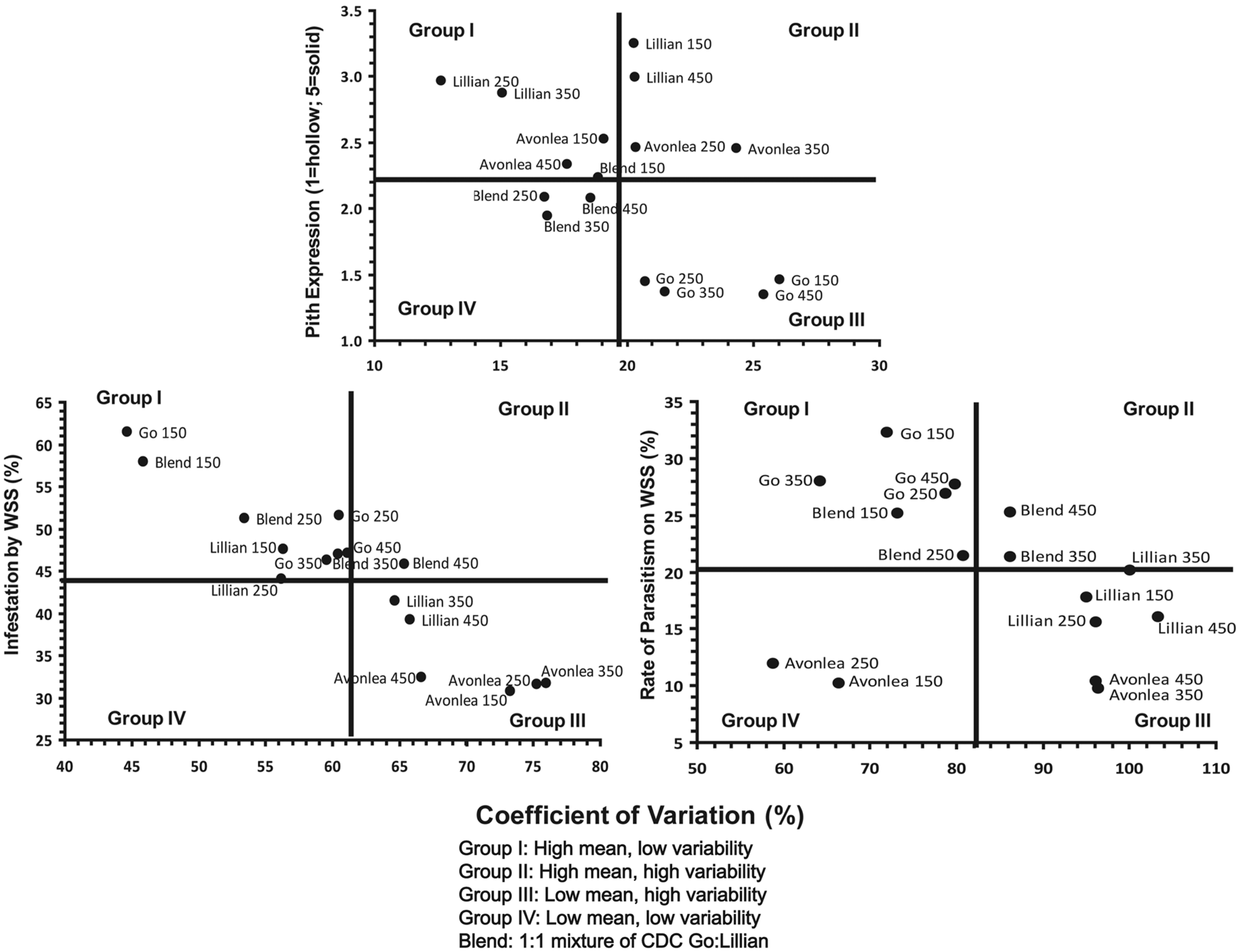

Fig. 3. Biplot (mean vs. CV) of variety and sowing density combinations for data from insect-related variables collected at Coalhurst and Nobleford, AB, Canada, 2006 to 2009. The prefix of the labels indicates the variety selected followed by the planting density (150, 250, 350, or 450 seeds m^{-2}).

reported in several studies involving winter wheat (Beres et al., 2010a), canola (Harker et al., 2003), and barley (Harker et al., 2009; O'Donovan et al., 2000, 2009). Increased sowing densities may also reduce the reliance on herbicides for weed control or increase the efficacy when herbicide rates are reduced (O'Donovan et al., 2006). However, the rationale for higher seeding rates to enhance crop performance and competitive ability for wheat would not apply to solid-stemmed cultivars as pith expression is reduced when sowing density is increased.

Grain protein accumulation did not differ between the bread wheat varieties CDC Go (13.2%) and Lillian (13.4%) when planted in monoculture or blended together (Table 3). Protein averaged 1% lower in AC Avonlea durum compared to the bread wheat variety treatments. All variety treatments produced sufficient protein to meet the minimum no. 1 grade criteria (≥11.5%) set by the Canadian Wheat Board, but were all lower than the uppermost protein premium of 14.5%. The inverse relationship between grain yield and protein content is apparent in Table 2 as increasing sowing densities from the lowest to the highest seeding rate reduced grain protein by 5%.

We conducted partial correlation analyses between each yield component and final yield (Littell et al., 2006). These analyses were conducted to examine the direct effect of a given yield component on final yield, where the effect of all other yield components are held constant. Averaged over all seeding rates and cultivars, Pearson partial correlation coefficients indicate that seed mass and spike density were primarily responsible for differences in grain yield (data not shown). This makes agronomic sense as the highest kernel weight was observed in the variety with the highest yield potential (AC Avonlea), and the single degree of freedom contrasts indicate a strong linear response in both stand establishment and grain yield with increasing seeding rates (Table 3).

Biplots were constructed (Fig. 3 and 4) to study the stability of insect- and crop-related variable responses and to determine which variety × seeding combinations offer the best integrated system for WSS management. Optimum pith expression over a range of environments is necessary for a solid-stemmed cultivar to effectively reduce the negative effects of WSS. Higher pith expression in Lillian was observed in the 150 seeds m^{-2} treatment but the result was not as consistent as it was for the 250 or 350 seeds m^{-2} treatments (Fig. 3). Poor pith expression in CDC Go is expected as it is a hollow-stemmed cultivar, and the most consistent rating for AC Avonlea occurred at the highest seeding rate. Infestation rates were consistently highest

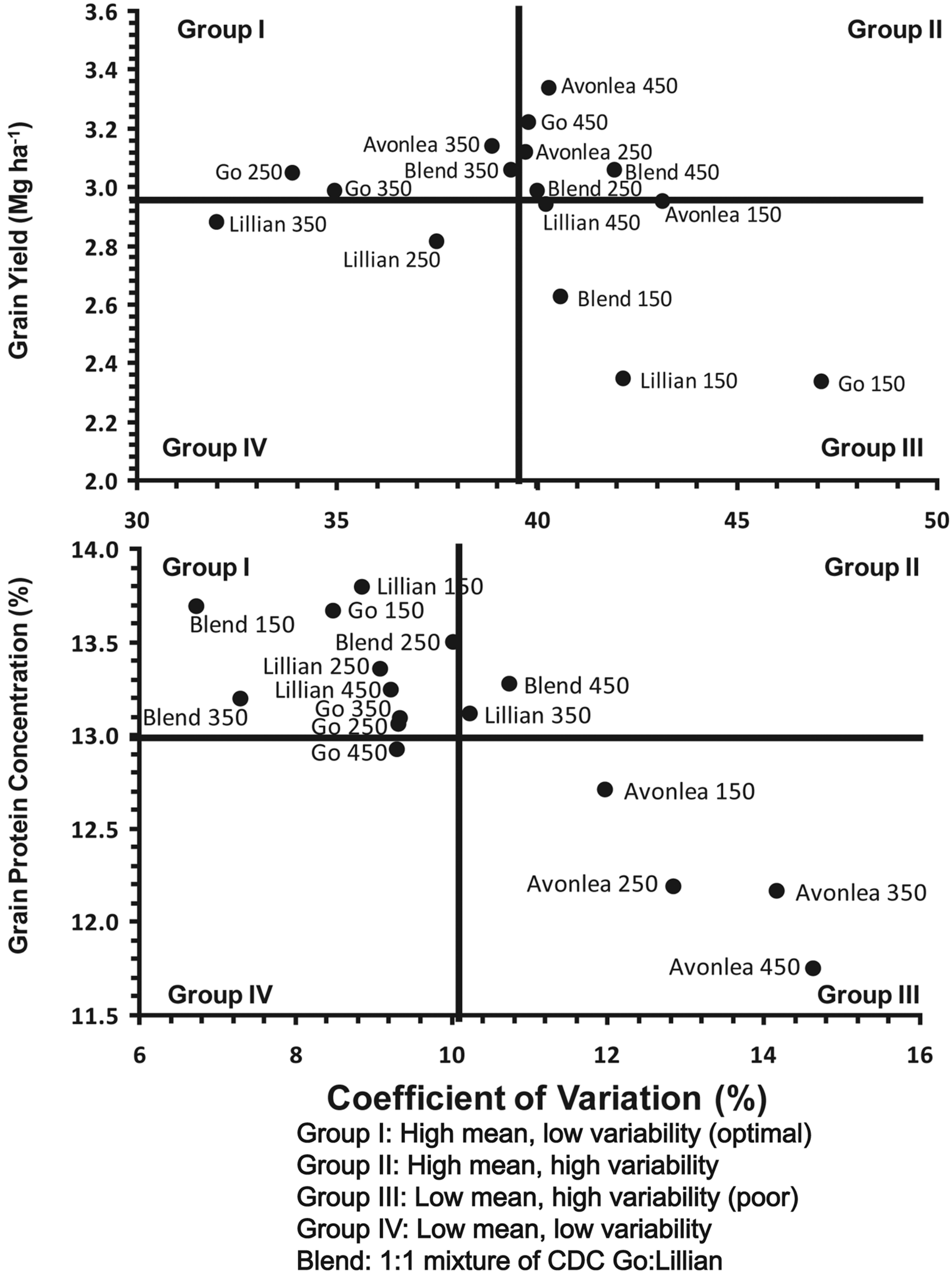

Fig. 4. Biplot (mean vs. CV) of variety and sowing density combinations for grain yield and protein concentration data collected at Coalhurst and Nobleford, AB, Canada, 2006 to 2009. The prefix of the labels indicates the variety selected followed by the planting density (150, 250, 350, or 450 seeds m^{-2}).

for CDC Go and Lillian in monoculture and when blended together at the lowest seeding rate. Infestation dropped at the higher seeding rates for these treatments but with higher variability. Infestation for AC Avonlea was low and variable at all sowing densities (Fig. 3). Rates of parasitism on WSS followed a similar pattern to WSS infestation but the results for Lillian were more variable than any other treatment. For hollow-stemmed treatments, sowing densities of 350 seeds m^{-2} generally produced above average yield and stability. A sowing density of 450 seeds m^{-2} often increased yield in the hollow-stemmed treatments but with greater instability (Fig. 4). Yield of Lillian was generally below average at all seeding rates but produced consistently stable yields at the 350 seeds m^{-2} rate. The lowest rate produced inferior grain yields with poor overall stability. The inverse of the yield results were generally observed in the protein biplot (Fig. 4).

Table 4. Correlation matrix of insect-related variables, grain yield, yield components, and grain protein in spring wheat grown in areas prone to wheat stem sawfly (WSS) attack.

Variable	Stem solidness	Rate of parasitism on WSS	Stems infested by WSS	Grain yield	Stand establishment	Spike density	Spikes per plant	Grain protein
	Pearson correlation coefficients							
Stem diameter	–†	–	–	–	–0.53	0.27	0.49	–
Stem solidness	1	–0.42	–	–0.22	–	–	–	–
Rate of parasitism		1	0.77	0.23	–0.53	–	0.42	–
Stems infested by WSS			1	–	–0.42	–0.26	–	–0.26
Grain yield				1	–0.48	0.71	0.70	–0.23
Stand establishment					1	–0.22	–0.82	0.25
Spike density						1	0.56	–
Spikes per plant							1	–
Grain protein								1

† '-' = $P > 0.05$; all other r values presented at $P \leq 0.05$.

Correlation coefficients were generated to further explore relationships between insect-related parameters, yield, and yield component parameters (Table 4). Positive correlations were observed between rates of parasitism on WSS and the crop parameters grain yield and spikes per plant. The positive effect of parasitism on crop yield or mitigation of crop yield losses caused by WSS has been reported in a Montana study (Buteler et al., 2008), however, the relationship has not been observed in studies in southern Alberta (Wu et al., 2011). Negative correlations were observed between infestation rates by WSS and stand establishment, spike density, and grain protein content. Larger stem diameter appears to positively affect the yield components spike density and spikes per plant but a negative relationship was observed for stand establishment. A negative relationship between grain yield and stand establishment was also observed. The negative association with stand establishment does not agree with a previous finding that reports a positive association (Beres et al., 2011c) which may be more plausible given that yield potential is dependent on optimum plant stand or a high degree of tillers per plant. The result may indicate some of the treatment combinations in this study had a higher tillering capacity than what has been previously observed.

CONCLUSIONS

The differential response between hollow- and solid-stemmed cultivars and varying rates of sowing density suggest that a management package for WSS must take into account the stem type. The solid-stemmed cultivar Lillian generally had optimized grain yield and high and stable pith at the 250 to 350 seeds m^{-2} sowing densities. A higher sowing density for hollow-stemmed treatment is warranted based on the findings that infestation rates tended to decrease with increased seeding rates, and parasitism of WSS was also high at the higher seeding rates. Moreover, there may be other benefits related to the enhancement of competitive ability that were not part of this study. For wheat produced in regions prone to WSS infestation we encourage seeding rates of ≤300 seeds m^{-2} for solid-stemmed cultivars and recommend increasing the rate into the range of 400 to 450 seeds m^{-2} for hollow-stemmed cultivars.

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REFERENCES

Ainslie, C.N. 1920. The western grass-stem sawfly. USDA Tech. Bull. 841. USDA, Washington, DC.

Ainslie, C.N. 1929. The western grass-stem sawfly: A pest of small grains. USDA Tech. Bull. 157. USDA, Washington, DC.

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

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

Beres, B.L., H.A. Cárcamo, D.K. Weaver, L.M. Dosdall, M.L. Evenden, B.D. Hill, R.H. McKenzie, R.C. Yang, and D.M. Spaner. 2011a. Integrating the building blocks of agronomy and biocontrol into an IPM strategy for wheat stem sawfly. Prairie Soils and Crops 4:54–65.

Beres, B.L., G.W. Clayton, K.N. Harker, C.F. Stevenson, R.E. Blackshaw, and R.J. Graf. 2010a. A sustainable management package to improve winter wheat production and competition with weeds. Agron. J. 102:649–657. doi:10.2134/agronj2009.0336

Beres, B.L., L.M. Dosdall, D.K. Weaver, D.M. Spaner, and H.A. Cárcamo. 2011b. The biology and integrated management of wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), and the need for continuing research. Can. Entomol. 143:105–125. doi:10.4039/n10-056

Beres, B.L., K.N. Harker, G.W. Clayton, R.E. Blackshaw, and R.J. Graf. 2010b. Weed competitive ability of spring and winter cereals in the Northern Great Plains. Weed Technol. 24:108–116. doi:10.1614/WT-D-09-00036.1

Beres, B.L., R.H. McKenzie, H.A. Cárcamo, L.M. Dosdall, M.L. Evenden, R.C. Yang, and D.M. Spaner. 2011c. Influence of seeding rate, nitrogen management and micronutrient blend applications on pith expression in solid-stemmed spring wheat. Crop Sci. (in press).

Beres, B.L., R.S. Sadasivaiah, R.H. McKenzie, R.J. Graf, and R.J. Dyck. 2008. The influence of moisture regime, N management, and cultivar on the agronomic performance and yield stability of soft white spring wheat. Can. J. Plant Sci. 88:859–872. doi:10.4141/CJPS07173

Bowden, R., J. Shroyer, K. Roozeboom, M. Claassen, P. Evans, B. Gordon, B. Heer, K. Janssen, J. Long, J. Martin, A. Schlegel, R. Sears, and M. Witt. 2001. Performance of wheat variety blends in Kansas. Kansas State Univ., Manhattan.

Bruckner, P.L., J.E. Berg, G.D. Kushnak, R.N. Stougaard, J.L. Eckhoff, G.R. Carlson, D.M. Wichman, K.D. Kephart, N. Riveland, and D.L. Nash. 2006. Registration of 'Genou' wheat. Crop Sci. 46:982–983. doi:10.2135/cropsci2005.07-0188

Bruckner, P.L., G.D. Kushnak, J.E. Berg, D.M. Wichman, G.R. Carlson, G.F. Stallknecht, R.N. Stougaard, J.L. Eckhoff, H.F. Bowman, and W.L. Morrill. 1997. Registration of 'Rampart' wheat. Crop Sci. 37:1004. doi:10.2135/cropsci1997.0011183X003700030052x

Buteler, M., D.K. Weaver, and P.R. Miller. 2008. Wheat stem sawfly-infested plants benefit from parasitism of the herbivorous larvae. Agric. For. Entomol. 10:347–354. doi:10.1111/j.1461-9563.2008.00396.x

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

Cárcamo, H., T. Entz, and B. Beres. 2007. Estimating *Cephus cinctus* wheat stem cutting damage-Can we cut stem counts? J. Agric. Urban Entomol. 24:117–124. doi:10.3954/1523-5475-24.3.117

Carlson, G.R., P.L. Bruckner, J.E. Berg, G.D. Kushnak, D.M. Wichman, J.L. Eckhoff, K.A. Tilley, G.F. Stallknecht, R.N. Stougaard, H.F. Bowman, W.L. Morrill, G.A. Taylor, and E.A. Hockett. 1997. Registration of 'Vanguard' wheat. Crop Sci. 37:291. doi:10.2135/cropsci1997.0011183X003700010060x

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

Clarke, J.M., J.G. McLeod, T.N. McCaig, R.M. DePauw, R.E. Knox, and M.R. Fernandez. 1998. AC Avonlea durum wheat. Can. J. Plant Sci. 78:621–623. doi:10.4141/P98-002

Cochran, W.G. 1954. Some methods for strengthening the common x^2 tests. Biometrics 10:415–451.

Comstock, J.H. 1889. On a saw-fly borer in wheat. Cornell Univ., Ithaca, NY.

Criddle, N. 1922. The western wheat stem sawfly and its control. Dominion of Canada Dep. of Agric. Pamphlet no. 6 New Ser.:1–8.

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

Damania, A.B., L. Pecetti, C.O. Qualset, and B.O. Humeid. 1997. Diversity and geographic distribution of stem solidness and environmental stress tolerance in a collection of durum wheat landraces from Turkey. Genet. Resour. Crop Evol. 44:101–108. doi:10.1023/A:1008629604766

DePauw, R.M., J.M. Clarke, R.E. Knox, M.R. Fernandez, T.N. McCaig, and J.G. McLeod. 2000. AC Abbey hard red spring wheat. Can. J. Plant Sci. 80:123–127. doi:10.4141/P99-089

DePauw, R.M., J.G. McLeod, J.M. Clarke, T.N. McCaig, M.R. Fernandez, and R.E. Knox. 1994. AC Eatonia hard red spring wheat. Can. J. Plant Sci. 74:821–823. doi:10.4141/cjps94-148

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

DePauw, R.M., T.F. Townley-Smith, G. Humphreys, R.E. Knox, F.R. Clarke, and J.M. Clarke. 2005. Lillian hard red spring wheat. Can. J. Plant Sci. 85:397–401. doi:10.4141/P04-137

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

Francis, T.R., and L.W. Kannenberg. 1978. Yield stability studies in short-season maize. I. A descriptive method for grouping genotypes. Can. J. Plant Sci. 58:1028–1034.

Gan, Y.T., T.D. Warkentin, C.L. McDonald, R.P. Zentner, and A. Vandenberg. 2009. Seed yield and yield stability of chickpea in response to cropping systems and soil fertility in northern latitudes. Agron. J. 101:1113–1122. doi:10.2134/agronj2009.0039

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

Harker, K.N., G.W. Clayton, R.E. Blackshaw, J.T. O'Donovan, and F.C. Stevenson. 2003. Seeding rate, herbicide timing and competitive hybrids contribute to integrated weed management in canola (*Brassica napus*). Can. J. Plant Sci. 83:433–440. doi:10.4141/P02-073

Harker, K.N., J.T. O'Donovan, R.B. Irvine, T.K. Turkington, and G.W. Clayton. 2009. Integrating cropping systems with cultural techniques augments wild oat (*Avena fatua*) management in barley. Weed Sci. 57:326–337. doi:10.1614/WS-08-165.1

Hayat, M.A., J.M. Martin, S.P. Lanning, C.F. McGuire, and L.E. Talbert. 1995. Variation for stem solidness and its association with agronomic traits in spring wheat. Can. J. Plant Sci. 75:775–780. doi:10.4141/cjps95-131

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

Holmes, N.D. 1979. The wheat stem sawfly. p. 2–13. *In* H.G. Philip (ed.) Proc. of the 26th Annual Meet. of the Entomological Soc. of Alberta, Lethbridge, AB. 19–21 Oct. 1979. Vol. 26. Entomol. Soc. of Alberta, Lethbridge.

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

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

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

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

Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 2006. SAS® System for mixed models. 2nd ed. SAS Inst., Cary, NC.

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

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

May, W.E., S.A. Brandt, Y. Gan, H.R. Kutcher, C.B. Holzapfel, and G.P. Lafond. 2010. Adaptation of oilseed crops across Saskatchewan. Can. J. Plant Sci. 90:667–677. doi:10.4141/CJPS09179

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

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

O'Donovan, J.T., R.E. Blackshaw, K.N. Harker, and G.W. Clayton. 2006. Wheat seeding rate influences herbicide performance in wild oat (*Avena fatua* L.). Agron. J. 98:815–822. doi:10.2134/agronj2005.0234

O'Donovan, J.T., G.W. Clayton, K.N. Harker, T.K. Turkington, and N.Z. Lupwayi. 2009. Relationship between seeding rate and plant density of hulled and hull-less barley as influenced by seeding depth in a no-tillage system. Can. J. Plant Sci. 89:645–647. doi:10.4141/CJPS08203

O'Donovan, J.T., K.N. Harker, G.W. Clayton, and L.M. Hall. 2000. Wild oat (*Avena fatua*) interference in barley (*Hordeum vulgare*) is influenced by barley variety and seeding rate. Weed Technol. 14:624–629. doi:10.1614/0890-037X(2000)014[0624:WOAFII]2.0.CO;2

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

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

Platt, A., and C.W. Farstad. 1949. Breeding spring wheats for resistance to wheat stem sawfly attack. Proc. 7th Pacific Sci. Congress 4:215–220.

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

Selles, F., J.M. Clarke, and R.M. DePauw. 2006. Quantification of the yield and protein response to N and water availability by two wheat classes in the semiarid prairies. Can. J. Plant Sci. 86:981–993. doi:10.4141/P05-007

Wallace, L.E., F.H. McNeal, and M.A. Berg. 1973. Minimum stem solidness required in wheat for resistance to the wheat stem sawfly. J. Econ. Entomol. 66:1121–1123.

Weiss, M.J., and W.L. Morrill. 1992. Wheat stem sawfly (Hymenoptera: Cephidae) revisited. Am. Entomol. 38:241–245.

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

Wu, X.-H., H. Cárcamo, B.L. Beres, and B.-P. Pang. 2011. Parasitoid (*Bracon cephi*) effects on grain yield of selected genotypes of wheat infested by *Cephus cinctus*. Aust. J. Crop Sci. 5:1102–1107.