THE INHERITANCE OF THE MARQUILLO TYPE RESISTANCE IN WHEAT TO THE GREAT PLAINS BIOTYPE OF THE HESSIAN FLY

by

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INTRODUCTION

The Hessian fly, *Mayetiola destructor* (Say) historically has been considered one of the most serious insect pests of wheat, *Triticum aestivum* L. em Thell. in the United States (9). It is an introduced pest, presumably brought to this continent in the bedding straw of Hessian mercenary soldiers during the Revolutionary War. The fly moved westward across the United States with the introduction of wheat as a crop. It is now found in most of the wheat production areas of North America, although it causes significant damage in more localized areas depending on regional and annual environmental conditions (27).

In 1915 an epidemic of the Hessian fly in the United States caused wheat losses of $100 million (27). In 1971 the average annual loss was about $16 million (27). Improved cultural practices and the use of resistant cultivars have reduced losses. For example, the release of the cultivar 'Pawnee' in Kansas in 1943 was responsible for a marked reduction in the overall fly population even though other susceptible cultivars were being grown at the same time (9).

Recently however, the trend in Kansas has been away from the use of resistant cultivars with increased dependence upon cultural practices. While good cultural practices are significant in the control of the Hessian fly, their exclusive use is not desirable for a number of reasons: 1) The community cooperation that is required for the success of the program may be difficult to maintain; 2) sacrifices may be necessary such as the expense of controlling volunteer wheat or the loss of fall pasture due to late planting; 3) unpredictable environmental conditions may make cultural controls unfruitful or impossible.

The trend away from resistance appears to be continuing with the advent of the popular new semi-dwarf type wheats. Most of these do not have adequate genetic protection against the Hessian fly. In order to improve this situation, breeders need to incorporate sources of genetic resistance to the fly into good adapted material that has promise of meeting the future requirements of the growers. In order to accomplish this task in the most expedient way, a knowledge of the inheritance of the resistance sources is desirable. Many of these sources will be considered briefly in the following literature review.

THE PURPOSE OF THE STUDY

The purpose of this study was to investigate the inheritance of the 'Marquillo' type resistance in wheat to the Great Plains biotype (GP) of the Hessian fly.

REVIEW OF THE LITERATURE

I. The Insect and the Infestation Process.

The adult Hessian fly is about 2.5 to 3.0 mm. in length, mosquito like in appearance having a dark gray to black body with transparent wings. Females have somewhat robust red abdomens due to the presence of the red eggs. Adults mate soon after emerging and die soon after mating and ovipositing, living only two or three days. The females lay their eggs on the upper surface of the leaves, often producing 100 eggs or more. The eggs are shiney red in color, about 0.5 mm. in length, cylindrical with bluntly rounded ends (9, 24, 27). With favorable conditions larvae hatch in three to five days and migrate down the leaf blade positioning themselves behind the leaf sheath to begin feeding by sucking plant juices (14, 29). The first instar larvae are roughly the same size and shape as the eggs. The Hessian fly is an obligate parasite. When the environment favors the development of the fly, the young red larvae turn white after a few days and mature in nine to twelve days. When the mature larva completes development, the cuticle hardens and turns brown forming a puparium. This is known as the "flaxseed" because of its resemblance to the seed of flax. The insect overwinters and oversummers as a larva inside the puparium.

The fly is favored by relatively cool, humid conditions. The eggs and young larvae are susceptible to desiccation. Regions with hot and dry conditions generally are not suject to severe Hessian fly infestations.

II. The Reaction of Susceptible Wheat Cultivars to the Fly.

The physiological and biochemical effects of the feeding process on the wheat plant has not been determined in detail, although certain aspects of the process have been observed.

Stunting is probably the most obvious effect of Hessian fly infestation. Plants are often severely stunted. When the infestation occurs in the seedling stage the affected tiller is usually killed. When the infestation occurs after jointing the affected tiller will have shortened internodes, decreased seed numbers and seed size. It will also be susceptible to lodging, usually breaking over at the feeding site. When a seedling leaf is infested, the next leaf to appear from the plant will be stunted, appearing dark green in color and broad at the base. Miller et al. (19) found that these center, stunted leaves had a higher percentage of the lipid soluble pigments chlorophyll, carotene, and xanthophyll than the older, outer leaves of the infested plants. The stunted leaves also had more of these pigments than did uninfested control plants. They concluded that the dark green color was due to increased chlorophyll concentration. Robinson et al. (31) found that the number of chloroplasts per gram of fresh weight was higher in the stunted leaves than in the normal leaves.

The current view is that while the insect inhibits the elongation of the stunted leaf, chloroplast and chlorophyll production remain the same as in an uninfested leaf. Therefore the dark color is due to the concentration of chlorophyll.

The length of time the larva feeds has been shown to directly influence the degree of stunting. Two days feeding or less did not cause significant stunting. Three days feeding caused minor stunting. Four or five days feeding caused permanent stunting (2).

Byers and Gallun (4) found using paper chromatography that more plant growth inhibitors were present in infested wheat plants than in uninfested plants. While plant growth promoting substances were found in the larvae that had been feeding on susceptible plants, there was no evidence that larval feeding reduced the amounts of these substances in the infested plants. In another paper these authors reported that a single small larva in only four days time was able to permanently stunt a wheat plant. The authors argued that the stunting was not caused by the removal of plant substances, but by the introduction into the plant of growth inhibitors which later caused the stunting on new leaves after the larva was removed (3).

Byers and Gallun (5) reported the effects of soil applied gibberellic acid (GA_3) on infested and uninfested wheat plants. They found that GA_3 greatly elongated the 2nd and 3rd leaves of uninfested plants but that the 3rd leaf of treated infested plants was stunted as compared to the 3rd leaf of treated uninfested plants. They concluded that stunting was not an effect of gibberellin deficiency since applied GA_3 did not correct the stunting.

Refai et al. (28) showed in vitro that Hessian fly larvae secreted hemicellulase as well as some substance which caused a decrease in wheat plant phosphorlase action. The nature of the inhibitory substance(s) has not yet been discovered.

III. <u>The Reaction of Resistant Wheats to the Hessian Fly</u>.

A number of studies have been conducted to examine the reason for resistance to the fly's attack. Gallun and Langston (11) found that the larvae feed on resistant wheats, but showed that the duration of feeding is limited. Their research found that Hessian fly larvae feeding on P^{32} labeled susceptible and resistant wheat cultivars fed for at least fifteen days on the susceptible cultivars but not more than two days on the resistant cultivar. The level of P^{32} in the resistant plants was higher than that of the P^{32} in the labeled susceptible plants of comparable age.

Refai et al. (28) proposed that resistance was based on higher levels of hemicellulose that were positively correlated with resistance in their study. They speculated that the leaf sheaths of the susceptible wheats gave way more easily to the developing larvae than those of the resistant cultivars. The idea being that the rigid leaf sheaths prevented normal larval development.

Miller et al. (20) reported that the leaf sheaths of some resistant cultivars had a very even and complete arrangement of silica deposits as compared to some other susceptible cultivars. They pointed out however, that since there are a number of known genetic sources of resistance, that silica distribution may be only one factor of many involved.

Roberts et al. (30) found that hairy leaves were responsible for reducing both oviposition and the survival of the larvae. This is probably not significant however.

None of these studies made an attempt to associate morphologic or physiologic traits with any of the genetic systems now known. Considering the number of resistance sources known and especially in the light of the number of biotypes of fly that have been identified, it appears that more is involved than those traits mentioned above.

IV. Control Methods for the Hessian Fly.

Due to the position of the larva during feeding as well as the expense, chemical control has not proven practical.

Cultural methods have been useful in controlling the Hessian fly. Probably the most valuable cultural practice is the late seeding of winter wheats to avoid infestation by the fall emergence of the fly. The so called "fly free date" is determined for different regions by entomologists and agronomists. Sowing after this date will generally avoid most of the fly problem in the fall as well as minimize the populations that overwinter in growing wheat. Plowing under infested stubble and the destruction of volunteer wheat are also important cultural control methods. Crop rotation will also reduce the infestation of wheat. Finally, good agronomic practices such as seedbed preparation, fertilizing, and all practices which increase the health and vigor of the crop will reduce losses due to the Hessian fly (9, 27).

The use of resistant cultivars has been considered the most important method for control of the Hessian fly (24). Several cultivars are available and a number of different sources of genetic resistance have been identified. A consideration of previous genetic work follows.

V. Previous Genetic Studies on Resistance to the Hessian Fly.

The Hessian fly is an obligate parasite surviving only on wheat and wheat relatives including rye and barley. Because of this close association the genetic systems in the wheat and the fly are similar to those in many obligate disease systems. The gene-for-gene relationship described in the flax-flax rust system by Flor (10) appears to be operating in the wheat-Hessian fly system.

A number of sources of resistance have been found. Many have been given 'H' designations. H_1, H_2, and so on, each representing known single genes for resistance to the Hessian fly. Most of these are dominant or partially dominant genes (dominance over susceptibility).

The cultivar 'Dawson' contains two resistance factors designated H_1 and H_2 (12). A spring wheat 'Ill. No. 1, W38' was found to have a gene designated H_3. The cultivar Java was reported to have a recessive factor designated h_4 which Allan et al. (1) reported was an allele or psuedoallele of the H_3 gene. The 'Ribeiro' resistance was designated H_5 (12). A number of resistance factors have been described in PI94587 (6). Allan et al. (1) identified and designated H_6 a gene for resistance from CI12855 which is a selection from the cross Pawnee/PI94587. H_7 and H_8 were found in 'Seneca' wheat (26). In recent work at Purdue University the genes H_9, H_{10} H_{11} (37, 38, 39), and H_{12} (21) have been named. Hatchett et al. (16, 17, 18) has described at least three sources of resistance derived from <u>Triticum tauschii</u> (Coss) Schmal., the D-genome donor of the hexaploid wheats (35). These have not yet been given 'H' designations. The cultivars 'Kawvale' and Marquillo contain sources for resistance that have not been thoroughly understood. These have not been given 'H' designations.

These sources of resistance to the Hessian fly have differing sensitivities to temperature. Cartwright et al. (8) described the break down of the resistance of the H_3 gene with increased temperature. Sosa et al. (32) used biotypes B, C, D, and the Great Plains biotype to infest wheats carrying the

H_3, H_5, H_6, H_7 and H_8 genes. The results showed significant temperature sensitivity of H_3 to the Great Plains biotype and to biotype C. There was a very high level of resistance breakdown of H_5 when attacked by biotype D under high temperature, and a threshold effect between 24 and 27 degrees C when attacked by the Great Plains biotype. The other genes showed trends toward resistance breakdown as temperature increased as well. Sosa (33) reported that the H_5 gene in 'Abe' wheat underwent resistance breakdown when exposed to one day old biotype B larvae for only one day at 27 degrees C and were then returned to 18 degrees for the remainder of the experiment. Host genes, Hessian fly biotype, and temperature all influenced the phenotypic response.

VI. Biotypes of the Hessian Fly.

The existence of Hessian fly biotypes was first shown by Painter (22) in the 1920's. Since that time at least ten biotypes have been named based on their varying abilities to attack wheats with different genes for resistance.

The Great Plains (GP) biotype of the Hessian fly is defined by its inability to attack wheats with any resistance genes. It can only attack so called "universally susceptible" wheats such as 'Triumph' (12). The GP biotype is considered the 'wildtype' of the Hessian fly (18).

Biotype A is similar to GP in that it can infest all of the wheats susceptible to GP but differs in that it is also able to infest wheats with the Kawvale, Marquillo, or H_7 and H_8 types of resistance (12, 15, 18).

Biotype B can infest all wheats that are susceptible to biotype A as well as wheats with the H_3 gene for resistance (12).

Biotype C is able to infest all wheats that are susceptible to biotype A and in addition can attack wheats with the H_6 gene (12).

Biotype D is capable of attacking wheats susceptible to any of the above named biotypes. Biotype D can infest wheats with the Kawvale or Marquillo types of resistance as well as H_1, H_2, H_3, H_6, H_7, and H_8.

Biotype E is similar to GP except that it can infest wheats with the H_3 gene such as Monon (15).

Biotype F is like GP except that it can attack wheats with the H_6 gene for resistance (12).

Biotype G is similar to GP except that it can infest wheats with either the H_3 or the H_6 genes for resistance (13).

Biotype J is able to infest all wheats susceptible to biotype D except for those with the H_6 gene. Biotype J is also able to infest wheats with the H_5 gene (34).

Biotype L is similar to biotype D except that L is also capable of infesting wheats with the H_5 gene (34).

Many other virulence combinations are possible that will distinguish new biotypes (12). These ten biotypes are the ones that have been identified in the field or selected in the laboratory.

Since the Great Plains biotype is the predominant biotype in the hard red winter wheat region, sources of resistance such as the Marquillo type are of value in this area. The intent of this study was to gain understanding regarding the inheritance of resistance derived from Marquillo wheat.

VII. Genetic Studies of the Marquillo Type Resistance.

Not much work has been done regarding the inheritance of the Marquillo resistance. Painter et al. (23) reported that the resistance comes from 'Iumillo' durum wheat and tends to be recessive. Painter reported that an unknown number of factors was involved. Allan et al. (1) using the cultivar 'Ponca', which Painter et al (25) said probably carried both the Marquillo and the Kawvale resistance, reported three levels of resistance among ten Ponca selections. Allan also reported that Pawnee, which carries the Kawvale type of resistance, had two recessive factors.

MATERIALS AND METHODS

All of the cultivars used in this study are hard red winter wheats adapted for use in the Southern Great Plains of the United States. The source of the Marquillo resistance in this study was 'Parker 76'. Parker 76 is a cultivar developed from a backcross program using 'Parker' as the recurrent parent. The object of the backcross program was to transfer the LR_{24} leaf rust resistance gene, derived from *Agropyron*, from the cultivar 'Agent' into the Parker background. The pedigree of Parker 76 is Parker 5*/Agent. The pedigree of Parker is 'Quivira'/3/'Kanred'/'Hard Federation'//'Prelude'/Kanred/4/ Kawvale/ Marquillo//Kawvale/'Tenmarq'. The Hessian fly resistance of Marquillo was transferred, but it is not known if all of the factors involved were fixed in Parker.

Five cultivars that are susceptible to the GP biotype of the Hessian fly were used in crosses with Parker 76 (Table 1).

All of the susceptible cultivars used are semidwarfs.

Table 1.-Susceptible cultivars used in crosses with Parker 76.

Variety	Pedigree*	Relative Maturity	Chaff Color	Characteristics of Interest
Newton	1	mid season	white	resists wheat soil-borne mosaic virus-WSBMV
KS75210	1	mid season	white	the same as Newton with higher test weight
TAM W-101	2	mid season	white	short; susceptible to WSBMV; large kernel
TAM 105	3	mid season	red	high yield; low test weight; susceptible to WSBMV
Plainsman V	4	early	red	short; resistant to WSBMV; high protein

*Pedigree

1 'Pitic 62'//II53-526 ('Chris' sib)/'Sonora 64'/3/Sonora 64 /'Klein Rendidor'/4/'Scout'

2 'Norin 16'/3/'Nebraska 60'//'Mediterranean'/'Hope'/4/'Bison'

3 Short Wheat/Scout

4 Privately developed. Pedigree unpublished.

Parker 76 was used as the female parent in all crosses. Reciporcal crosses were made except for the cross with KS75210. The initial crosses were made in the field in May, 1979. F_1 seeds were harvested in the summer of that year. The F_1's were divided into two groups. One group was planted in the greenhouse and advanced a generation. The other group was planted in the field in the fall of 1979.

The greenhouse F_1's were grown to maturity and harvested in early 1980. The F_2 seed was immediately seeded in the greenhouse, vernalized, and transplanted to the field in the early spring. F_3 seed was harvested in the summer of 1980. These were treated as plant progenies representing individual F_2 plants.

The field F_1's produced a large number of F_2 seeds. These and the F_3 lines were evaluated in January, 1981 against the GP biotype of the Hessian fly using the methods described by Cartwright and LaHue (7).

Painter et al. (25) reported that the resistance of Marquillo was recessive. Backcrosses using the Parker 76 parent as the recurrent female were made in the spring of 1980. BC_1 seed was harvested in the summer and tested in the greenhouse in January, 1981. One inch diameter plastic tubes, each containing one plant, were held in a rack of 200. The plants were uniformly infested. Plants with a high resistance reaction were individually examined for dead larvae. The backcrosses tested are listed in Table 3.

A large F_1 test was designed using the cultivar Marquillo spring wheat as the resistance source. The spring wheat cultivars 'James' and 'Eureka' were used as the susceptible parents. Each Marquillo parent plant was tested against the GP biotype of the fly prior to crossing in order to verify its resistance. The susceptible lines had previously been tested in the Hessian fly program and were verified to be susceptible to the GP biotype.

The F_1 seeds of each cross used in this experiment were divided equally and planted in two identical groups in racks of one inch diameter plastic tubes as described for the BC_1 test. The racks each held 200 tubes and the tubes were numbered 1-200, seeds from the same cross having the same numbers in each of the two racks. The first seven tubes in each group of forty were check cultivars and parents. Tubes #1-7, #41-47, #81-87 and so on contained the checks. The checks in the order of planting were: #1 'Knox 62' (H_6), #2 Eureka (S), #3 Marquillo, #4 James (S), #5 Marquillo, #6 Eureka (S), #7 'Larned' (H_3). Each of the two racks was infested with a different fly culture. Rack #1 was infested with fly collected in South Dakota that was thought to be somewhat less virulent than the general fly population of the Great Plains states. Rack #2 was infested with the GP biotype of the fly collected in Western Kansas. This test was conducted on an air-conditioned bench in August, 1981.

In all of these materials, those found to have off type parents or no segregation were discarded.

RESULTS AND DISCUSSION

I. The F_1 Test. James and Eureka by Marquillo.

The results of the F_1 test are presented in Table 2.

A chi-square test comparing the two fly cultures in ability to infest the F_1's produced a chi-square value of 0.42. A value of chi-square this small occurs with a probability of about 0.50 (36). At this level, it must be assumed that any differences between the fly cultures were random.

Table 2.-The reaction of F_1 plants, parents, and checks to South Dakota and Kansas cultures of the Hessian fly.

Tube Nos.	Cross No.	Pedigree	South Dakota Fly Nos. of Plants			Kansas Fly Nos. of Plants		
		F_1 Crosses	FF	S	Dead	FF	S	Dead
8-13	H	James/Marquillo	4	2	0	3	3	0
14-16	BJ	"	0	3	0	2	1	0
17-36	AS	Eureka/Marquillo	9	11	0	6	14	0
37-40	AU	"	0	4	0	1	3	0
48-56	W	James/Marquillo	3	5	1	1	8	0
57-73	AR	Eureka/Marquillo	2	15	0	1	15	0
74-80	BL	"	1	6	0	0	6	1
88-96	Z	James/Marquillo	1	8	0	0	9	0
97-117	AH	Eureka/Marquillo	1	19	1	0	21	0
118-120	BE	"	0	3	0	1	2	0
128-132	V	James/Marquillo	0	5	0	0	5	0
133-136	AA	"	1	3	0	0	4	0
137-149	AD	Eureka/Marquillo	0	13	0	1	10	2
150-160	AZ	"	1	10	0	0	11	0
168-173	BH	James/Marquillo	0	6	0	0	6	0
174-176	BK	"	0	3	0	0	3	0
177-189	BS	Eureka/Marquillo	0	13	0	0	13	0
190-200	AL	"	0	11	0	1	10	0
Totals			23	140	2	18	144	3
		Parents and Checks						
		Knox 62 (H_6)	3	0	2	4	0	1
		Eureka (S)	1	9	0	1	9	0
		James (S)	0	5	0	0	5	0
		Marquillo (R)	9	1	0	10	0	0
		Larned (H_3)	5	0	0	5	0	0

FF= Fly Free Plants

S= Susceptible

Phenotypically resistant and susceptible plants were observed from the same crosses (see Table 2). The possibility of these resistant phenotypes all being escapes was ruled out because of the low level of escapes in the susceptible checks. Dead larvae were not found on most of the fly free F_1 plants; however, they were not found on the known resistant cultivars either. The plants may have been too old when the microscopic work was done. The red larvae tend to lose their color with time. The faster growing spring type wheats may also have pushed the dead larvae out of the plant before they were examined. Some stunted and dead larvae were observed on a few of the F_1 plants with the appearance of resistance. Plants from the same cross side by side in the same rack were observed to have apparently different reactions to the fly. Assuming that there were not a significant level of escapes, an explanation of this observation cannot be based solely on the genetics of the F_1 host. F_1 plants descended from the same two homozygous parents would be expected to react the same under identical conditions of Hessian fly attack. There are two variables to be considered, the fly population, and the environment. The GP culture used in this study had been purified and was homogeneous in its ability to infest homozygous wheats. The effect of the number of larvae on an individual plant with Marquillo resistance has not been determined. Based on observations of Parker plants, as many as 40 larvae on an individual under the proper environment will not cause the breakdown of resistance. It is not known what the effect of the number of larvae is on heterozygous plants.

The Marquillo resistance appears to be very temperature sensiive in the greenhouse (18). In an F_2 test in the greenhouse in February, 1981, the author observed the breakdown of resistance in Parker ckeck rows that were nearer to the greenhouse heating system than the ~~same~~ ckeck rows less than three feet away on the opposite side of the bench. The F_2 plants in this test had more than twice the proportion of susceptible plants than an earlier F_2 test of the same material done under cooler greenhouse conditions. If the known homozygous resistance breaks down in increasing proportion with increasing temperature, the reaction of heterozygous material under the same conditions will be totally unpredictable.

Observation of the F_1 test data shows that the proportion of resistant phenotypes in both racks decreased very much after tube number 50. The racks were placed end to end in front of the air-conditioning unit in August. It is possible that the orientation of the racks to the air-conditioning unit caused slightly cooler conditions over the first 50 tubes of each rack which allowed the resistant phenotype to be expressed. The one Marquillo plant in which the resistance broke down was in the center of the rack infested with the South Dakota fly, away from the end where the phenotypically resistant F_1's were observed.

A serious problem is encountered in attempting to complete a genetic analysis under these conditions. There is no observed relationship between the phenotypic response of an individual and that individual's true genetic condition. The results of this test indicate that the effect of small environmental variations masked the true expression of the genotype. Thus, all of the results of this study must be considered in the light of this problem.

II. The BC_1 Test.

Up to five tillers per individual female Parker 76 plant were used so that seed production would be maximized. Crosses having less than 20 seeds were not included in the backcross test. Backcrosses involving Newton and KS75210 did not produce enough seed to be included in the test. The data are presented in Table 3.

Table 3.-The reaction of BC_1 plants to the GP biotype of the Hessian fly.

Cross	Pedigree	Resistance Rating					Nos. of Plants	
		R1	R2	R3	R4	R5	S	Total
X80110	Parker 76 2*/TAM W-101	16	16	12	7	12	15	78
X80111	"	3	9	4	7	3	8	34
X80112	Parker 76 2*/TAM 105	1	13	5	3	1	1	24
X80114	Parker 76 2*/Plainsman V	0	1	4	1	0	50	56

R1=highly resistant phenotype
R2=resistant phenotype but not as good as R1
R3=resistant phenotype but stunting observable
R4=resistant phenotype but plants obviously stunted
R5=plants severely stunted but new growth beginning to emerge
S= completely susceptible phenotype

Progeny tests were not completed on plants rated R1 or R2 in order to verify resistance. Plants rated R1 or R2 were examined however, for the presence of Hessian fly larvae in order to verify infestation.

A high level of resistance was noted in the TAM W-101 and the TAM 105 BC_1's. Because of the unknown response of heterozygous material these data were not considered reliable enough to propose a genetic hypothesis. The Plainsman V backcross had a very low level of resistance. This was inconsistent with the other Plainsman V cross data and therefore it was suspected that the backcross Parker 76 female did not carry the resistance. Insufficient selfed seed from the Parker 76 female prevented verification by a progeny test.

III. The F_2 Test.

The problem of environmental confounding would be expected to be more severe in the F_2 generation than in the BC_1 because of the higher proportion of heterozygous plants. These data were not considered reliable for founding a genetic hypothesis. The data are presented in Table 4.

Table 4.-The reaction of F_2 plants to the GP biotype of the Hessian fly.

Cross No.	Pedigree	Nos. of Plants Observed		
		Resistant Phenotype	Susceptible Phenotype	Total
X7932	Plainsman V/Parker 76	219	292	511
X7982	Newton/Parker 76	346	184	530
X7988	Parker 76/Newton	270	202	472
X79114	TAM W-101/Parker 76	323	156	479
X79113	Parker 76/TAM W-101	186	114	300
X79111	"	202	35	237
X79119	TAM 105/Parker 76	285	126	411
X79115	Parker 76/TAM 105	251	207	458
X79122	Parker 76/KS75210	173	307	480

The infestation of the F_2's was light and a number of escapes were noted in the susceptible Triumph checks. More than 12% of the Triumph plants were uninfested. In order to correct for the light infestation, all plants rated as resistant visually, were examined under the microscope for the presence of dead larvae. Plants in which no dead larvae were found were discarded.

The incidence of the breakdown of the Marquillo type resistance in the Parker check rows was very low. Only two out of 269 Parker plants were rated as susceptible.

There was a large proportion of resistant phenotypes in this test. All but two of the crosses tested had more plants with the resistant phenotype (after discarding escapes) than plants with the susceptible phenotype. There was not a high enough proportion of resistant plants however, to establish that the resistance was dominant over susceptibility. It would appear that the resistance is nondominant in nature and that under the environment in the greenhouse the heterozygous types express either the resistant or the susceptible phenotype depending on the microenvironment and possibly on the number of larvae on a given plant. It is also possible that the relative proportion of resistant and susceptible phenotypes is governed by the temperature. This F_2 test was done under cooler temperatures than any of the other experiments. This test had the lowest incidence of resistance breakdown in this study. Perhaps under cool temperatures a low proportion of the heterozygous types undergo the breakdown of resistance, while under progressively warmer temperatures an increasingly higher proportion of the heterozygous plants exhibit resistance breakdown.

IV. Progenies of Individual F_2 Plants.

Seed numbers were low in both the F_1 and F_2 greenhouse generations. For this reason F_3 lines having four or fewer plants per line were not included in the study.

The F_3 lines were classified into three categories based on the proportions of resistant and susceptible phenotypes in the line. The categories were 'R' signifying a homozygous resistant line, 'H' signifying a segregating line (a heterozygous F_2 plant), and 'S' signifying a homozygous susceptible line. Lines having 90% or more resistant plants were classed as 'R'. Lines having between 10% and 90% resistant plants were rated as 'H' lines. Lines having 10% or fewer resistant phenotype plants in the line were classed as 'S' lines. About 8% of the susceptible Triumph checks were escapes, and about 5% of the Marquillo type checks demonstrated resistance breakdown. These data are presented in Table 5.

The F_3 data were considered the most reliable in the light of the presumed environmental sensitivity of the heterozygous individuals. It was assumed that the homozygous types, both the resistant and the susceptible, would not vary beyond the 10% limits set in this experiment. It was also assumed that the conditions were such that the heterozygous genotypes, even though expected to vary in reaction, would not vary below 10% resistant plants on the susceptible side, or above 90% resistant plants on the resistant side.

V. Consideration of Some Possible Genetic Hypotheses.

All hypotheses which include complete dominance were ruled out based on the low level of resistance observed in

Table 5.-The reaction of F_3 lines to the GP biotype of the Hessian fly.

		No. of Lines Per Cross		
Pedigree	Cross No.	R	H	S
Newton/Parker 76	X7985	0	3	0
Parker 76/Newton	X7992	3	6	0
"	X7988	1	5	3
Parker 76/KS75210	X79121	1	4	1
"	X79122	0	0	1
Total of Newton type crosses		5	18	5
Parker 76/TAM W-101	X79111	2	4	0
"	X79112	4	6	1
Total of TAM W-101 type crosses		6	10	1
Parker 76/TAM 105	X79115	0	2	1
"	X79117	1	8	2
TAM 105/Parker 76	X79119	0	2	0
"	X79120	2	36	8
Total of TAM 105 type crosses		3	48	11
Plainsman V/Parker 76	X7932	1	17	1
"	X7934	5	11	0
Total of Plainsman V type crosses		3	48	11
Total of all crosses		20	104	18

R=F_3 lines having 90% or more phenotypically resistant plants in the line.

H=F_3 lines having more than 10% but fewer than 90% resistant phenotypes in the line.

S=F_3 lines having fewer than 10% resistant phenotypes in the line.

the F_1 test. Likewise, the F_2 and F_3 data do not demonstrate a high enough level of resistance to support a dominance hypothesis. The BC_1 test of itself does not rule out the possibility of complete dominance, but in the light of the unpredictable nature of the heterozygous types, these results are not unreasonable if incomplete dominance were operating.

Complete recessiveness, like complete dominance, was ruled out based on the observance of resistant plants in the F_1 test as well as the relatively high levels of resistance in the BC_1, F_2, and F_3 tests. Some form of nondominance is probably operating. Environment is an important factor in considering a nondominance hypothesis.

Assuming a nondominance hypothesis, the number of factors involved in the resistance was considered. The possibility of a single nondominant factor acting alone was eliminated based on the high level of heterozygosity observed in the F_3 lines. If a single nondominant factor was controlling the resistance, a 1:2:1 ratio would be expected among the F_3 lines rated as described on page 21. The data have more than two times this level of heterozygosity overall.

A two factor model in which one major nondominant factor in the homozygous condition and a minor nondominant factor in either homozygous or heterozygous state would produce 90% or more resistant progeny under the conditions of the F_3 study was considered. This hypothesis depends upon a high proportion of the plants which are heterozygous for the minor factor and homozygous for the major factor expressing the resistant phenotype under the conditions of the F_3 test. The expected F_3

line ratios would be 3:10:3.

A chi-square test for heterogeneity between the proportions of resistant plants in each cross produced a chi-square value of 19.63 with 12 degrees of freedom. This corresponds to a probability of about 0.075 that the level of heterogeneity observed would occur by chance if the crosses were truly homogeneous (36). This may be partially because of the small sample numbers in the F_3 test. Because of the heterogeneity in the F_3 test, statistical comparisons to genetic models are not valid.

A three factor model in which any two of the factors being in the homozygous resistant state would condition phenotypic resistance was considered. This model gives and expected F_3 ratio of 10:44:10. This model could explain the high levels of resistance observed in the BC_1 and the F_2. It could also explain why a number of wheats with Marquillo type cultivars in their pedigree such as Lindon, 'Vona', and 'Centurk' have the Marquillo type resistance although these lines were not selected for Hessian fly resistance during the breeding procedure.

CONCLUSIONS

The Marquillo type resistance to the Great Plains biotype of the Hessian fly has proven to be an effective and stable means of controlling the Hessian fly in the field. Cultivars such as Ponca, Parker, Parker 76, Lindon, Vona, and Centurk carry some if not all of the resistance derived from Marquillo. This source of resistance continues to have promise of protecting future wheats against the Hessian fly in the Great Plains since it does not appear to select for biotypes.

This study verified the results of Allan et al. (1) and Painter et al. (23) in that the resistance appears to be complex. A form of nondominance seems to be operating in this system. Possibly two of three factors are involved.

The Marquillo resistance appears to be highly sensitive to temperature and possible other environmental effects in the greenhouse. Homozygous types of wheat will exhibit resistance breakdown under the influence of relatively warm temperatures. The effect of warm temperatures on heterozygous wheats is not known, but would be expected to be even more sensitive to slight differences in temperature. F_1 plants from the same two parent plants demonstrated both resistant and susceptible phenotypes under very similar greenhouse conditions. This presumably is the result of slight environmental differences.

Futher research into the nature of the environmental sensitivity of Marquillo resistance will be required before meaningful genetic data can be aquired. A study of heterozygous wheats grown under various temperature conditions would be profitable.

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THE INHERITANCE OF THE MARQUILLO TYPE RESISTANCE IN WHEAT TO THE GREAT PLAINS BIOTYPE OF THE HESSIAN FLY

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ABSTRACT

The Hessian fly, Mayetiola destructor (Say) historically has been one of the most serious insect pests of wheat, Triticum aestivum L. em Thell. in the United States. The Great Plains (GP) biotype is defined by its avirulence on wheats with any genes for low host reaction. The GP biotype is the prevalent biotype in Kansas.

The 'Marquillo' type resistance to the Hessian fly has proven to be a stable and effective means of controlling the GP biotype. A knowledge of the inheritance of the Marquillo type of resistance is desirable in order to expedite the breeding of new wheats with the Marquillo type resistance.

A number of different biotypes of Hessian fly have been described based on their abilities to infest wheats with different genes for resistance. A gene-for-gene relationship appears to be operating in the wheat-Hessian fly system. The Marquillo resistance was reported in earlier work to have a complex inheritance that tended to be recessive in nature.

In this study five susceptible semi-dwarf hard red winter wheat cultivars were crossed with 'Parker 76' as the resistance source. The susceptible lines were: 'Newton', 'KS75210', 'TAM W-101', 'TAM 105', and 'Plainsman V'. Progenies were advanced to the F_2 and F_3 generation. Backcrosses of F_1's were also made using Parker 76 as the recurrent parent. These materials were tested in the greenhouse against the GP biotype of the Hessian fly. An F_1 test was designed using the cultivar Marquillo spring wheat at the resistance source. The susceptible cultivars 'James' and 'Eureka' were used in this study. The

results of the F_1 test indicate that the expression of heterozygous types is extremely sensitive to environmental effects, probably temperature. The reaction of F_1 plants descended from the same two homozygous parents differed from resistant to susceptible in phenotype. This was presumed to be due to microenvironmental effects. Because of the unpredictable reaction of heterozygous types under the conditions of this study, the analysis of segregating material for the purpose of establishing genetic hypotheses must be seriously questioned.

The results of this study indicate that a form of non-dominance is probably operating in this system. The resistance appears to be complex in nature with possibly two or three factors controlling the inheritance.

Research into the nature of the environmental sensitivity of Marquillo resistance to the Hessian fly will be required before meaningful genetic data can be accumulated. A study of heterozygous wheats grown under various temperature conditions would be profitable.