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RESISTANCE STABILITY OF THE SECONDARY TILLER OF 'CALDWELL' WHEAT AFTER THE PRIMARY CULM WAS INFESTED WITH VIRULENT HESSIAN FLY (DIPTERA: CECIDOMYIIDAE) LARVAE

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ABSTRACT

Secondary tiller resistance of 'Caldwell' wheat, *Triticum aestivum*, with the H_6 gene for larval resistance to Hessian fly, *Mayetiola destructor*, was maintained, after the primary culm had been previously infested with virulent larvae. Earlier studies showed that a primary culm infested initially with a virulent larva allowed subsequent normally avirulent larvae to survive on that cultivar; however, in our study the resistance of secondary tillers was maintained even though the primary culm was infested earlier with virulent Hessian fly larvae. This gene stability for resistance is important for optimizing wheat yield of those cultivars that possess genes resistant to the Hessian fly that are tillering and infested with different biotypes.

Wheat, *Triticum aestivum*, is a very adaptable crop being grown across a wide range of environments, and leads in production and acreage of all crops (Briggle and Curtis 1987). It is also quite tolerant of insect attack due to its ability to produce secondary tillers. Wheat usually has eight tiller buds, but generally only three or four of these develop fully (Williams and Langer 1975). Thus, an insect may feed upon and destroy the primary culm, while later-developing tillers may not be damaged and often produce seeds. Three major components affect wheat yield: density of fertile heads per unit area, number of seeds per head, and seed weight (often expressed as the weight per 1000 seeds) (Schlehuber and Tucker 1967). At maximum yield levels, a substantial increase in one yield component generally results in a decrease in one or both of the others.

Biotic and abiotic conditions influence tillering. Most studies of tillering in Gramineae have focused on cultivar differences and the effects of a wide range of environmental factors. The physiology of tillering has been investigated by studying the effects caused by various growth substances and inhibitors (Leopold 1964, Williams et al. 1975, Williams and Langer 1975). Little information, however, is available about the impact of insect numbers on wheat tillering. Multi-tillering wheat varieties were able to tolerate heavier infestations of the wheat bulb fly, *Delia coarctata* (Fällen), but this had the disadvantage of greater pest survival the following season (Oakley 1980).

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Successful Hessian fly, *Mayetiola destructor* (Say), infestation of the primary culm usually kills it, and may result in the production of tillers; however, young plants do not tiller under severe infestation; abundantlytillering wheat cultivars appear to survive Hessian fly infestations better (Barnes 1956). Buntin and Raymer (1989) noted that low to moderate Hessian fly damage levels reduced forage yield primarily by reducing tiller size and weight, rather than tiller density. Tillering of 'Arthur 71' (H_3H_5 genes for resistance), 'Monon' (H_3), and 'Seneca' (H_7H_8) increased when infested with Hessian fly biotypes B, D, or GP at higher temperatures (Sosa and Foster 1976). Tillering of 'Knox 62' (H_6 and perhaps H_7H_8) was relatively stable when infested with biotypes B, C, D, or GP, and biotype C did not cause an increase in tiller numbers in any of the four cultivars.

'Monon' and 'Newton' wheat cultivars differ in their tillering response when infested by Hessian fly (unpublished data, Wellso and Hoxie). Although 'Newton' tillered less than 'Monon' at the 0 infestation level, infestations of 1–3 puparia (indicative of the number of infesting larvae per seedling) per primary culm resulted in a greater number of tillers. 'Monon' had the same number of tillers at 0–3 puparia per primary culm; however, both cultivars tillered less at 4 or more puparia than at 1–3 puparia per primary culm. Thus, the Hessian fly may or may not increase tillering under light infestations; however, higher infestation levels lessened tillering, perhaps due to the depletion of soluble carbohydrates (Wellso et al. 1989).

The main resistance mechanism of wheat to the Hessian fly is larval antibiosis, resulting in the death of young larvae due to their inability to maintain sustained feeding (Gallun 1965, Shukle et al. 1990) and the resistant plant continues to grow with little evidence of insect feeding. Grover et al. (1989) noted that infestation by a single virulent larva resulted in an alteration of resistance of the plant, allowing survival of all normally avirulent larvae that concurrently or subsequently infested the plant. Their research dealt only with the primary culm. They used four cultivars ('Abe', Purdue line 6549, 'Caldwell' and 'Monon') with various combination of infestation with four Hessian fly biotypes (B, C, D, and L).

Little information is available about the effectiveness of Hessian fly resistant wheat genes when the primary culm is infested with a biotype that is either virulent or avirulent and a secondary tiller is subsequently infested with the same or another biotype. The objective of this study was to evaluate the stability of resistance in the primary culm and secondary tiller of 'Caldwell' wheat infested by virulent or avirulent Hessian fly biotype combinations.

MATERIALS AND METHODS

Test Insects. Hessian fly biotypes B and L, originally isolated in Indiana approximately 21 and 13 years ago, respectively, have subsequently been maintained in culture at the Insects and Weed Control Research Unit, U.S. Dept. of Agriculture, Purdue University, Ind. To maintain biotype cultures for these studies, mated females oviposited on susceptible wheat (e.g., 'Newton' CI 17715, H_0 gene for resistance) maintained in a growth chamber at 21.1°C, a 16:8 (L:D) photoperiod, light intensity of 300 μEinsteins/m^2/sec, and 65% R.H. Biotype purity was verified periodically with wheat cultivars having known resistance genes (Sosa and Gallun 1973).

Test Plants. Three 'Caldwell' wheat (CI 17897; H_6 gene; resistant to Hessian fly biotype B, but susceptible to biotype L) seeds, obtained from Purdue University's wheat breeding program, were soaked for 1 h, planted in a mix-

ture of soil-vermiculite in forty 10 cm diameter plastic pots (with 4 replicates), and later thinned to one seedling per pot (24 seedlings of each cultivar per treatment). Plants were maintained in a growth chamber set at 21.1°C, 65 ± 10% RH and 14:10 (L:D), and provided with Hoagland's solution biweekly and watered as needed.

Treatments. 'Caldwell' seedlings were exposed to ovipositing Hessian fly as follows:

- Control, not infested;
- Primary culm infested 1 wk after planting with biotype B;
- Primary culm not infested; secondary tiller infested 3 wk after planting with biotype B;
- Primary culm infested 1 wk after planting with biotype B; secondary tiller of the same seedling infested 3 wk after planting with biotype B;
- Primary culm infested 1 wk after planting with biotype L; secondary tiller of the same seedling infested 3 wk later with biotype B.

Adult Hessian fly of the desired biotype were released in a growth chamber to oviposit on the first or second leaf of the primary culm, and oviposition was verified within 24 h. Leaves without eggs were exposed to adults until eggs were found on each seedling. Secondary tiller leaves were infested by confining a mated female in a cylindrical screen cage (2.5 x 12 cm) with plastic foam plugs supported by a metal rod enclosing a normal leaf [as opposed to dark green leaves on a primary culm that previously had been infested successfully by virulent larva(e)]. The cage was removed after oviposition was confirmed. The plants were scored 6 wk after planting relative to the number of tillers, plant length from the crown to the apex of the longest leaf, above ground fresh weight, live Hessian fly larvae or puparia and dead larvae (usually small red larvae about 0.5 mm in length). The experiment was replicated on four dates.

Data Analysis: After analysis of variance (ANOVA, SAS Institute 1985) using a split-plot design, significantly different means ($P \leq 0.05$) were separated by Student-Newman-Keuls test (Steel and Torrie 1980).

RESULTS AND DISCUSSION

There was a significantly higher ($P=0.05$) level of infestation of primary culms of 'Caldwell' seedlings by virulent biotype L than by avirulent biotype B larvae (Table 1). Secondary tillers also were resistant to biotype B larvae, including those from seedlings on which the primary culm was infested by virulent biotype L larvae.

The mean numbers of tillers (stems) per plant was not significantly different among the Hessian fly treatments (Table 1). Plant length and fresh weight did not differ significantly between control plants infested by avirulent biotype B larvae on either the primary or secondary tiller, however, plant length was significantly less when both the primary culm and secondary tiller were infested with biotype B larvae. Virulent biotype L larvae had the greatest effect on plant parameters. Infestation of the primary culm by biotype L larvae resulted in a significant decrease in plant weight, length and number of leaves per plant. The greatest impact to the plant by biotype L larvae was reduction in fresh plant weight, which decreased 50% of that of the control. Wellso et al. (1989, 1990) reported that uninfested plants of 'Winoka' and 'Monon', respectively, had significantly greater plant length, weight, and number of leaves than plants infested with virulent larvae. The 50% reduction in fresh plant weight of 'Caldwell' was less than the 65 to 89% reduction in

Table 1. Effect of virulent (biotype L) and avirulent (biotype B) larval infestation of the Hessian fly (FH) on the primary culm and/or second;ary tillers of 'Caldwell' winter wheat in the laboratory[a]

Treatments[b]		% HF infestation ± SD		HF[c] per tiller ± SD		Stems per plant ± SD	Leaves per plant ± SD	Plant length (cm ± SD)	Fresh plant wt (g ± SD)
Primary culm	Secondary tiller	Primary culm	Secondary tiller	Primary culm	Secondary tiller				
B	–	21.9± 2.6b	–	3.7 ± 2.0	–	3.9 ± 1.1a	16.8 ± 3.3a	46.3 ± 2.3a	4.8 ± 1.4a
–	B	–	18.8 ± 12.5a	–	5.8 ± 4.5	4.1 ± 1.4a	18.2 ± 4.1a	45.4 ± 2.9a	6.0 ± 1.5a
B	B	15.6 ± 12.0b	12.5 ± 10.2a	11.8 ± 9.6	2.3 ± 1.0	3.7 ± 1.2a	16.3 ± 3.7ab	43.2 ± 4.1b	4.4 ± 1.5a
L	B	75.0 ± 49.9a	9.4± 1.2a	8.2 ± 5.4	13.7 ± 6.0	3.6 ± 1.5a	13.6 ± 1.5a	36.0 ± 6.1c	2.4 ± 1.3b
–	–	–	–	–	–	3.6 ± 0.9a	15.9 ± 3.2b	46.0 ± 3.0a	4.8 ± 1.3a

[a]Means in the same column followed by the same letter are not significantly different ($P \leq 0.05$), according to a Fisher's Protected LSD test, for % HF infestation of BB and LB ($df = 1$; $F = 21.7$), stems per plant ($df = 4$; $F = 1.1$), leaves per plant ($df = 4,5$; $F = 5.9$), plant length ($df = 4$; $F = 38.9$), and fresh plant weight (df = 4; $F = 28.9$). This experiment included four replicates and 8 plants per replicate.

[b]HF biotype on primary colm and/or a secondary tiller.

[c]Larvae and puparia per tiller.

weight of 'Winoka' infested with 1 to 3 or 7 to 9 larvae, respectively, for 8 wk old plants (Wellso et al. 1989). The greater loss in weight of 'Winoka' plants may have been due, in part, to environmental differences between the test parameters and to the longer duration of the study.

The adverse impact (stunting) of infestation by virulent biotype L larvae on development of the primary culm of susceptible 'Caldwell' seedlings was clearly demonstrated in this study. Of significance, however, was the fact that secondary tillers which developed from stunted primary culms (susceptible to biotype L), retained resistance to the avirulent biotype B larvae. This is in contrast to the finding that resistance of the primary culm to normally avirulent larvae is lost following feeding by a virulent larva (Grover et al 1989). The response of tillers observed in this test would be beneficial where different biotypes are present in the same field, because tillers would be capable of surviving and producing grain, even after the primary culm was destroyed by a virulent biotype.

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