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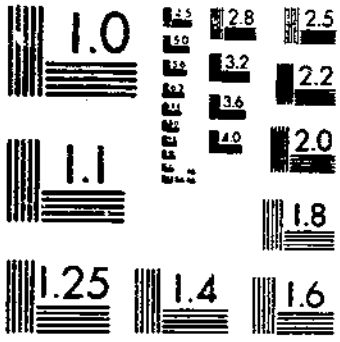

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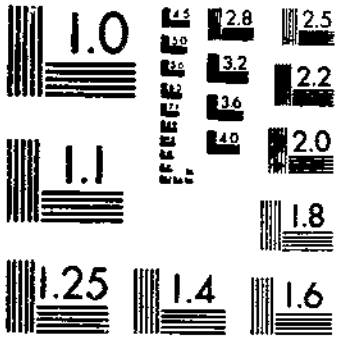

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Further Differentiation of Genetic Factors in Wheat for Resistance to the Hessian Fly [1]

By C. A. Suneson, *agronomist, Division of Cereal Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering,* and W. B. Noble, *entomologist, Division of Cereal and Forage Insect Investigations, Bureau of Entomology and Plant Quarantine, Agricultural Research Administration*

CONTENTS

INTRODUCTION

In 1936 Department workers in California began an investigation of the genetic constitution of six American wheat varieties that were known to be resistant to the strain of hessian fly prevalent in the vicinity of Rio Vista, Calif. One of the varieties, Dawson, had already been studied in crosses with two susceptible wheats, Poso and Big Club, and a backcrossing program had been initiated to effect the transfer of its two dominant resistance genes to these commercially important varieties (*4*).[2] This breeding program has now been completed, and the wheat acreage in the area has been taken over by the derived resistant varieties, Poso 42 and Big Club 43. The resultant destruction of natural infestation precludes further inheritance studies, so the accumulated data are presented here.

REVIEW OF LITERATURE

The available genetic information on hessian fly resistance has come from three sources. In California, the Dawson variety has been shown to possess two dominant genes for resistance (*4*). Their separation into genetic testers designated as H_1H_1 and H_2H_2 has

[1] Submitted for publication September 12, 1949. This work was carried out in cooperation with the Division of Agronomy, University of California.

[2] Italic numbers in parentheses refer to Literature Cited, p. 7.

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also been effected (*7*). The variety W38 when crossed with Dawson produced susceptible progeny in the F_3 generation, thus establishing that its resistance is independent from the Dawson genes (*6*).

A more specific analysis of W38 was made in Indiana (*1*), revealing an incompletely dominant resistance gene for which the symbol H_3H_3 has been designated. Dawson is susceptible in Indiana (*2*). Cartwright and Shands have also reported results from crosses between W38 and 11 foreign wheats, 6 of which "apparently possess the H_3H_3 factor" and the other 5 one or more genes different from H_3H_3 (*3*). The identity of these genes and of the two or more dominant genes reported in P. I. 94587 [3] has not been determined more specifically (*1*). None of these 12 resistant varieties have been studied genetically in California, but their resistance has been confirmed by work as yet unpublished. Of greater pertinence to the present study, however, are the biological-race studies showing that a culture of flies reared through 4 generations on W38 (*2*) is capable of producing a much higher infestation in W38, Dixon, and Java, than does the wild Indiana fly.

Painter and coworkers in Kansas (*9*), working with the variety Marquillo in F_1, F_2, and F_3 generation crosses, were unable to resolve their data on factorial basis, but they indicated that resistance in this variety tends to be inherited as a recessive character. Marquillo crosses often result in F_1 lethals (*5*).

MATERIALS AND METHODS

The hessian fly has persisted in the Rio Vista area in California bordering San Francisco Bay for at least 70 years (*8*). Outside of this belt, high summer temperatures and low humidities have prevented its permanent establishment. Within the belt where it can survive there has been a continuous diminution of the wheat and barley acreage. Equally important, the very susceptible varieties Pacific Bluestem and Big Club wheat have predominated in this belt for more than 70 years (*10*), thus offering little inducement for the increase of mutants or segregates having the capacity to infest other varieties.

The experiments here reported have been conducted on various field sites chosen for their proximity to infested stubble.[4] Seed stocks were produced in the fly-free area at Davis.

As in previous studies, plants were classified as infested or uninfested, depending on whether or not puparia were present. Check rows of susceptible Poso or Big Club wheat were grown in each eleventh row throughout the nurseries. A sample of 25 plants was generally used to establish the level of infestation in either parent rows, or F_3 generation rows. Errors due to sampling and heterogeneity of fly dispersal were most serious when mean infestations were

[3] P. I. denotes accession number of the Division of Plant Exploration and Introduction.

[4] Previous to 1942 the sites were always on the Hoyt ranch near Birds Landing, but a change in ownership and in cropping interests forced a move. Subsequently several farmers provided experimental sites and furnished services for the furtherance of the work.

relatively low and the range of observed infestations in susceptible varieties widespread. Genetic study plantings were abandoned because of low infestations during the years 1945 and 1946.

In previous experiments in which approximately 95 percent infestation occurred in susceptible checks, the F_2 generation of Dawson × Poso contained about 14 percent of infested plants (*4*), the F_2 generation of the H_1H_1 or H_2H_2 testers × Poso about 20 percent infested plants (*7*), and the F_2 generation of W38 × Wabash gave 32 percent infested plants (*1*). These relative infestations were used as a basis for interpreting the data from later experiments.

RESULTS

Responses of parent varieties in tests from 1938 to 1944 are shown in table 1. It is evident that significant differences in levels of infestation occurred in different years, and that resistance is only relative and may permit moderate infestations when fly populations are large. These considerations are also pertinent in interpretations of F_2 data given in table 2 and of the F_3 data in table 3. The reaction in crosses involving each variety follows.

TABLE 1.—*Hessian fly infestations in parent varieties of wheat in California, 1938–44*

Variety	C. I. No.[1]	Plants infested with puparia in—						
		1938	1939	1940	1941	1942	1943	1944
		Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Poso	8891	76	52	67	85	68	95	51
Dawson	3342	0	0	2	2	0	0	0
H_1H_1 tester	------	------	------	0	6	12	0	------	2
H_2H_2 tester	------	------	------	0	4	14	16	------	4
W38	12061	3	1	11	29	5	0	4
Java	10051	------	5	2	8	------	15	0
Marquillo	6887 1	6	5	2	12	1	10	0
Dixon	6049	------	------	0	12	------	20	0
Kawvale	8180	------	1	17	0	0	8	0

[1] C. I. refers to accession number of the Division of Cereal Crops and Diseases.

TABLE 2.—*Hessian fly infestations in various F_2 generation hybrids grown in California, 1938–44*

Cross	Plants													
	1938		1939		1940		1941		1942		1943		1944	
	Total	Infested	Total	Infested	Total	Infested	Total	Infested	Total	Infested	Total	Infested	Total	Infested
	No.	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*
Java × Dawson									459	15				
Java × H_1H_1 tester	41	10			120	15			410	17				
Java × H_2H_2 tester	60	15			275	20			814	20				
Java × Poso											150	50	50	28
Java × W38													209	21
Java × Dixon											404	9	76	3
Marquillo × Dawson	76	11	65	15	250	4	912	13						
Marquillo × H_1H_1 tester			48	15	234	11	767	23						
Marquillo × H_2H_2 tester			163	9	40	20	146	19						
Marquillo × Poso											275	41		
Marquillo × Dixon							496	10						
Dixon × Dawson									867	2				
Dixon × H_1H_1 tester									350	3				
Dixon × H_2H_2 tester									815	4				
Dixon × W38													275	5
Dixon × Poso											255	24	89	11
Kawvale × Dawson							990	1						

TABLE 3.—*Distribution of F_3 families of various crosses and of susceptible parent checks in California tests, 1939–44*

Variety or cross	Year grown	Number of rows in classes (percentage) of hessian fly infestation																
		2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	Total
Poso	1940	0	0	0	0	0	0	2	0	3	0	0	2	4	3	4	6	24
Big Club	1941	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	9
Do	1942	0	0	0	0	0	0	0	0	1	0	0	4	2	5	1	27	40
Poso	1944	0	0	0	0	0	0	2	0	2	0	0	2	1	0	1	0	8
Java × Poso	1944	46	9	8	10	7	1	6	9	2	3	3	8	1	1	3	6	123
Java × H_1H_1	1940	13	2	1	6	1	0	1	3	0	0	0	0	1	0	0	3	31
Java × H_2H_2	1940	25	6	5	7	2	4	1	4	1	0	0	0	0	1	0	1	57
Java × Dixon	1944	18	3	2	0	1	0	0	0	0	0	0	0	0	0	0	0	24
Marquillo × Poso	1944	1	3	2	2	1	4	3	2	1	1	1	0	0	1	0	1	23
Marquillo × Dawson	1939	67	9	2	3	1	0	0	3	0	0	0	0	0	0	0	0	85
Marquillo × H_1H_1	1940	6	2	2	4	1	0	0	1	0	1	0	0	0	0	0	0	17
Marquillo × H_2H_2	1940	12	5	4	5	2	2	0	2	1	2	1	0	1	0	0	1	38
Marquillo × Dixon	1941	82	13	7	4	1	2	1	1	1	1	1	0	0	0	1	3	118
Dixon × Poso	1944	2	0	1	2	3	0	2	4	1	1	1	5	2	2	1	1	28
Dixon × Dawson	1942	134	15	2	4	5	1	2	1	0	2	0	0	0	0	0	0	166
Dixon × H_1H_1	1942	81	11	4	8	2	2	0	0	1	2	1	0	0	0	1	0	113
Dixon × H_2H_2	1942	175	35	13	21	8	1	2	3	0	0	0	0	1	0	1	0	260
Kawvale × Dawson	1942	135	5	2	1	1	1	1	0	1	2	0	0	0	0	0	0	149

Crosses With Java

Resistance in the Java (C. I. 10051) variety in California has not been so high as in the Dawson variety. In the F_2 generation of the cross Java × Poso resistance appears to be recessive. In crosses with Dawson, or with the H_1H_1 and H_2H_2 testers derived from it, the F_2 populations were nearly as susceptible as comparable Poso crosses. Small F_2 populations from crosses with H_1H_1 and H_2H_2 testers suggest a 13 : 3 ratio. Since dominance is less complete in W38 than in H_1H_1 or H_2H_2, it is logical for the F_2 crosses of W38 × Java to show a greater average infestation than do the H_1H_1 or H_2H_2 testers crossed with Java. The available data suggest that the recessive resistance factor in Java is independent of the factors H_1H_1, H_2H_2, or H_3H_3. Hence the symbol h_4h_4 for the Java resistance factor is suggested.

Crosses With Marquillo

Among the several strains of Marquillo (C. I. 6887–1) crossed with Dawson was one that did not produce lethals (*5*), although all crosses with Java were lethal. Resistance in Marquillo behaved as a recessive and was independent of the factors H_1H_1 and H_2H_2. Since the gene action is unlike that of W38 in crosses with either a susceptible variety or Dawson, independence of H_3H_3 also seems logical. It is not possible to distinguish between the resistance in Java and that in Marquillo from the data at hand, but they probably differ, inasmuch as a selected population of hessian fly attacks one much more severely than the other (*2*).

Crosses With Dixon

Resistance in Dixon (C. I. 6049) was partly dominant in crosses with Poso. In crosses with Dawson and with H_1H_1 or H_2H_2 testers practically no susceptibles were recovered in the F_2, and relatively few in the F_3 generation. Their occurrence, however, establishes independence from H_1H_1 or H_2H_2. The F_2 generation from a cross with W38 gave inconclusive results as regards the H_3H_3 factor. Crosses with Java (h_4h_4) suggest the possibility of a common recessive gene, since no susceptible rows were found among the 24 F_3 lines sampled. Crosses with Marquillo produced 4 susceptible rows among 118, however.

Crosses With Kawvale

Studies with Kawvale (C. I. 8180) do not permit differentiation with any known genes except those in Dawson. In this cross only 1 percent infestation was observed in the F_2 generation, and only 14 out of 149 lines fell outside the range of the Kawvale parent in the F_3 generation. The fact that 3 of the 14 segregating F_3 lines fell in the susceptible class would seem to preclude any common genes with Dawson. Such a distribution confirms the dominance of resistance in Kawvale and its independence from the H_1H_1 or H_2H_2 factors.

DISCUSSION

Genetic interpretations of the nature of resistance, as well as the practical use of this resistance in breeding, often depend upon specific

biological races of insect or parasite for a given expression. This is certainly the case with hessian fly (*2* and *9*). In the major wheat belt of America the Dawson variety was resistant for many years. Since the appearance of new races of hessian fly the H_1H_1 and H_2H_2 genes from Dawson are now practically useless for breeding wheats for that region. All wheat varieties that have been reported to be resistant to hessian fly show resistance when tested in California. It is unfortunate that our practical breeding program for resistance in California was completed before we were able to isolate all of the genes for resistance.

The geographical isolation and the localized confinement of the hessian fly in California, coupled with the dominance of two highly susceptible wheat varieties in this area for a period of more than 70 years, should have been conducive to a stable population of hessian fly. Thus, mutations with a differential capacity to infest resistant varieties had no selective advantage, and mutations capable of enduring greater summer heat and lower humidity apparently did not appear. Furthermore, the resistance of Dawson, first recognized in experimental tests in 1921, has persisted at the first observed level. This is the evidence for homogeneity of the hessian fly in California.

Considerable interest will focus on the stability of the $H_1H_1H_2H_2$ resistance in Poso 42 and Big Club 43 in California. The fact that the general population of hessian fly was low and that these varieties replaced their prototypes rather quickly from 1944 to 1946 makes it seem likely that no biological variant of hessian fly capable of infesting Dawson ($H_1H_1H_2H_2$) survived in the exchange. If such a race of hessian fly should survive, the most certain and durable protection from the new races would come from combining the $H_1H_1H_2H_2$ factors with another source of resistance like H_3H_3 or h_4h_4 and not by constituting a new and separate single or double gene resistance.

SUMMARY

The genetic aspects of a study of resistance to hessian fly begun in 1931 were terminated by near area-wide acceptance of the derived resistant varieties, Poso 42 and Big Club 43, that were bred during the course of these experiments. Natural infestation is now too low to permit further studies.

In addition to three previously reported dominant genes for hessian fly resistance, viz, H_1H_1 and H_2H_2 (Dawson) and H_3H_3 (W38), an independent recessive gene pair designated as h_4h_4 (Java) is herewith established. Further evidence for the recessive behavior of resistance in Marquillo also is presented. Resistance in Dixon and in Kawvale is shown to be independent of H_1H_1 and H_2H_2.

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