EFFECT OF TEMPERATURE ON THE EXPRESSION OF RESISTANCE IN WHEAT DERIVED FROM *TRITICUM TAUSCHII* AND IN RYE TO HESSIAN FLY, *MAYETIOLA DESTRUCTOR* (SAY)

by

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INTRODUCTION

Since its introduction into the United States during the American Revolution, the Hessian fly [*Mayetiola destructor* (Say)] has been a major pest of common wheat, *Triticum aestivum* L. em Thell. Epidemics of Hessian fly have occurred throughout the major wheat growing areas of the United States and have resulted in millions of dollars of damage. State and USDA research agencies have been involved in developing wheat cultivars resistant to Hessian fly. However, the vast genetic variability (biotypes) found in most Hessian fly populations has allowed the insect to adapt and survive despite discovery and employment of resistant genes (Hatchett and Gallun 1968). This adaptability will likely overcome todays resistant cultivars and make them vulnerable to virulent biotypes in just a few years. Thus, wheat breeders and entomologists must continue to find and incorporate new sources of resistance into adapted wheats to avoid future outbreaks.

New sources of genetic resistance to Hessian fly have been identified in goatgrass, *Triticum tauschii*, the donor of the D-genome in common wheat (Hatchett and Gill 1981) and in rye, *Secale cereale* (Hatchett 1976, unpublished data). A recent study indicated that Hessian fly resistance derived from *Triticum tauschii* was expressed as antibiosis and conditioned by a single-dominant genetic factor (Hatchett et al. 1981). Resistance derived from rye is also being investigated as a potential source of Hessian fly resistance in wheat. Resistance is being transferred by x-ray induced rye-wheat chromosomal translocation. This technique was successful in transferring resistance to greenbug, *Schizaphis graminum* (Rondani) from

rye to wheat (Sebesta and Wood 1978). The mechanism of Hessian fly resistance in rye is also larval antibiosis but the inheritance of resistance is unknown. Resistance derived from *T. tauschii* and rye is presently being transferred to adapted wheat genotypes (J. H. Hatchett, personal communication).

Hessian fly biotypes and the increased susceptibility of resistant wheats at high temperatures are the most critical factors affecting the permanence of resistance to Hessian fly. The latter factor is considerably important in the southern Great Plains since short periods of above-normal temperatures are common in the fall and spring when Hessian fly infestations occur. Ideally, the source of Hessian fly resistance used in breeding hard red winter wheat should be stable at high temperature to provide maximum protection.

The objectives of this study were to: 1) determine the effect of temperature on expression of resistance to Hessian fly in synthetic hexaploid wheat having resistance derived from *Triticum tauschii*, 2) determine for *T. tauschii* derived resistance whether the heterozygous genotype differs from the homozygous dominant genotype in expressivity of resistance at high temperature, and 3) determine the effect of temperature on expression of resistance in two rye cultivars, Balbo and Gator.

REVIEW OF LITERATURE

Sources and Genetics of Resistance to Hessian fly

A number of genetically different sources of resistance to Hessian fly have been identified in wheat. The genetics of resistance in Kawvale, which exhibits tolerance, is not understood. Marquillo resistance is not totally understood, although it is believed to involve several

recessive genes for antibiosis (Gallun 1977).

The genetics of resistance of other sources has been studied. The number of genes involved and the linkage groups of some genes have been determined.

The genetics of resistance in wheat and the interactions of resistant genes with Hessian fly biotypes were reviewed by Gallun (1977). Resistance in Dawson wheat is determined by two genetic factors, designated H_1 and H_2 (Gallun and Patterson 1977). The H_1H_2 genes provide resistance to Hessian flies in California, but are not highly resistant to Hessian flies in the midwest and eastern United States (J. H. Hatchett, unpublished data). Two independent dominant genes, designated H_7H_8 are resistant to the Great Plains (GP) biotype and biotype E but are susceptible to biotypes A, B, C, and D. A single dominant gene designated H_3 provides resistance to biotypes A, C, and GP, but not to biotypes B, and D. This gene was found to condition resistance in Illinois No. 1 W 38 wheat (Gallun and Patterson 1977). A single dominant gene designated H_6, transferred from PI 94587 to the cultivar Knox 62, provides resistance to biotypes A, B, and GP, but not to biotypes C and D. The dominant genetic factor designated H_5 is derived from Ribeiro (Gallun and Patterson 1977) and is resistant to GP biotype and biotypes A to E. Two biotypes, J and L, which can infest wheats having the H_5 gene were found in 1978 in an Indiana wheat field (Sosa 1981). Two linked dominant genetic factors designated H_9H_{10} were found in a Portuguese wheat which after selection was named Elva (CI 17714) (Carlson et al. 1978). H_9H_{10} genes provide resistance to all known biotypes. A single dominant gene designated H_{11}, found in PI 94587, confers resistance to Hessian fly biotype D (Stebbins et al. 1981). Hessian fly resistance found in *Triticum tauschii* was shown to be conditioned by a single dominant

gene and provides resistance to all known biotypes (Hatchett et al. 1981). The following table summarizes the interactions of Hessian fly resistant genes with Hessian fly biotypes. Genes H_3 and H_6, and H_9H_{10} are located on chromosome 5A (Stebbins et al. 1981).

Effect of Temperature on Expression of Resistance in Wheat to Hessian Fly

Previous studies have shown that temperature affects the expression of Hessian fly resistance in wheat. Generally, as temperatures increase, the susceptibility of wheats having specific resistant genes also increase (Cartwright and Shands 1944). In the fall of 1938 a field seeded to resistant spring wheat Illinois No. 1 W 38 (CI 12061) (H_3) in Indiana showed an unexpectedly high infestation (Cartwright et al. 1946). Cartwright et al. (1946) grew and infested plants at two temperature ranges, 18-21° C and 24-27° C. They found that Illinois No. 1 W 38 (H_3) in the warm environment showed a mean infestation of 35.8% compared to 4.8% in the cool environment. Cartwright et al. (1946) also showed that the durum wheat PI 94587 maintained its resistance at high temperatures. Sosa and Foster (1976) later reported that this source of resistance actually does break down at high temperatures although to a lesser degree. Knox 62 (H_6), a derivative of PI 94587, showed only slight decrease in resistance at high temperatures to biotypes B and GP. Sosa and Foster (1976) investigated the temperature stability of resistance in four cultivars having H_3, H_5, H_6, and H_7H_8 genes and the interaction with four Hessian fly biotypes. In almost every case biotypes that were avirulent to a cultivar, became increasingly virulent on that cultivar as temperatures increased. However, the breakdown of resistance did not apply equally to

Interactions of Genes for Hessian Fly

Resistance with Hessian Fly Biotypes

Genetic Factor	Biotypes						Chromosome Location
	GP	A	B	C	D	L	
H_1H_2	R	S	S	S	S	S	unknown
H_7H_8	R	S	S	S	S	S	unknown
H_3	R	R	S	R	S	S	5A
H_6	R	R	R	S	S	S	5A
H_5	R	R	R	R	R	S	unknown
H_9H_{10}	R	R	R	R	R	R	5A
H_{11}	R	R	R	R	R		unknown
derived from *T. tauschii*	R	R	R	R	R	R	unknown

R = resistant, S = susceptible.

all biotypes. For example, Arthur 71 (H_5) was resistant to biotype C at all temperatures, whereas resistance to biotype D declined with higher temperatures. These findings suggest complex interactions between temperature, resistance, and biotype.

Gallun and Langston (1963) found that larvae stopped feeding after two days on a resistant cultivar (H_5) at 18-20° C and later died. Permanent stunting of a susceptible cultivar requires six days of larval feeding (Prompichai 1974). Sosa (1979) found that permanent stunting of 100% of the resistant plants occurred after seven days of feeding at 27° C. In contrast, when the first four days of feeding were at 18° C, 100% of the plants were resistant regardless of later exposure to high temperatures.

Recently, Carlson et al. (1978) identified Hessian fly resistance in *Triticum turgidum* (Elva, CI 17714) and showed that resistance was maintained at 27° C.

Resistance in Rye to Hessian Fly

Although rye is a host of the Hessian fly, there has been little effort to identify resistance in rye germplasm or develop resistant rye cultivars. Hatchett (unpublished data 1976) evaluated a diverse group of ryes and triticales for Hessian fly resistance and found a large number of lines or cultivars resistant (antibiosis) or segregating for resistance. Cultivars Balbo and Gator were homogeneous resistant to biotype D Hessian fly. Painter (1951) also reported Balbo to be nearly immune to Hessian fly. The effect of temperature on the expression of resistance in rye has not been studied.

EXPERIMENT I

Temperature Stability of Hessian Fly Resistance Derived from *Triticum tauschii*

Materials and Methods

Seed Sources. Two synthetic hexaploid wheats (KU221-14 and KU221-19) with Hessian fly resistance derived from *T. tauschii* were crossed with common wheats Eagle and Amigo for genetic studies (Hatchett et al. 1981). The parentages of the synthetic hexaploid wheats were: KU221-14 (*T. durum* cv. 'Gulab' x *T. tauschii*) and KU221-19 (*T. persicum* var. *stramineum* x *T. tauschii*). F_3 plants of several homozygous resistant families were selected and grown to maturity. The F_4 seed of individual plant selections was used in this study as representative of *T. tauschii* resistance.

Hessian fly culture. The biotype D Hessian fly culture used in these experiments was obtained from Purdue University and has been maintained at Kansas State University for four years. Larvae of biotype D stunt and survive (virulent) on wheats having H_1H_2, H_3, H_6, and H_7H_8, but cannot stunt or survive (avirulent) on wheats having H_5 and H_9H_{10} or the single dominant resistant gene derived from *T. tauschii*. Flies used in these experiments were reared on a Purdue wheat having H_3 and H_6 genes.

The GP biotype was used in one portion of experiment II only. Larvae of GP biotype cannot stunt or survive on wheats having any of the known genes for resistance. The GP biotype used had been reared in a greenhouse on Triumph wheat for about 10 generations and selected for avirulence to wheats having H_3, H_6, and H_7H_8 genes. Techniques for routine rearing and handling of Hessian flies and for infesting wheat were similar to those described by Cartwright and LaHue (1944).

Specific testing procedures: The resistance of selected F_4 lines representing *T. tauschii* resistance (hereafter referred to as synthetic hexaploid wheat) was compared to Arthur 71 (H_5), Elva (H_9), and Seneca (H_7H_8) wheats at four temperatures; 18, 23, 28, and 31° C. Arthur 71 is resistant to biotype D at low temperature, but susceptible at high temperature (27° C) (Sosa and Foster 1976). Elva is resistant to biotype D at 27° C (Carlson et al. 1978). Seneca has no genes for resistance to biotype D and was used as a susceptible check.

For each temperature, seed of each of the four entries was seeded in small plastic tubes (12 x 3 cm) containing soil. The tubes were placed in a plastic rack designed to hold the tubes. Enough seed was germinated to obtain about 50 seedlings of each entry for each temperature (1 plant/tube). The seeds were germinated and plants were grown and infested in a controlled growth chamber programmed for 18 $\pm$ 1° C and 12:12 light:dark cycle.

When the plants were at the one leaf stage (ca 5 cm tall) the entire group of plants was covered with a cheesecloth tent and biotype D gravid females were released to infest the plants. Females were allowed to oviposit for 8 hours so that eggs would hatch at approximately the same time. After the plants were infested, 30 plants of each entry were selected for similar size, vigor, and number of eggs (6-12/plant). The 30 plants of each entry were placed in three rows (10/row) with the rows randomized in the rack. Four entries, 30 plants/entry for each temperature constituted one replication. When the larvae had migrated to the base of the plants (5 days after oviposition) each rack was placed in a growth chamber programmed for the desired temperature. The growth chambers were calibrated for constant temperatures of 18, 23, 28, and 31 $\pm$ 1° C

at soil level and programmed for a 12:12 light:dark cycle. Temperatures were monitored several times daily during the tests with a digital centigrade thermometer (Cole-Parmer Instrument Co. Model 8502-20).

Twenty days after infestation the plants were removed from the tubes and recorded either susceptible or resistant on the basis of their reaction to larval feeding. Susceptible plants were stunted and dark blue-green in color with broad second or third leaves. Resistant plants were not stunted and retained their yellowish-green color. The effect of temperature on the level of antibiosis was also studied by determining the condition (live or dead) and size (length)of larvae on susceptible and resistant plants. All plants were examined under a stereoscopic microscope (30X) for presence of larvae at the base of the first leaf sheath. Dead and live larvae were counted and measured with an ocular micrometer. Dead larvae retained the normal red body color of first instar larvae whereas live larvae were translucent white.

Experiment I was replicated four times over time. Each replication required about four weeks for completion. Analysis of variance tests were performed on the data and significance of means was tested at the $P = 0.05$ level.

An experiment was also conducted to determine if heat stress prior to larval feeding affects the subsequent expression of resistance. Arthur 71 seed was germinated in 10 cm diam. plastic pots (20 seeds/pot) and the plants were grown and infested at $28 \pm 1°$ C. When the plants were in the one-leaf stage biotype D females were released to infest the plants for 2 hours so that eggs would hatch approximately the same time. One day before the larvae began feeding, 200 plants were moved to a growth chamber programmed for $18 \pm 1°$ C and remained there for the duration of the

experiment. A second group of 200 plants were maintained at 28° C through the first day of larval feeding after which they were moved to the 18° C chamber and retained at 18° C for the remainder of the experiment. About 20 days after infestation plants were rated resistant or susceptible on the basis of feeding symptoms. Plants that appeared resistant were examined for presence of larvae at the base of the first leaf sheath to verify that they were infested.

RESULTS

The reactions of Seneca, Arthur 71, Elva, and the synthetic hexaploid wheat to biotype D larvae at four temperatures are shown in Table 1. All of the Seneca plants at all temperatures showed susceptible reactions which indicated a uniform infestation. As expected, Arthur 71 and Elva were resistant to biotype D larvae at 18° C. Arthur 71 showed some reduction in resistance at 23° C, as 81% of the plants were resistant at that temperature. Elva and the synthetic hexaploid wheat maintained their resistance at 23° C; all plants of both entries were resistant. The expression of resistance in Arthur 71 was further reduced at 28° C, as only 16% of the plants were resistant. Elva and the synthetic hexaploid wheat showed no significant reduction in resistance at 28° C, although one Elva plant and two synthetic hexaploid wheat plants showed susceptible reactions. The appearance of many of the Elva and synthetic hexaploid plants during the first 3-5 days of larval feeding at 28° C suggested that the plants were severely stressed. The plants were initially stunted and appeared susceptible, but they recovered later and ultimately expressed resistance. Only three (2.5%) of the 120 Arthur 71 plants at 31° C were

Table 1. Reactions of Seneca (H_7H_8), Arthur 71 (H_5), Elva (H_9H_{10}), and a synthetic hexaploid wheat (*T. tauschii* resistance) to biotype D of Hessian fly larvae at four temperatures.

Entry	18° C			23° C			28° C			31° C		
	No. plants[1/]		Mean % resistant[2/]	No. plants		Mean % resistant	No. plants		Mean % resistant	No. plants		Mean % resistant
	R	S		R	S		R	S		R	S	
Seneca	0	100	0.00 e	0	100	0.00 e	0	100	0.00 e	0	100	0.00 e
Arthur 71	119	1	99.17 a	98	22	81.67 c	20	100	16.67 d	3	117	02.50 e
Elva	120	0	100.00 a	120	0	100.00 a	119	1	99.17 a	107	13	89.17 b
Synthetic hexaploid (*T. tauschii* resistance)	120	0	100.00 a	120	0	100.00 a	118	2	98.33 a	90	30	75.00 c

[1/] R = resistant S = susceptible

[2/] Means with the same letter in horizontal rows do not differ significantly ($P<0.05$).

resistant, indicating a nearly complete loss of resistance due to temperature. Resistance in Elva and the synthetic hexaploid wheat was significantly reduced at 31° C. Thirteen (11%) of the 120 Elva plants were rated susceptible, and 30 (25%) of the 120 synthetic hexaploid plants showed susceptible symptoms. Larvae that survived on resistant and susceptible plants of all entries at 31° C were small and appeared less vigorous than those surviving at other temperatures. Foster and Taylor (1975) reared Hessian fly larvae at constant temperatures of 15.6, 18.3, 21.1, 23.9, and 26.7 $\pm$ 1.1° C and showed that 21.1° C was optimum for growth, developmental time, and adult emergence.

Larval survival on resistant and susceptible plants was studied to determine likelihood of population increases when infestations occur during periods of high temperatures. The mean numbers of live and dead biotype D larvae/plant on Arthur 71, Elva, and the synthetic hexaploid wheat plants at four temperatures are presented in Table 2. Arthur 71 plants hosted live larvae at all temperatures, but there were significant increases in larval survival associated with increases in temperature. Arthur 71 plants averaged 1.33 live larvae/plant at 23° C and 3.97 live larvae/plant at 28° C. Elva plants hosted no live larvae at 18° C, and an average of only 0.03 live larvae/plant were present at 23° C. At 28 and 31° C Elva plants averaged 0.31 and 0.65 live larvae/plant, respectively. The synthetic hexaploid plants hosted no live larvae at 18 and 23° C. A mean of 0.14 and 0.98 live larvae/plant were on the synthetic hexaploid plants at 28 and 31° C, respectively. About 7 times more larvae were present on the synthetic hexaploid plants at 31° C than were present at 28° C. But a constant temperature of 31° C probably places more stress on plants than commonly occurs in wheat fields in the southern Great Plains

Table 2. Survival of biotype D larvae on resistant and susceptible plants of Arthur 71 (H_5), Elva (H_9H_{10}), and a synthetic hexaploid wheat (*T. tauschii* resistance) at four temperatures.

Entry	Total no. of plants/ temperature	18° C Mean no. larvae/plant		23° C Mean no. larvae/plant		28° C Mean no. larvae/plant		31° C Mean no. larvae/plant	
		Dead	Live	Dead	Live	Dead	Live	Dead	Live
Arthur 71	120	4.26	0.24 b[1/]	2.31	1.33 d	0.36	3.97 e	0.21	4.11 f
Elva	120	5.75	0.00 a	4.72	0.03 a	5.22	0.31 b	5.87	0.65 c
Synthetic hexaploid (*T. tauschii* resistance)	120	5.05	0.00 a	4.69	0.00 a	4.04	0.14 b	6.11	0.98 d

[1/] Means (No. live larvae/plant) with the same letter in horizontal rows do not differ significantly ($P < 0.05$).

region during periods of larval feeding in the spring and fall.

Level of antibiosis. Death of all larvae on a plant indicates a high level of antibiosis. In general, as the temperature increased, larval survival also increased on Arthur 71, and to a lesser extent on Elva and the synthetic hexaploid wheat. The size (length) of surviving larvae was used as a measure of low level antibiosis, i.e. nonlethal effect on larvae. Table 3 shows the larval length data. At 28° C, biotype D larvae surviving on wheat plants (Seneca) having no genes for resistance to biotype D, were significantly larger than those larvae that survived on susceptible Arthur 71 (H_5) plants. This indicated that the gene (H_5) adversely affected the development of biotype D larvae on plants that did not express resistance.

Larvae surviving on resistant plants of Arthur 71, Elva, and the synthetic hexaploid wheat were not smaller than those surviving on susceptible plants of the same entry. For example, at 28° C the mean length of live larvae on resistant and susceptible Arthur 71 plants was 3.29 and 3.22 mm, respectively. This may have been due to the fact that resistant plants usually harbored low numbers of live larvae, thus decreasing competition between larvae. There was no larval survival on resistant Elva and synthetic hexaploid wheat plants at 18° and 23° C. At 28° C resistant Elva and synthetic hexaploid wheat plants hosted 0.27 and 0.13 live larvae/plant respectively. At 31° C resistant Elva and synthetic hexaploid wheat plants hosted 0.34 and 0.44 live larvae/plant respectively. Increased larval survival (associated with temperature increases) on resistant plants is interpreted as an intermediate condition between full expression of resistance (no larval survival) and complete loss of resistance (stunting of plant).

Table 3. Size (length) of live biotype D larvae on susceptible Arthur 71 (H_5) and Seneca (H_7H_8) plants at 28° C.

Entry	Total number larvae measured	Mean length in mm of larvae at 28° C
Arthur 71	80	3.22 a[1/]
Seneca	80	3.42 b

[1/] Means with different letters differ significantly ($P < 0.05$).

Heat stress prior to larval feeding. Of the Arthur 71 plants that were exposed at 28° C through the first day of larval feeding, 48% were resistant. Thus, one day of larval feeding at 28° C caused significant reductions in resistance as was also reported by Sosa (1979). Of the Arthur 71 plants that were moved to the 18° C chamber one day before larval feeding began, 96% were resistant. Exposure to 28° C prior to larval feeding did not significantly reduce subsequent expression of resistance in Arthur 71 plants.

DISCUSSION AND CONCLUSIONS

Sensitivity of Hessian fly resistant genes to high temperature combined with frequent high temperatures during spring and fall in the southern Great Plains wheat region make expression of resistance at high temperatures an important criterion for evaluating new sources of resistance. The level of antibiosis expressed at high temperatures is also an important consideration since larval survival may allow populations to increase.

Resistance derived from *T. tauschii* was compared to Ribeiro (H_5) derived resistance, a source known to be temperature sensitive (Sosa and Foster 1976), and to Elva wheat (H_9H_{10}), a source that is resistant at 27° C (Carlson et al. 1978) at four temperatures. Resistance derived from *T. tauschii* in synthetic hexaploid wheat to biotype D larvae was not significantly affected at 18, 23, and 28° C. However, resistance of the synthetic hexaploid wheat declined significantly at 31° C, but this constant temperature may have produced more heat stress than normally occurs in the field.

One can only speculate about the amount of heat stress that wheat plants are subjected to during periods of Hessian fly larval feeding in wheat fields during the fall and spring. There has been no field study to determine fluctuations in soil temperatures at critical times. Constant temperatures were used in this study, but temperatures fluctuate in field conditions. Therefore, it is difficult to make accurate estimations of field performance on the basis of these experimental results. The results of this study can be used however, to compare a new source of

resistance to one that is known to be temperature sensitive. *T. tauschii* derived resistance was markedly superior to Ribeiro (H_5) derived resistance in expression of resistance at 23, 28, and 31° C and equal to resistance from Elva at 18, 23, and 28° C. However, at 31° C resistance in Elva was superior to resistance derived from *T. tauschii*. Elva has two genes for resistance while the synthetic hexaploid wheat carries one. The additional gene in Elva may provide a degree of buffering against temperature effects. Although resistance derived from *T. tauschii* was significantly reduced at 31° C, it should be emphasized that the majority of the synthetic hexaploid plants (75%) were resistant at that temperature.

A high level of antibiosis (low larval survival) was expressed by the synthetic hexaploid wheat plants at 18, 23, and 28° C. This suggests that population buildups are unlikely to occur if *T. tauschii* derived resistance is employed.

Measurements of larvae on susceptible Arthur 71 plants at 28° C indicated that their mean length was less than that of larvae on Seneca plants at the same temperature. The H_5 gene can adversely affect the growth and development of the larvae, despite a "break down" of resistance due to high temperature. This implies that susceptible plants may exhibit low level antibiosis (non-lethal effect).

Sosa (1979) reported that when duration of exposure to high temperatures was varied during critical larval feeding periods, expression of resistance was affected. In those experiments there was no exposure prior to larval feeding. In this study, an experiment was conducted to determine if exposure prior to larval feeding only affects subsequent

expression of resistance. Prior exposure did not result in significant reductions in expression of resistance. The implication is that the high temperature effect is on the plant-insect interaction and/or on the level of virulence expressed by the insect.

EXPERIMENT II

Temperature Stability of Hessian Fly Resistance in the Heterozygous Dominant Condition Derived from *T. tauschii*

MATERIALS AND METHODS

Seed sources. Some of the F_4 synthetic hexaploid wheat plants having resistance derived from *T. tauschii* were used in crosses with the susceptible wheat Amigo (CI 17609) to produce F_1 plants for testing the temperature stability of *T. tauschii* resistance in the heterozygous condition.

In previous research on interaction of temperature and resistance there has been no attempt to measure the penetrance of the dominant allele in heterozygotes in a high temperature environment. This aspect of genotype-environmental interaction is important from the aspect of understanding the nature of dominance and allelic behavior of the gene. From a practical viewpoint, the information would be useful in hybrid wheat development.

Crossing procedures. The synthetic hexaploid was used as the pollen (male) parent, while Amigo was emasculated and used as the female parent. Emasculation is the removal of male flower parts to prevent self-pollination. The anthers of the Amigo spikelets were removed with forceps before the pollen was mature, and the spikes were covered with glycine bags to prevent outcrossing. About 3 to 5 days after emasculation, the stigmas appeared fluffy and expanded; this indicated maximum receptivity to pollen. Spikes from synthetic hexaploid plants that held mature pollen were inverted and twirled over the selected Amigo spikes causing

pollen to fall on the receptive stigmas. The number of seeds harvested (successful pollinations) per spike ranged from 0 to 22. About 75 wheat spikes were emasculated and pollinated, yielding about 450 F_1 seeds.

Specific testing procedures. The reaction of F_1 plants heterozygous for resistance was compared to that of the homozygous resistant synthetic hexaploid parent, the susceptible parent Amigo, and Arthur 71 at two temperatures (18 and 28° C). Enough seed of each entry was planted to obtain about 75 plants/entry for each temperature. Biotype D Hessian flies were released to infest the plants. Procedures for growing the plants, infestation and selection of the test plants, randomization of the plants, and all other procedures were the same as in Experiment I. Fifty plants/entry for each temperature constituted one replication. The experiment was replicated twice over time.

Differences in expression of resistance at high temperature due to biotypes have been demonstrated before (Sosa and Foster, 1976). Because the expression of resistance in the F_1s at 28° C may be variable because of biotype differences, a test of F_1 plants was repeated using the GP biotype. The experimental procedures were identical to those used in the F_1 test described for biotype D.

RESULTS

The reactions of the F_1 plants, the Amigo and synthetic hexaploid parent plants, and Arthur 71 to biotype D Hessian fly larvae are shown in Table 4. Two of the Amigo plants at 18° C were resistant. Their resistant reactions were due, most likely, to low infestation as each plant was infested with only one larva. The infestation of the test plants overall was uniform but not heavy, averaging 5.4 larvae/plant.

Table 4. Reactions of F_1 plants heterozygous for *T. tauschii* resistance to biotype D Hessian fly larvae at two temperatures.

Entry	18° C			28° C		
	No. plants 1/		Mean % resistant plants 2/	No. plants		Mean % resistant plants
	R	S		R	S	
Arthur 71	100	0	100.00 a	39	61	39.00 b
Synthetic hexaploid (*T. tauschii* resistance)	100	0	100.00 a	96	4	96.00 a
Amigo	2	98	2.00 d	0	100	0.00 d
F_1	100	0	100.00 a	17	83	17.00 c

1/ R = resistant S = susceptible

2/ Means with the same letter in horizontal rows do not differ significantly ($P < 0.05$).

The dominant allele conferring resistance in heterozygous plants was effective at a low temperature (18° C) as all 100 of the F_1 plants were resistant. At 28° C however, only 17 of the 100 F_1 plants were resistant. Since the F_1 plants have identical genotypes for the resistant trait, all F_1 plants should have reacted uniformly to the biotype D larvae. The presence of live larvae on the resistant F_1 plants at 28° C indicated that their effect (nonlethal) on feeding larvae was the same as that of the susceptible plants. Resistance shown by 17 of the F_1 plants was possibly the result of low numbers of larvae on those plants (1-4/plant).

All of the synthetic hexaploid parent plants were resistant at 18° C. There was essentially no larval survival (0.05 larvae/plant) on these plants. At 28° C, 96 of the 100 synthetic hexaploid parent plants were resistant. On those resistant plants 0.16 live larvae/plant were found, however, the majority of larvae found were dead (4.91 dead larvae/plant). The four plants rated susceptible were overwhelmed by unusually high numbers of larvae (25-35/plant). Resistance in the heterozygotes was less effective at 28° C than that of Arthur 71; 39 of the 100 Arthur 71 plants at 28° C were resistant.

Although the F_1 plants were mostly susceptible at 28° C, larval measurements indicated that the dominant resistant allele effected low level antibiosis in that larval size was reduced (Table 5). The biotype D larvae that survived on the susceptible F_1 plants were significantly smaller than those surviving on susceptible Amigo plants.

The reactions of the F_1 plants, Amigo, synthetic hexaploid parent plants, and Arthur 71 to the GP biotype Hessian fly larvae are shown in Table 6. All of the Amigo plants were susceptible, again indicating

Table 5. Size (length) of live biotype D larvae on susceptible F_1 and Amigo plants at 28° C.

Entry	Total number larvae measured	Mean length in mm of larvae at 28° C
Amigo	80	3.47 a[1/]
F_1	80	3.08 b

1/ Means with a different letter differ significantly ($P < 0.05$).

a uniform infestation. The F_1 plants were all resistant to the GP biotype larvae at 18° C, however, only 13 of the 100 F_1 plants at 28° C were resistant. Thus, the reactions of the heterozygotes did not differ significantly due to the biotype used. The synthetic hexaploid parent expressed its resistance at 18° C to the GP biotype as all 100 of the plants were resistant. Of the Arthur 71 plants, 94% were resistant to the GP biotype at 28° C. This was in contrast with results from the biotype D test where only 39% of the Arthur 71 plants were resistant at 28° C. These data confirm the results obtained by Sosa and Foster (1976) that "break down" of H_5 gene resistance at high temperatures varies in degree due to fly biotypes.

Table 6. Reactions of F_1 plants, heterozygous for *T. tauschii* resistance, to the Great Plains biotype Hessian fly larvae at two temperatures.

Entry	18° C			28° C		
	No. plants		Mean % resistant plants [2/]	No. plants		Mean % resistant plants
	R	S		R	S	
Arthur 71	100	0	100.00 a	94	6	94.00 a
Synthetic hexaploid (*T. tauschii* resistance)	100	0	100.00 a	95	5	95.00 a
Amigo	0	100	00.00 c	0	100	00.00 c
F_1	100	0	100.00 a	13	87	13.00 b

[1/] R = resistant S = susceptible.

[2/] Means with the same letter in horizontal rows do not differ significantly ($P < 0.05$).

DISCUSSION AND CONCLUSIONS

The F_1 study was designed to measure the penetrance of the dominant allele in a low and high temperature environment. The penetrance of a gene is the proportion of individuals showing the expected phenotype. A gene may be fully penetrant in some individuals, but not in others because of environmental and/or genetic effects. Results of the F_1 study indicated complete penetrance of the dominant allele conferring *T. tauschii* resistance in heterozygotes in a low temperature environment. In a high temperature environment, however, the penetrance of the dominant allele was reduced. These results indicated that the dominant allele must be in the homozygous condition for full expression of resistance at 28° C.

Results of the F_1 temperature study also suggest that hybrid wheat breeders wanting to incorporate Hessian fly resistance into their programs should have resistance donated by both parents. This practice would produce F_1s homogeneous for resistance. This is not to conclude that all genes for Hessian fly resistance must be provided in double allele dose to maintain resistance at high temperatures. But if resistance breaks down in the homozygous condition at high temperatures, then it is likely to break down in the heterozygous condition at lower temperatures. Before using a gene in the heterozygous condition, tests should be conducted to determine the temperature stability of the gene in that condition.

EXPERIMENT III

Temperature Stability of Hessian Fly Resistance in Gator and Balbo Ryes

Materials and Methods

Gator and Balbo rye plants were evaluated for resistance to biotype D Hessian fly larvae at 18, 23, and 28° C. Arthur 71, Elva, and Seneca wheats were used for comparison. For each temperature, seed of each entry was seeded in small plastic tubes (12 x 3 cm) containing soil. The tubes were placed in a plastic rack designed to hold the tubes. Enough seed was seeded to obtain about 50 seedlings of each entry for each temperature. Biotype D Hessian flies were released to infest the plants. Procedures for growing the plants, infestation and selection of the test plants, randomization of the plants, and all other procedures were the same as in Experiment I. Thirty plants/entry for each temperature constituted one replication. The experiment was replicated four times over time. Poor germination of the rye seed in the last replication, reduced the number of test plants/temperature to 15-20.

RESULTS

Prior to the experiment it was assumed that both ryes were homogeneous for Hessian fly resistance. However, Balbo was segregating for resistance to the biotype D Hessian fly larvae. The reactions of Gator and Balbo to biotype D larvae at 18, 23, and 28° C are presented in Table 7. The rye experiment was done in conjunction with Experiment I so results listed for the checks are the same as those shown in Table 1.

Table 7. Reactions of Balbo and Gator ryes to biotype D Hessian fly larvae at three temperatures.

Entry	18° C			23° C			28° C		
	No. plants 1/		Mean % resistant plants 2/	No. plants		Mean % resistant plants	No. plants		Mean % resistant plants
	R	S		R	S		R	S	
Gator	103	3	97.17 a	102	2	98.08 a	102	2	98.08 a
Balbo	96	8	92.31 b	91	13	87.50 b	92	13	87.62 b
Arthur 71	119	1	99.17 a	98	22	81.67 b	20	100	16.67 c
Seneca	0	100	00.00 d	0	100	00.00 d	0	100	00.00 d
Elva	120	0	100.00 a	120	0	100.00 a	119	1	99.17 a

1/ R = resistant S = susceptible

2/ Means with the same letter in horizontal rows do not differ significantly ($P < 0.05$).

Analysis of variance revealed no significant differences in expression of resistance for Balbo or Gator due to temperature treatments. Gator resistance was effective at all temperatures; 98% of the Gator plants at 28° C were resistant. Gator plants exhibited potent antibiosis at all temperatures. Only 10 biotype D larvae (0.1 live larvae/plant) survived on the 104 Gator plants at 28° C.

Although there were Balbo plants rated susceptible at all temperatures, larval survival on resistant Balbo plants was comparable to that on resistant Gator plants at all temperatures. Balbo derived resistance in the homozygous condition will likely provide a high level of antibiosis in a warm temperature environment.

The susceptible reactions of Gator plants listed in Table 7 occurred in the last replication of the test. Poor germination of the Gator seeds, and reduced vigor of Gator plants was noted in that replication, and the latter probably caused the susceptible reactions.

DISCUSSION AND CONCLUSIONS

Results of the rye temperature experiment indicated that rye (Balbo and Gator) derived Hessian fly resistance has the temperature stability needed in warm wheat growing regions. At this time it is not known if the resistant gene(s) in Balbo is the same as that in Gator.

The low survival of larvae on Gator and resistant Balbo plants at 28° C indicated that fly population increases are unlikely to occur in the field if Gator or Balbo derived resistance is employed.

The effectiveness of rye derived resistance should encourage further work in transfer of rye resistant genes into wheat genotypes, and subsequent use in breeding programs. In the past, genes conferring Hessian fly resistance that were used in breeding programs came strictly from the *Triticum* genus. Now, however, the feasibility of employing sources of Hessian fly resistance outside of *Triticum* can be readily seen.

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EFFECT OF TEMPERATURE ON THE EXPRESSION OF RESISTANCE IN WHEAT DERIVED FROM *TRITICUM TAUSCHII* AND IN RYE TO HESSIAN FLY, *MAYETIOLA DESTRUCTOR* (SAY)

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Experiments were conducted in controlled growth chambers in 1980 and 1981 to determine the effect of high temperatures (constant temperatures ± 1° C) on expression of resistance in wheat derived from *Triticum tauschii*, and in rye to biotype D of Hessian fly, *Mayetiola destructor* (Say). *T. tauschii* derived resistance was examined in the homozygous dominant resistant genotype and in the heterozygous genotype. Larval survival and size were used as measures of antibiosis in the plant.

T. tauschii derived resistance represented in synthetic hexaploid wheat in the homozygous condition was fully expressed at constant temperatures of 18, 23, and 28° C, but not at 31° C. In the heterozygous condition, resistance derived from *T. tauschii* was fully expressed in F_1 plants at 18° C, but resistance of F_1 plants was greatly reduced at 28° C. Hessian fly resistance in Balbo and Gator rye cultivars was expressed at 18, 23, and 28° C, although Balbo was segregating for Hessian fly resistance. Low larval survival at 28° C on synthetic hexaploid wheat plants having *T. tauschii* resistance and on Balbo and Gator rye plants indicated high level antibiosis and suggests that Hessian fly populations are unlikely to increase if these sources of resistance are employed. Rye and *T. tauschii* derived sources of resistance appear to have the stability that is required in high temperature environments of the southern Great Plains.

Larvae that survived on resistant plant genotypes that reacted susceptible because of heat stress were smaller in size than those on susceptible genotypes (control). This suggests that those plants exhibited low level antibiosis even though the plants reacted susceptible.

Exposure to high temperature prior to larval feeding did not signi-

ficantly affect subsequent expression of resistance in a temperature sensitive cultivar. This suggests that the high temperature effect is not on the plant alone, but rather on the plant-insect interaction or the insect.