Resistance to Hessian fly (Diptera: Cecidomyiidae) in a Canadian spring wheat cultivar[1]

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Abstract—The Canadian spring wheat (*Triticum aestivum* L.; Poaceae) cultivar 'Superb' was less susceptible to damage by Hessian fly, *Mayetiola destructor* (Say), than the spring wheat cultivars 'AC Barrie', 'AC Foremost', 'McKenzie', 'AC Domain', and 'Glenlea' in Manitoba. The partial resistance of 'Superb' was similar, at the seedling stage, to that of 'Guard', which possesses the resistance gene *H18*. Females laid eggs readily on all cultivars, providing no evidence for antixenosis, but few larvae developed on seedlings of 'Superb' and 'Guard', showing that antibiosis against larvae is the mechanism of resistance in these seedlings. In the field, where infestation of spring wheat takes place about 4 weeks after the seedling stage, 'Guard' continued to show high levels of resistance, but 'Superb' was less resistant, although still more resistant than highly susceptible cultivars. Infested stems of 'Superb' and 'Nordic' were less likely to break than infested stems of other cultivars, showing that these two cultivars are partially tolerant to infestation. Infested stems of 'Guard' and other cultivars showed high levels of stem breakage and are intolerant. Yield losses due to infestation by Hessian fly were mostly caused by the breakage and falling over of infested stems, which prevented the seeds on these stems from being harvested. Infested stems of all susceptible cultivars that remained standing at harvest had lower seed masses and fewer seeds per spike than uninfested stems, which contributed to yield loss. 'Grandin', a parent of 'Superb', is the probable source of resistance in 'Superb', but the pedigree of 'Grandin' provides no clue as to the gene(s) involved. The partial antibiosis and tolerance expressed by 'Superb' is sufficient to reduce losses to Hessian fly by 65% in comparison with a susceptible cultivar such as 'AC Barrie'. 'Superb' is the first Canadian spring wheat cultivar identified to have an agronomically useful level of resistance to Hessian fly.

Résumé—Au Manitoba, le cultivar canadien 'Superb' de blé de printemps (*Triticum aestivum* L., Poaceae) est moins vulnérable aux ravages de la mouche de Hesse, *Mayetiola destructor* (Say) que les cultivars de blé de printemps 'AC Barrie', 'AC Foremost', 'McKenzie', 'AC Domain' et 'Glenlea'. La résistance partielle de 'Superb' est semblable, au stade de jeune pousse, à celle observée chez 'Guard' qui possède le gène de résistance *H18*. Les femelles pondent spontanément sur tous les cultivars, sans indication d'antixénose, mais peu de larves se développent sur les jeunes pousses de 'Superb' et de 'Guard', ce qui indique que l'antibiose contre les larves est le mécanisme de résistance qui agit chez les jeunes pousses. Dans les champs, où l'infestation du blé de printemps se produit environ quatre semaines après le stade de jeune pousse, 'Guard' continue à être résistant, mais 'Superb' l'est moins, bien qu'il soit plus résistant que les cultivars très vulnérables. Les tiges infestées de 'Suberb' et de 'Nordic' risquent moins de se rompre que les tiges infestées des autres cultivars, ce qui indique que ces deux cultivars sont partiellement tolérants à l'infestation. Les tiges infestées de 'Guard' et d'autres cultivars se brisent fréquemment et sont intolérantes. Les pertes de rendement dues à l'infestation de la mouche de Hesse sont causées principalement par la rupture des tiges infestées et de leur recourbement, ce qui empêche la

Received 31 May 2005. Accepted 24 July 2006.

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récolte des graines sur ces tiges. Par rapport aux tiges saines, les tiges infestées qui sont encore dressées au moment de la récolte ont des graines de masse réduite et un nombre restreint de graines par épi, ce qui contribue à la perte de rendement. ‘Grandin, un cultivar apparenté à ‘Superb’, est la source probable de la résistance chez ‘Superb’, mais la généalogie de ‘Grandin’ ne fournit aucun indice sur le ou les gènes impliqués. L’antibiose partielle et la tolérance observées chez ‘Superb’ suffisent à réduire de 65 % les pertes dues à la mouche de Hesse par comparaison à un cultivar vulnérable tel que ‘AC Barrie’. ‘Superb’ est le premier cultivar canadien de blé de printemps connu à posséder un niveau de résistance à la mouche de Hesse d’intérêt agronomique.

[Traduit par la Rédaction]

Introduction

Hessian fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), infests winter and spring wheat, *Triticum aestivum* L. (Poaceae), throughout most of North America (Ratcliffe and Hatchett 1997). Damage occurs when larvae feed at the base of the plant or on stems immediately above nodes. The extraction of nutrients by larvae is less damaging than the injection of salivary fluids by the larvae during feeding (Hatchett *et al.* 1990). Necrotic lesions often form at the feeding site, reducing internodal elongation and the flow of nutrients. Infestation by Hessian fly of autumn-sown winter wheat can kill seedlings or stunt plants by destroying the apical meristem (Byers and Gallun 1972). Larval feeding the following spring can reduce subsequent seed production, with yield and test mass losses in winter wheat exponentially related to the number of larvae per stem (Buntin 1999). For spring-sown wheat, which dominates in western Canada, feeding by larvae weakens infested stems. Infested stems often break and fall over in a characteristic way, with the upper part of the stem remaining attached to the lower part at the point of the break. Spikes of broken stems lie on or near the soil, where they cannot easily be harvested. Some infested stems of spring wheat remain sufficiently upright for seed to be harvested; the effect of infestation on the productivity of this wheat is not known.

Although planting of resistant crops is an important strategy for managing Hessian fly in winter wheat grown in North America (Ratcliffe and Hatchett 1997), no spring wheat cultivars from western Canada are known to express resistance genes (Patterson *et al.* 1992) and, therefore, all are likely susceptible to damage. The level of damage, however, is not well documented. Infestation levels of over 10% in spring wheat occur periodically in localized areas, but in most years damage probably is lower. A survey of spring wheat fields in Manitoba in 1987 found Hessian fly in all fields, resulting in 0.2% to 3.2% stem breakage (McCullough 1987). In 1990, 6 of 11 fields surveyed in Manitoba had 3% to 11% stem breakage from Hessian fly attack (Turnock and Timlick 1990). In Saskatchewan, Hessian fly damage is mostly <1%, but localized outbreaks causing up to 30% stem breakage have been reported (Harris 1991).

The spring wheat cultivar ‘Superb’ was registered for commercial use in Canada in 2000. In field trials conducted during its development, ‘Superb’ appeared to suffer less of the stem breakage characteristic of Hessian fly infestation than other spring wheat cultivars, particularly the commonly grown ‘AC Barrie’. Greenhouse and field experiments were conducted to evaluate the level of resistance to Hessian fly of some commonly grown spring wheats, including ‘Superb’. Resistance was measured by the relative number of eggs deposited on plants of each cultivar, which reveals oviposition preferences of females (antixenosis); the relative proportion of larvae able to survive and develop on the cultivars, which reflects differences in larval mortality (antibiosis); and the relative ability of stems to withstand feeding without breaking (tolerance). Another aspect of tolerance to Hessian fly damage was assessed by comparing the number and mass of seeds from infested and uninfested stems that did not break.

Materials and methods

Seedling antixenosis and antibiosis

In 2001 and 2002, seeds of five spring wheat cultivars and ‘Superb’ were planted 1 cm deep in rows of 25 seeds per line in flats (47 cm × 25 cm × 5 cm) filled with a sandy loam soil, with four replicates for each cultivar. Plants were grown at Agriculture and Agri-Food Canada,

https://doi.org/10.4039/n05-051 Published online by Cambridge University Press

London, Ontario, in a greenhouse that was maintained at 24 °C for 8 days until leaves were 10 cm high. Flats were then moved to an insectary at 21 °C, 16L:8D, and 70% RH, and each was covered with a mesh cage. Newly emerged and mated female Hessian flies were placed in the cages, 25 per cage, from a culture reared for many generations in the laboratory and originally collected in southern Manitoba. Cages were removed after 3 days and eggs were counted on all leaves 3 to 4 days after female flies commenced oviposition. Puparia were counted on all plants 18–20 days later by peeling back the leaves to the base of the plant to expose any puparia under the sheath. Counts were transformed by log(x + 1) and analyzed by Tukey's studentized multiple range test.

Resistance in the field

The resistance of the spring wheat cultivar 'Superb' was assessed against resistant standards, the spring wheat cultivars 'Guard' and 'Nordic', which are registered for production in the United States but not in Canada. 'Guard' possesses the Hessian fly resistance gene *H18*, transferred from winter wheat, and is antibiotic (Cholick *et al.* 1984). 'Nordic' was observed to be tolerant to infestation in preliminary tests in Manitoba. 'AC Barrie', 'AC Foremost', 'McKenzie', and 'Glenlea' were included for comparison because they are widely grown spring wheats in western Canada and are expected to be susceptible. 'AC Domain' and 'Grandin' were included because these cultivars are parents of 'Superb'. The cultivars were seeded by hand in the first week of June in 2000–2003, in blocks of single-row plots 4–5 m long and 0.3 m apart, with 0.5 m between blocks, or by a press drill in single 1 m rows on 19 June 2004. The plots were seeded at least 1–2 weeks later than recommended for commercial fields (Wolfe *et al.* 1978) because preliminary experiments often showed that spring wheat seeded later had higher Hessian fly populations than wheat seeded earlier. Plots were replicated four times in 2000 and 2001 and three times in 2002, 2003, and 2004 in a randomized complete block design. In a separate test, 'Superb', 'AC Barrie', and 'Nordic' were seeded on 4 June 2002 with a double-disc press drill in four-row plots 4 m long and with 18 cm between rows. Plots were replicated five times in a randomized complete block design. All field plots were at the Agriculture and Agri-Food Canada Research Farm, Glenlea, Manitoba (49°38′N, 97°09′W).

The plots in 2000–2003 were assessed in early September, soon after the crop ripened, by counting the numbers of standing and lodged stems from a 1 m length of row in the middle of each plot or by counting all stems in the plot. Lodged stems had fallen to the ground because of breakage caused by Hessian fly feeding or poor straw strength. Up to 40 lodged stems and 40 standing stems were collected from each row, without a formal randomization procedure, by severing the stem near ground level. Stems were assessed for the type of breakage typically caused by Hessian fly, and then the leaf sheaths were removed to reveal puparia, which were counted. The total number of infested standing stems in each plot was estimated by multiplying the number of standing stems in the plot by the proportion of infested stems in the subsample. The proportion of broken infested stems was added to determine the proportion of stems infested by Hessian fly.

In 2004, plots were not assessed by sampling individual stems because few stems broke. On 27–28 September, four mature plants from the central area of each plot were uprooted and stems were severed at the internode just above the first node that had no adventitious roots. Ten stems per sample were selected randomly and puparia were counted. The puparia on the lower part or crown (McCall 1934) of all plants were exposed by removing the stem sheaths to the roots. The number of puparia per plant was estimated by adding the number of puparia on the crown and on the stems, based on the mean number of stems per plant. The numbers of puparia per plant crown, per tiller, and per plant were analyzed by Tukey's studentized multiple range test (SAS 1989).

Three components of plant tolerance to infestation by Hessian fly were assessed by quantifying stem breakage, the number of seeds, and the size of seeds. Breakage was estimated from the proportion of broken infested stems divided by the proportion of total infested stems in each plot and analyzed by Tukey's studentized multiple range test. Seed production was estimated by comparing the number of seeds per spike on each infested standing stem and on 10 randomly selected uninfested stems in each plot for two tests in 2002 (ANOVA, least squares means) (SAS 1989). Seed size was estimated by comparing the mass of 1000 seeds from infested

Table 1. Oviposition and survival of Hessian fly on seedlings of six spring wheat cultivars in the laboratory.

Year	Cultivar	No. of eggs/plant	% of plants with eggs	No. of pupae/plant	% of plants with pupae	% survival, egg to pupa
2001	Superb	8.5*a*	90.6*a*	0.5*c*	10.4*cd*	5.9
	AC Barrie	8.5*a*	86.9*a*	4.5*a*	85.0*a*	52.9
	Guard	7.5*a*	82.6*a*	<0.1*c*	1.3*d*	0.9
	Nordic	1.4*b*	43.2*b*	1.1*bc*	38.5*bc*	78.6
	Grandin	9.8*a*	86.1*a*	0.3*c*	3.9*cd*	3.1
	AC Domain	3.6*a*	78.5*a*	2.8*ab*	61.7*ab*	77.8
2002	Superb	8.0*a*	80.9*a*	0.2*b*	10.0*b*	2.5
	AC Barrie	9.2*a*	85.7*a*	5.3*a*	80.0*a*	57.6
	Guard	7.0*a*	80.0*a*	0.1*b*	5.6*b*	1.4
	Nordic	9.5*a*	72.7*a*	6.9*a*	66.7*a*	72.6
	Grandin	4.9*a*	68.7*a*	0.1*b*	3.9*b*	2.0
	AC Domain	3.4*a*	71.0*a*	2.7a	72.2*a*	79.4

Note: Within years, means followed by the same letter do not differ ($P > 0.05$, Tukey's studentized multiple range test). Data were transformed by $\log(x + 1)$ before analysis; untransformed means are presented.

and uninfested standing stems in the same plots (ANOVA, least squares means) (SAS 1989).

Yield loss caused by Hessian fly was estimated for each plot of each cultivar from the following variables: b, the proportion of infested broken stems; i, the proportion of infested standing stems; u, the proportion of uninfested stems; s_i and s_u, the number of seeds per spike on an infested standing stem and an uninfested standing stem, respectively; and w_i and w_u, the average mass of a seed in an infested standing spike and an uninfested standing spike, respectively. Assuming that all seeds from broken stems are lost and the yield of uninfested stems from plants where other stems are infested is not affected, yield loss (as a proportion of potential yield) = $[bw_u s_u + i(w_u s_u - w_i s_i)]/[w_u s_u(b + i + u)]$.

Results

Seedling antixenosis and antibiosis

The proportion of plants with eggs and the number of eggs per plant were similar on all wheat cultivars in 2002 and on all wheat cultivars except 'Nordic' in 2001 (Table 1). Few of the eggs on 'Superb', 'Grandin', or 'Guard' produced larvae that developed into pupae (<6%) (Table 1). Pupal populations on 'AC Barrie', 'AC Domain', and 'Nordic' were at least 8 times higher than those on 'Superb', and nearly all the plants of these three cultivars that were infested with eggs produced puparia.

Resistance in the field

At least one cultivar in each year had more than 30% of all its stems infested naturally by Hessian fly (Tables 2, 3). The proportion of stems infested was at least twice as high on 'AC Barrie', 'AC Foremost', 'McKenzie', and 'AC Domain' as on 'Superb'. 'Glenlea' had similar infestation levels as 'Superb' in 2002 but higher levels in 2003. In both 2000 and 2002, 'Nordic' and 'Superb' had similar infestation levels, whereas 'Guard' had few infested stems (Tables 2, 3). 'Grandin' had fewer infested stems than 'Superb' in 2003 and a similar number in 2004 (Tables 2, 3). The six cultivars tested in 2000–2003 had similar numbers of puparia per infested stem, ranging from 1.62 ± 0.47 (SE) for 'AC Foremost' to 2.57 ± 0.37 for 'Glenlea' in broken stems and from 1.06 ± 0.06 for 'Nordic' to 1.38 ± 0.07 for 'Superb' in standing stems. Because infested stems had similar numbers of puparia, the overall densities of Hessian fly puparia followed the same pattern as the proportions of infested stems (Table 2). 'AC Barrie', 'AC Foremost', 'Glenlea', and 'AC Domain' had more than twice as many puparia as 'Superb'. When counts in 2004 included puparia from the bases of stems or the crown as well as from excised stems, 'AC Barrie', 'McKenzie', and 'AC Domain' had at least twice as many puparia as 'Superb' (Table 3). Few puparia were ever found on 'Guard'.

A large proportion of the infested stems of 'AC Foremost', 'AC Barrie', and 'AC Domain' had broken just above a node and fallen over by

Table 2. Proportions of stems infested by Hessian fly and the relation of stem breakage to infestation for eight cultivars of spring wheat.

	Infested	Infested and broken		Broken	
Cultivar	% of stems	% of stems	% of infested stems	% of stems	% of infested stems
Single-row plots, 2000					
Superb	7.6±5.0*b*	3.0±0.9*b*	39	5.5±1.1*c*	54.5
AC Barrie	16.3±3.9*ab*	16.3±3.9*ab*	100	16.3±3.9*b*	100
Guard	0*b*	0*b*	—	0.7±0.4*c*	0
Nordic	19.2±6.0*ab*	2.4±0.7*b*	13	3.6±0.8*c*	66.7
AC Foremost	44.1±10.6*a*	39.4±12.1*a*	89	65.3±8.8*a*	60.3
Single-row plots, 2002					
Superb	10.1±1.7*bc*	5.0±1.3*b*	49	6.4±1.3*b*	78.1
AC Barrie	32.0±8.3*ab*	20.7±7.4*ab*	65	23.9±8.8*ab*	86.6
Guard	0.9±0.8*c*	0.9±0.8*b*	100	0.9±0.8*b*	100
AC Foremost	43.1±3.2*a*	33.7±1.5*a*	78	34.5±1.9*a*	97.7
Glenlea	12.1±3.9*bc*	3.9±1.7*b*	32	4.3±1.9*b*	90.7
AC Domain	27.5±10.5*abc*	19.6±9.5*ab*	71	21.0±9.5*ab*	93.3
Single-row plots, 2003					
Superb	34.9±2.0*b*	18.8±1.2*c*	54	24.5±1.7*c*	76.7
AC Barrie	69.0±3.4*a*	60.9±2.4*a*	88	73.0±3.8*a*	83.4
Guard	0.3±0.2*d*	0.3±0.2*d*	100	1.3±0.3*d*	23.1
Glenlea	60.8±2.5*a*	41.0±5.1*b*	67	45.8±5.7*b*	89.5
Grandin	19.2±1.6*c*	11.9±1.4*cd*	62	15.5±2.8*cd*	76.8
Multi-row plots, 2002					
Superb	13.4±1.8*b*	6.8±1.0*b*	51	8.9±1.3*b*	76.4
AC Barrie	41.6±4.1*a*	32.7±5.5*a*	79	34.8±5.6*a*	94.0
Nordic	12.3±2.8*b*	6.1±1.4*b*	50	10.1±2.3*b*	60.4

Note: Results for 2001 were excluded because <1% of stems of all cultivars were infested. Within each test, means followed by the same letter do not differ ($P > 0.05$, Tukey's studentized multiple range test).

Table 3. Densities of Hessian fly puparia (mean ± SE) on spring wheat cultivars in field plots in 2004.

	No. of puparia/plant			
Cultivar	Crown	Stems	Total	% of stems infested
Superb	0.6±0.2*bc*	0.8±0.4*abc*	1.4±0.3*bc*	10
AC Barrie	1.9±0.2*ab*	2.1±1.0*abc*	4.0±1.0*ab*	23
Guard	0*c*	0*c*	0*c*	0
Grandin	0.8±0.2*bc*	1.0±0.3*abc*	1.8±0.3*bc*	15
AC Domain	2.9±0.6*a*	2.9±0.8*ab*	5.8±1.3*a*	33
McKenzie	3.0±0.2*a*	3.0±0.2*a*	6.0±0.3*a*	33

Note: The crown is defined as the part of the plant up to the first node without adventitious roots, and the stem is defined as the part of the plant above this node. Means followed by the same letter do not differ ($P > 0.05$, Tukey's studentized multiple range test).

Table 4. Seed production (mean ± SE) for spikes of uninfested stems (U) and unbroken stems infested by Hessian fly (I) in field plots of five spring wheat cultivars.

	Mass of 1000 seeds, g				No. of seeds per spike			
Cultivar	U	I	*F*	*P*	U	I	*F*	*P*
Single-row plots								
All cultivars	27.5±0.9	22.8±0.8	88.2*	<0.0001	34.6±0.6	31.6±0.3	4.5*	0.060
Superb	29.1±0.4	20.3±1.8	62.3†	<0.0001	32.4±2.0	32.3±4.3	0†	0.98
AC Barrie	23.4±1.6	19.4±2.3	13.1	0.005	32.5±1.3	27.7±0.4	2.5	0.148
AC Domain	30.6±1.3	28.0±0.6	5.4	0.043	29.8±0.8	26.2±1.9	1.0	0.347
Glenlea	35.9±2.8	29.4±3.8	33.8	0.002	37.1±3.4	30.5±3.7	4.5	0.060
AC Foremost	18.4±0.6	16.8±0.3	1.9	0.202	41.6±2.5	41.5±1.5	0	0.98
Multi-row plots								
All cultivars	26.8±0.9	21.5±1.4	23.7*	0.0009	35.5±1.0	32.6±1.7	5.9*	0.038
Superb	28.8±0.8	20.9±1.2	17.1†	0.0025	33.3±0.3	32.2±2.0	0.3†	0.61
AC Barrie	21.1±1.2	18.6±1.0	1.7	0.229	33.1±1.1	29.1±2.4	3.9	0.081
Nordic	30.6±2.1	24.9±2.7	9.0	0.015	40.0±2.6	36.5±1.2	2.9	0.122

**F* values of infestation effect for all stems (ANOVA).
†*F* values for least squares means for infestation effect by cultivar (ANOVA).

the time the crop matured (Table 2). Infested stems of 'Nordic', 'Superb', 'Glenlea', and 'Grandin' also broke, but fewer infested stems broke in these cultivars than in the other cultivars. Although few 'Guard' stems were infested, those that were frequently broke. Stem breakage for 'Glenlea' and 'Grandin' was similar to that of 'Superb'.

In both single- and multi-row plots, spikes on infested unbroken stems produced seeds that were 17% and 20% lighter, respectively, than those produced by spikes on uninfested stems when cultivars were pooled to increase sample size (Table 4). Average seed mass for the individual cultivars was always lower for infested stems than for uninfested stems, and usually significantly so (Table 4). Similarly, for individual cultivars, the mean number of seeds per spike was lower for infested unbroken stems than for uninfested stems, although the differences were sometimes small (Table 4). Pooling cultivars to increase sample size revealed an 8% or 9% reduction in the number of seeds per spike on infested stems for the two tests, but only in the multi-row experiment, where many more stems were available, did the difference reach statistical significance (Table 4). The yield losses from reductions in seed size and number for all cultivars were 24% and 26% in the two experiments, estimated by comparing the product of seed mass and number for infested and uninfested stems.

Although yield was reduced by about 25% in infested standing stems, the largest yield loss occurred as the result of stem breakage. Assuming that all seeds from broken stems were lost, and based on the proportion of broken stems (Table 2) and loss of seed production (Table 4), about 80% of yield loss due to Hessian fly damage in 'Superb' and 'Glenlea' occurred from stem breakage. In 'Nordic', about 60% of yield loss was due to stem breakage, and for 'AC Barrie', 'AC Foremost', and 'AC Domain', over 90% of the yield loss was due to stem breakage. Yield loss as a result of Hessian fly infestation was lower for 'Superb' than for any other cultivar except 'Guard' (Table 5). In four field tests the losses for 'AC Barrie' were at least 2.5 times higher than those for 'Superb'. Losses for 'AC Foremost' and 'AC Domain' were equal to or higher than those for 'Superb'. Yield losses for 'Superb', however, were much higher than those for 'Guard' (Table 5).

Discussion

Natural infestations by Hessian fly reduced the yield of Canadian spring wheats in Manitoba. Stem breakage caused most of the yield loss associated with Hessian fly infestation. For cultivars such as 'AC Barrie', 'AC Foremost', and 'AC Domain' that are very susceptible to stem breakage, 90% or more of the yield loss was due to stem breakage. For cultivars with a higher tolerance to infestation, such as 'Superb'

https://doi.org/10.4039/n05-051 Published online by Cambridge University Press

Table 5. Yield loss, as a percentage of the yield of uninfested control plants, for spring wheat infested by Hessian fly in replicated field plots over three seasons.

	2000	2002		2003
Cultivar	Single-row	Single-row	Multi-row	Single-row
Guard	0	1	—*	0
Superb	4	7	9	24
AC Barrie	16	24	35	63
AC Domain	—	21	—	—
AC Foremost	40	35	—	—

*Not tested.

and 'Glenlea', about 80% of the yield loss was caused by stem breakage. Even if they did not break, stems infested by Hessian fly produced lighter and often fewer seeds, which reduced yield of these stems by about 25%. This type of damage has not been included in estimates of crop losses for spring wheat infested by Hessian fly in western Canada (Mitchener 1923; Turnock and Timlick 1990; Harris 1991).

The level of resistance of 'Guard' to Hessian fly in Manitoba was the same as that in South Dakota (Cholick *et al.* 1984), making 'Guard' a suitable spring wheat standard against which the resistance of Canadian wheat lines could be assessed. Hessian fly females oviposited readily on 'Guard', showing that antixenosis played no role in the resistance. Very few larvae that hatched from these eggs survived to be detected as puparia. The few infested stems of this cultivar found in the field broke in the characteristic way, indicating that 'Guard' is intolerant of infestation. The resistance of 'Guard' results only from antibiosis, which prevents larvae from feeding and surviving, and this antibiosis provides a high level of resistance under field conditions in Manitoba, although the cultivar is not registered for production in Canada.

The spring wheat cultivar 'Nordic', used as a second standard, showed neither antixenosis to oviposition nor antibiosis to larvae and was sometimes as heavily infested as susceptible wheat. However, fewer stems of this wheat broke in the way characteristic of infested stems of the susceptible cultivars. Although infested stems of 'Nordic' often remained standing, the losses in seed mass and seed numbers on these stems were similar to those on infested stems of 'AC Barrie'. Thus, 'Nordic' exhibits some resistance, but the resistance is expressed only as tolerance to infestation and is at a much lower level than the resistance due to larval antibiosis in 'Guard'.

'Superb' was the only Canadian spring wheat to show consistent resistance to Hessian fly. Antixenosis did not contribute to the resistance, but unexpectedly 'Superb' seedlings were antibiotic to Hessian fly larvae. This antibiosis did not hold up completely in older plants, at least not as well as the antibiosis expressed by 'Guard'. Nevertheless, infestation levels of 'Superb' usually were less than half those of susceptible spring wheats, and stem breakage was similar to that of 'Nordic'.

'Superb' is a selection from the cross 'Grandin//Grandin/AC Domain'. 'AC Domain' (Neepawa/Columbus/BW90) was highly susceptible to Hessian fly and, therefore, is not likely the source of the antibiosis and tolerance observed in 'Superb'. On the other hand, 'Grandin' expressed levels of seedling antibiosis in the laboratory and infestation in the field similar to those of 'Superb', as well as tolerance to infestation intermediate between that of 'Superb' and that of the susceptible spring wheats. The presence of Hessian fly resistance in 'Grandin' in this study contrasts with its reportedly high susceptibility to the 'Great Plains' biotype in more than 96% of assessments (USDA-ARS 2003). The lineage of 'Grandin', a North Dakota wheat (Len// Butte×2/ND507/3/ND593), provides no information on any possible source of resistance to Hessian fly. 'Len', although reported to be slightly more resistant than 'Grandin', resisted Hessian fly in only 2.5% of observations and was highly susceptible in 83% of observations, based on seedling assays (USDA-ARS 2003). 'Butte' and ND507 were equally susceptible. The pedigree of ND593 includes only 'Len', 'Butte', and ND507 (USDA-ARS 2003).

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Nevertheless, 'Grandin', which makes up three quarters of the parentage of 'Superb' and shows antibiosis and tolerance levels similar to those of 'Superb' in the Manitoba tests, is the most likely candidate for the source of the resistance genes expressed by 'Superb'. Whether the resistance in 'Superb' is due to previously unrecognized resistance genes or one or more of the well-known resistance genes expressed by winter wheats developed in the United States will not be known until the gene or genes can be characterized against the various races of Hessian fly used to identify resistance genes (Ratcliffe and Hatchett 1997).

In laboratory studies of seedlings, 'Superb' killed most of the newly emerged larvae, an antibiosis comparable to that of 'Guard', whereas resistance of more mature plants in the field was less effective. Cellular hypersensitivity is considered to be the basis for resistance to the Hessian fly (Grover 1995). Hypersensitive cells of resistant plants collapse in response to feeding by larvae, reducing the ability of larvae to increase cuticular-membrane permeability at the feeding site (Shukle *et al.* 1992). Studies of antibiotic resistance to Hessian fly have been conducted on seedlings, following the methods of Cartwright and LaHue (1944), because seedling resistance is required to protect winter wheat, the main host in the United States. The effectiveness of the *H18* 'Marquillo' type resistance in the spring wheat 'Guard' (Cholick *et al.* 1984) in Manitoba shows that the resistance persists in plants at stem elongation and perhaps later. Plants were attacked by Hessian fly at least 4 weeks later in their development in our field studies than in the greenhouse studies. Although the antibiosis of 'Guard' was comparable for seedlings and more mature plants, the antibiosis of 'Superb' was weaker in more mature plants than at the seedling stage. The difference in expression of resistance in 'Superb' and 'Guard' at different growth stages suggests that *H18* is not the gene responsible for resistance in 'Superb'.

Although 'Superb' has a lower level of antibiosis than 'Guard' at the growth stages when spring wheat is attacked in western Canada, this partial resistance reduces puparium densities by at least one half compared with other Canadian spring wheat cultivars. Furthermore, 'Superb' exhibits a useful level of tolerance to infestation compared with other Canadian spring wheats. The combination of antibiosis and tolerance in 'Superb' makes this cultivar an excellent choice for minimizing Hessian fly damage in western Canadian wheat. Nevertheless, the partial resistance may not always be adequate at high Hessian fly densities, which may warrant the introduction of well-known resistance genes such as *H18* to Canadian spring wheat germplasm.

Acknowledgments

We thank M. Glasgow, F. Ortiz, L. Verdon, and S. Wolfe for technical assistance, and S. Woods for statistical advice. W. Turnock, B. Timlick, and R. Bilodeau contributed to collecting preliminary data that led to the identification of 'Nordic' and 'Glenlea' as possible sources of tolerance. Financial support was provided by the Agri-Food Research and Development Initiative.

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