RELATIONSHIP OF RESISTANCE TO GREENBUGS AND HESSIAN FLY IN SEGREGATING POPULATIONS OF HARD RED WINTER WHEAT

by

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INTRODUCTION

Stable and efficient production of hard red winter wheat depends on the absence of plant diseases, insects, and unfavorable climatic conditions. Greenbug /<u>Schizaphis</u> <u>graminum</u>, (Rondani)/, and hessian fly /<u>Phytophaga</u> <u>destructor</u>, (Say)/ are two damaging insects of wheat in the United States.

Some consider these two insects of second importance to weather as a limiting factor in growing wheat in Kansas. According to the Kansas State Board of Agriculture, it was estimated that 95 million bushels of wheat were lost because of hessian fly destruction during 1924, 1925, and 1926. The annual loss during the period 1941 to 1951 is estimated at 9,389,000 bushels of wheat valued at about $16,000,000. Painter (1960) mentioned an estimated million dollars of damage per year on the average to the Kansas Wheat crop, due to hessian fly. Losses in wheat production due to hessian fly for 1944-1945 in the United States were estimated at $84,400,000.

The hessian fly, introduced about 1776 into North America in straw brought by Hessian soldiers, has spread over most of the winter wheat growing areas of the United States. This insect becomes abundant only occasionally. During 1962 and 1963 it was common in many areas of Kansas, Nebraska, and Missouri.

The greenbugs are considered as one of the most destructive insects of small grain crops. Fifteen serious outbreaks have occurred since 1882, when it was first reported in Virginia. The most serious outbreaks were in 1907, 1949, and 1951. Each of these outbreaks caused an estimated loss of about 50 million dollars each season in the United States. Munro and Davis (1949) stated that a severe outbreak in 1949 in North Dakota caused a damage to some small grain fields as high as 100 per cent. Fenton and Dahms (1951) showed there was an outbreak of greenbug in Oklahoma about once every four years. Losses in wheat were estimated over 42 million dollars in these outbreaks. For Kansas, the estimated loss in wheat in 1960, and 1961 was $302,400, even though there was no outbreak during this period.

The information presented in this thesis is concerned with the relationship between hessian fly and greenbug resistance, and the possibility of combining these factors in one variety.

REVIEW OF LITERATURE

Related Studies

Plants that are damaged or infested less by insects than others under comparable conditions are called resistant. So far, resistant plants offer one of the most reliable and economical means for insect control. Three components appear to be involved in resistance, Painter (1951). Plants may be non-preferred for egg laying, shelter, or food, because they lack certain physical or chemical properties. Resistant plants may affect the biology of the insects adversely, causing mortality or reducing the fecundity of an insect feeding on the plant. Tolerant plants are those that survive and produce satisfactory yield under levels of infestation that would kill or severely injure susceptible plants but not affect the insect development. These three components are complex and concerned with effects rather than causes. Frequently they are concerned with physiological characteristics either in the plant or in the insect or in both. Information on the components and basis of resistance may or may not be helpful in the practical problems of selecting insect resistant plants but may explain differences that occur among varieties.

Studies on Differences Among Varieties. McColloch and Salmon (1923) thought the amount of silica was related to resistance. Miller et al (1960) using spodograms, indicated that silica was deposited in rod shaped forms arranged in rows in the susceptible varieties. This arrangement would allow hessian fly larvae to feed between the rows of silica. In case of some resistant varieties there was not enough free space to permit unrestricted feeding by the larvae. Robinson et al (1960) found an increase in number of chloroplasts in both inner and outer leaves of the hessian fly infested plants. The inner leaf became dark green and ceased to grow but the plant tissue did not dry up. The damage tended to move from inside the plant to outside, but those treated with Malic hydrizide (growth inhibitor), seemed to move from the outer layer inward and is followed by general break down and drying up. They found no relationship between concentration of pigments and resistant varieties. The larvae may reach their feeding place in resistant varieties but do not mature (Painter, 1951). On resistant varieties they die on the fourth or fifth day after hatching (Cartwright et al 1959). The larvae are considered as sap feeders, and obtain their food through sucking action.

As far as greenbug-host plant relationship is concerned, there is only moderate resistance and tolerance. Maxwell and Painter (1959) measured the degree of resistance by the rate of honey dew deposition by aphids. Recently (1962) they found higher concentrations of plant hormones in the extracts of greenbugs that feed on susceptible varieties compared with resistant varieties. The explanation was that free auxins exist in tolerant host plants in sufficient concentration in plant sap, but aphids may fail to penetrate into parts of the vascular system where free auxins exist in greater concentration. Or perhaps the plant hormones are bound to certain protein fractions or enzyme systems which prevent them from being detected by the biological assay method employed.

Races of Hessian Fly

Biological race studies showed that a culture of flies reared through four generations on W38 (Cartwright and Shands, 1946) is capable of producing a much higher infestation in W38, Dixon, and Java, than does the wild Indiana fly.

Races of hessian fly which differ in their ability to infest different varieties of wheat have been known for a long time (Painter, 1930). Laboratory studies in Indiana (Gallun, 1961) isolated four different races. Each race is adapted to feeding on specific varieties of wheat. These varieties have been shown to carry different genetic factors for resistance. These races of hessian fly selected in the greenhouse have not occurred as "pure" races in the field (Gallun et al, 1961). Recent (1963) information on races from Dr. R. H. Painter is that these races have been found in the field in Indiana.

Races of Greenbug

Races of greenbug were first demonstrated by Wood (1961). He isolated, in the greenhouse, a race called the "tiger" strain which was capable of destroying the resistant varieties, Dickinson Sel 28-A, and CI 9058. When this strain was cultured on Dickinson Sel 28-A, for eight generations they remained normal, whereas, those collected from the field populations decreased in size, fecundity, and longevity. Singh and Wood (1963) related the fecundity of this field strain to the changes in temperature. The fecundity of the field strain on Dickinson 28-A was much lower at optimum temperature than that of the greenhouse strain.

Inheritance Studies for Hessian Fly Reaction

Cartwright and Wiebe (1936), Noble et al (1940), described four genes affecting resistance to hessian fly. They showed that resistance of Dawson in crosses with the susceptible varieties Poso and Big Club depended upon two factors. Later, Noble and Suneson (1943), isolated the Dawson factor in the third backcross of Dawson x Poso to Poso. Selection No. 6179 was designated as having the genetic constitution $H_1H_1h_2h_2$ and selection No. 6232 was designated as $h_1h_1H_2H_2$. Analysis of the variety W38 made in Indiana (Caldwell et al, 1946), revealed an incompletely dominant gene for resistance and assigned the symbol H_3H_3 for this factor. The Dawson variety is susceptible to hessian fly in Indiana. Cartwright and Shands (1946) reported results from crosses between W38 and 11 other varieties of wheat, six of which apparently possessed the H_3H_3 factor, and the other five, one or more genes different than H_3H_3. Suneson and Noble (1950), in genetic studies of Java found that its resistance was different from the previous three and assigned the symbol h_4h_4 to the Java gene pair. Shands and Cartwright (1953), reported the presence of a fifth gene in Ribero and assigned the symbol H_5H_5. A partially-dominant factor possessed by Pawnee x PI 94587 (CI 12855) was designated, H_6H_6, (Allan et al 1959).

Painter et al (1940), working with the variety Marquillo in F_1, F_2, and F_3 generations were unable to resolve their data on a factorial basis but they indicated that resistance in this variety appears to be inherited as a recessive character.

Fly 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, independance of H_3H_3 also seems logical, (Noble and Suneson 1943). This agrees also with the finding of Suneson and Noble (1950), and Painter et al (1952), in that hessian fly resistance in Marquillo was complex and tended to be inherited in a recessive manner. Hollingsworth (1933), indicated that fly resistance was dependent upon more than a single pair or factors, and the resistance to the fly in the cross Kawvale x Tenmarq was probably dependent upon multiple factors. He concluded that the resistance in the case of Kawvale is more complex than Illini Chief.

Allan et al (1959), indicated that at least three dominant factors for hessian fly resistance and as many as five recessive factors are being utilized in Kansas wheat breeding program. They concluded that it appears that several factors are involved in the expression of Ponca's resistance. Ponca apparently is a mixture of different genetypes which differ in their response to the Great Plains hessian fly. However it was not possible to determine whether all the resistance possessed by Ponca came from Marquillo. Kawvale may contribute resistance to some or all individuals of the Ponca variety.

Inheritance Studies for Greenbug Reaction

Inheritance of greenbug resistance has been reported by a number of investigators. Wadley (1931), reported the reactions of greenbugs to several varieties of common durum and emmer wheat. The aphids did not thrive on Vernal, a variety of emmer, *Triticum dicoccum*.

The inheritance of resistance of barley to the greenbugs was studied in Oklahoma where difference involving one or two dominant genes for resistance was found, but none of the wheat and rye varieties showed a high degree of resistance, Dahms et al (1955). However, Gardenhire and Chada (1961), and Smith et al (1962), found that resistance in barley is conditioned by a single dominant gene.

Resistance of wheat to the greenbug, involving crosses between Dickinson selection and three winter wheat varieties was studied in Kansas. The F_2 population appeared to show the presence of a single recessive gene for the tolerance of resistance as expressed in ability to survive infestation (Painter and Peters 1956). However the F_1 of these crosses appeared to be more like the resistant parent in the lack of chlorosis following aphid feeding. These results are in agreement with those obtained later by Daniels and Porter (1958). In crosses of Dickinson with five other varieties, the F_1 plants tended to be intermediate to the parents indicating a lack of dominance. Chada et al (1961), working on barley and wheat suggested the possibility of modifying genes in the inheritance of greenbug resistance. Curtis et al (1960), studied the F_1, F_2, and F_3, among the crosses between the resistant varieties DS 28A and CI 9058 crossed with the susceptible varieties Ponca, Concho, and Crockett and with each other revealed that resistance is conditioned by a single recessive gene pair common to the resistant strains. The gene symbol gb gb was assigned. Resistance was transferred from DS 28A and CI 9058 to other strains of wheat. Porter and Daniels (1963), showed that the greenbug resistance was highly heritable. The influence of environmental factors intorduced complications in the interpretation of the results.

Association of Insect Resistance and Other Characteristics

Evidence has been secured that genetic factors for insect resistance can be transferred from one species of wheat to another. Genes for resistance of wheat to hessian fly have been transferred from Triticum durum by way of Marquillo spring wheat to varieties of winter habit Triticum vulgare. No relationship was evident between resistance to either leaf rust or stem rust or fly, and any other characteristics recorded (Painter et al 1931, 1940). However Allan et al (1959), found a linkage between hessian fly and leaf rust resistance in the Kansas selection 52400. Dual, CI 13083, is resistant to fly and leaf rust (Patterson, 1959). Ponca is resistant to hessian fly and leaf rust (Painter et al 1952).

Atkins and Dahms (1945), found that the most resistant strains of wheat to greenbug were selections from crosses Marquillo x Oro, which are resistant to hessian fly.

These studies for both hessian fly and greenbug resistance indicated that resistance is generally simple, highly heritable, and it can be transferred from resistant sources to adapted or commercial winter wheat.

MATERIAL AND METHODS

Parents and Crosses Studied

Three parents carrying resistance to greenbug, Concho x Dickinson (Cch-Di), K61293; Bison x Dickinson (Bsn-Di), K61296; and Pawnee x Dickinson (Pn-Di), K61299, were crossed with three varieties resistant to hessian fly. The hessian fly resistant varieties were Ottawa (Ot), CI 12804; Comanche x Ottawa (Com-Ot), CI 13548; and Ponca, CI 12128. The parents are listed on table 1 with their important characteristics.

Table 1. Parental characteristics of varieties used in hessian fly and greenbug resistant studies

Parents and Sel. No.	greenbug	hessian fly	leaf rust	stem rust	SBM
Concho x Dickinson, K61293	res.	susc.	susc.	susc.	susc.
Bison x Dickinson, K61296	res.	susc.	susc.	susc.	susc.
Pawnee x Dickinson, K61299	res.	susc.	susc.	susc.	susc.
Ottawa, CI 12804	susc.	res.	res.	res.	res.
Ottawa x Comanche, CI 13548	susc.	res.	res.	res.	susc.
Ponca, CI 12128	susc.	res.	res.	susc.	susc.

Dickinson in crosses with Concho, Bison, and Pawnee, probably possesses the gene pair gb gb for greenbug resistance. Ottawa and Ottawa x Comanche may possess the gene pair H_3H_3 for hessian fly resistance and Ponca probably of three recessive factors from Marquillo. The crosses made are given in table 2.

Table 2. List of crosses of hessian fly and greenbug resistant varieties

Cross No.	No. of Seeds	Parental name
X6267,68,72	4,1,1	Concho-Dickinson x Ottawa
X6269,70,71	5,1,11	Ottawa x Concho-Dickinson
X6273,74	7,3	Bison-Dickinson x Ottawa
X6275,76,77	8,5,5	Ottawa x Pawnee-Dickinson
X6278,79	2,11	Pawnee-Dickinson x Ottawa
X6280	5	Concho-Dickinson x Ponca
X6281	3	Ponca x Concho-Dickinson

Table 2. List of crosses of hessian fly and greenbug resistant varieties (concl.)

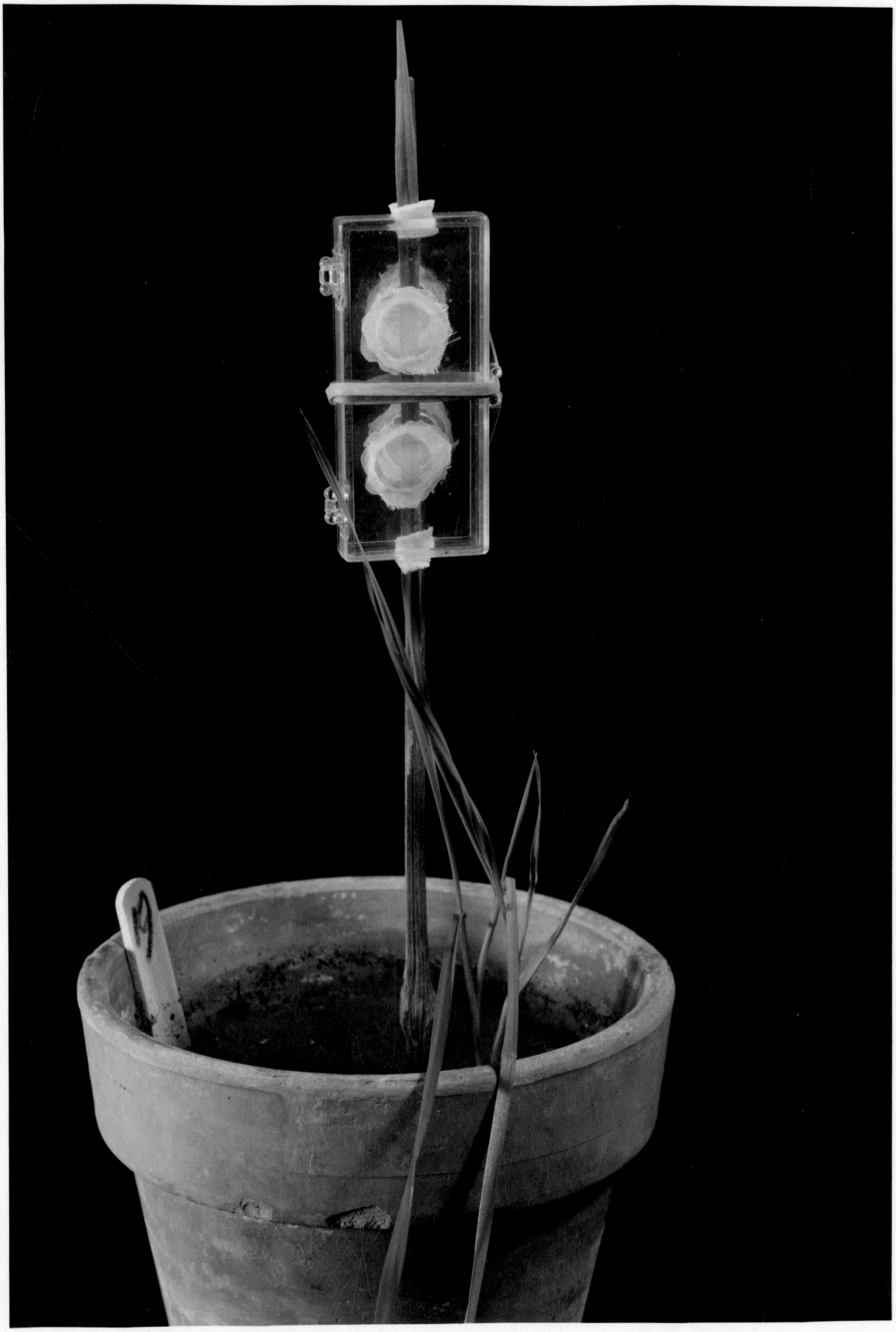
Cross No.	No. of Seeds	Parental name
X6282	5	Bison-Dickinson x Ponca
X6283	1	Pawnee-Dickinson x Ponca
X6284,85	4,1	Ponca x Pawnee-Dickinson
X6286,87,88,89	5,2,8,4	Comanche-Ottawa x Concho-Dickinson
X6290	9	Concho-Dickinson x Comanche-Ottawa
X6291	1	Bison-Dickinson x Comanche-Ottawa
X6292,93	3,2	Comanche-Ottawa x Pawnee-Dickinson
X6294,95	2,4	Pawnee-Dickinson x Comanche-Ottawa
Total	123	

Studies With F_1 Plants

Effects on The Greenbug And Wheat Plants. Antibiotic studies described by Chada et al (1961) were used. The single plant or entire flat was caged using cheese cloth. Aphids were introduced into the cage when the plants were about 8 days old. However, to obtain more information on the aphid-host relationship the technique used by Peters and Painter (1958) was used to cage seperate leaves (Figure 1). The cages were plastic cases $3 \times 1\frac{1}{4} \times \frac{1}{2}$ inch, which had two hinges on the back and one snap type fastener on the front to hold the cage closed. Two holes were drilled in the tops of these cages and covered with fine cloth mesh. A ⊔ shaped groove was made in both ends of the box to

EXPLANATION FOR PLATE I

Plastic cage for rearing aphids on individual plants in tests of aphid fecundity. (See text for explanation.)



insert the leaf and a damp cotton plug for protection. The clear plastic sides made it possible to see the aphids in the cage at all times, and the cloth windows allowed for transpiration of the leaves without condensation of water in the cage.

The boxes were held in place on the plants by fastening them with rubber bands to stakes. Fourth instar nymphs were selected and placed in the cage with a camel's hair brush. In some experiments only one aphid was used per cage, in others, five aphids were used. Infestation was made on plants when the third leaf was completely developed. Observations were made daily to ascertain whether the introduced aphids had molted and also to record notes of the appearance of progeny. The nymphs produced were counted on the seventh day after infestation where the leaf was cut and the number of all aphids, living and dead were recorded.

The leaves were arranged on a chart using $\frac{1}{2}$ inch cellophane tape. The damage on each leaf was measured in mm^2. Rating for damage on a scale of 1 to 5 was made. A rating of 1 indicated little or no damage and 5 indicated the leaf was injured beyond recovery.

Eight families were studied by planting the wheat in flats. A total of 23 F_1 seeds and their parents were sown at random in a flat $22\frac{1}{2}$ x $12\frac{1}{2}$ x $3\frac{1}{2}$ inches. Dickinson was used as a resistant check and Pawnee as the susceptible check. The soil flat contained 10 rows which were divided. Growth was rapid in the insectary. After one week when the plants were 5 inches tall and in the 2-leaf stage, they were infested with greenbugs by placing infested Reno barley leaves on a wire tray across the middle of the flat. Some aphids also were scattered, among the plants as uniformly as possible. After two weeks the Pawnee plants and the susceptible parents were completely destroyed by aphids. The same scale described earlier was made to evaluate the damage done to the plants. The plants which survived were sprayed with Malation to kill aphids and transplanted in seperate pots.

Effect on The Hessian Fly And Wheat Plants. The hessian fly used in this study were originally collected in a field in Marshall County, Kansas. This population had the characteristics of flies found in eastern Kansas and Missouri. The same F_1 plants and their parents used in greenbug tests were saved for this test. The plants were 8 weeks old when infested with hessian fly.

A cheesecloth tent was placed over the potted plants to provide a high relative humidity for the adult flies, for hatching the eggs, and migration of the larvae. Adult flies were released into the cage and the adults allowed to oviposit on the plants at random. The tent was left over the plants for one week. Infestation readings were made when the instars had developed or some puparia were present on the susceptible check plants. The plants were classified as resistant when no observed larvae were present at the base; intermediate, when larvae developed, but generally were smaller and fewer in number and often pushed up from the base of the plant; susceptible, when larvae were fully developed, and had normal size, and the plants showed typical symptoms of hessian fly damage.

After the test, the larvae and damaged tillers were removed, and the remaining parts of the plants were grown to maturity.

Studies With F_2 Plants

F_2 seeds were produced on F_1 plants used in the studies for the reaction of F_1 plants to greenbugs, and hessian fly, and the antibiotic studies. Other F_1 plants were grown to use in backcrossing to both parents. About one-half of the F_2 seeds were planted in the field in the fall 1963 and the remaining used for inheritance studies.

Inheritance Studies For Hessian Fly Resistance. F_2 seeds were sown in flats. There were 20 rows per flat and 25 seeds were planted in each row. Epidor, a variety very susceptible to hessian fly, was used as a check. The parents also were planted. The rating scale was resistant, intermediate, and susceptible. These three classes are illustrated in Figure 2. A tent was used to insure infestation as described for studies on F_1 plants.

Inheritance Studies For Greenbug Resistance. The tests were conducted in a basement. Flourscent light provided the necessary light for 16 hours a day. The temperature was maintained at 70°F. The greenbugs used in 1962 were lost during August, 1963. A new supply of greenbugs was obtained from

EXPLANATION FOR PLATE II

(1) Resistant plant "left": no larvae present and the plant normally developed.

(2) Intermediate plant "middle": a few flaxseed have been pushed up and out of their normal feeding area at the base of the stem. Later any larvae will dry out and die. The plants soon recover but have a reduced diameter of the stem.

(3) Susceptible plants "right": the larvae and flaxseed are generally at the base of the stem and develop normally. The plants have thin stems, injury at the base and reduction in the root size. The central leaves are absent or stunted.

Oklahoma State University. F_2 seeds were sown in flats. Rating damage was made three times, 12, 14, and 16 days after infestation. The scale used was zero to 6. Zero indicated little or no damage; 1 indicated $\frac{1}{4}$ of the leaf was damaged; 2, $\frac{1}{2}$; 3, 3/4; and 4, the entire leaf was damaged; 5, the plant was beyond recovery. Observations made on the basis of the first leaf reaction. Infestation were made as described for F_1 plants.

Eighteen days after infestation, most of the susceptible plants were dead, at that time the surviving plants were sprayed by Malation.

Statistical analysis. F test was used to differentiate between the averages of the number of tillers in hessian fly test, and the number of aphids produced in greenbug test. Chi square test was used in F_2 studies for the goodness of fit to the suggested hypothesis.

EXPERIMENTAL RESULTS

Hessian Fly Inheritance Studies

F_1 Generation

The data on 25 F_1 plants are given in Table 3. According to F test, there was no significant difference between the average number of tillers among F_1 plants and the parents. The F_1 plants had nearly as many larvae per plant as the susceptible parents. The F_1 plants averaged 3.56 larvae per plant, the

Table 3. Response of 15 F_1 hybrids and their parents for number of tillers, number of larvae, reaction and average rating of the plants when infested with hessian fly.

Cross No.	F1 Reaction: No. plts.	Total No. of tillers	Total No. of larvae	Reaction	Aver. rating	susc. parents: Kind of & name	Total No. of tillers	Total No. of larvae	Reaction	Aver. rating	res. parents: Kind of & name	Total No. of tillers	Total No. of larvae	Reaction	Aver. rating
6267	2	8	4	R-I	1.5	♀ Cch-Di	6	13	R+S	2	♂ Ot	6	-	R	1
6269	1	5	1	I	2	♂ do	3	-	R	1	♀ do	5	-	R	1
6271	1	5	-	R	1	do	4	1	S	3	do	3	-	R	1
6274	1	4	5	I	2	♀ Bsn-Di	5	4	S	3	♂ Ot	4	-	R	1
6276	1	5	-	R	1	♂ Pn-Di	3	-	R	1	♀ Ot	4	-	R	1
6277	2	9	3	R-I	1.5	do	10	8	S	3	do	10	-	R	1
6279	5	19	25	I	2	♀ do	15	8	S	3	♂ do	21	-	R	1
6281	1	3	2	I	2	♂ Cch-Di	5	1	S	3	♀ Ponca	1	-	R	1
6286	1	3	18	I	2	do	2	1	S	3	♀ Com-Ot	5	-	R	1
6287	1	3	2	I	2	do	4	-	R	1	do	1	-	R	1
6289	2	12	7	I	2	do	6	8	S	3	do	14	-	R	1
6290	4	12	5	R-I	1.5	♀ do	14	13	S	3	♂ do	19	9	I	1.5
6292	1	3	-	R	1	♂ Pn-Di	6	28	S	3	♀ Com-Ot	5	2	I	2
6293	1	4	5	I	2	do	3	9	S	3	do	4	3	I	2
6294	1	4	12	S	3	♀ do	4	10	S	3	♂ do	6	1	I	2
otal 15	25	99	89	R-I-S	26.5		91	104	R+S	38		108	15	R I	18.
verage		3.96	3.56	I	1.7		3.64	4.16	S	2.5		4.32	0.6	R	1.

susceptible parents 4.16; and the resistant parents 0.6. X6294 was found to be completely susceptible and no selfing was involved, because it segregated in greenbug tests. The explanation could be that the F_1 was an outcross plant.

F_2 Generation

Crosses With Ottawa. The data on F_2 plants and the parents of crosses involving Ottawa are given in Table 4. Ottawa possessed the H_3 factor for resistance to hessian fly and had no infestation in three tests. The three susceptible parents; Concho x Dickinson, Pawnee x Dickinson, and Bison x Dickinson were 100 percent infested. All F_2 families segregated in the ratio 3 resistant to 1 susceptible plant. Chi square analysis indicated that the data fit this hypothesis and that all families came from the same population.

Crosses With Ponca. Table 5 gives the distribution of infested F_2 plants and parents to hessian fly and Chi square analysis. Ponca varied in percentage infestation from 12 to 38 percent. Two crosses fit the ratio of 1 resistant : 3 susceptible. One cross fits the ratio 27 resistant : 37 susceptible and the other a ratio of 1:15. This indicated that the resistance of Ponca to hessian fly is complex.

It also was noticed that, 1) only few hybrids involving Ponca were successful and gave few seeds; 2) a high reduction in germination in both F_1 and F_2 that seemed to be correlated with the susceptibility of Ponca; and 3) the number of F_2 segregating

Table 4. Distribution of F_2 plants for reaction to hessian fly infestation the average number of larvae per plant the reaction of the parents to hessian fly in crosses involving Ottawa.

Cross No.	No. of families	F_2 reaction: res. No. plts.	inter. No. plts.	inter. Av. larv.	susc. No. plts.	susc. Av. larv.	% susc.	X^2 P	Parental reaction: Female name	res. No. plts.	susc. No. plts.	susc. Av. larv.	% susc.	Male name	res. No. plts.	susc. No. plts.	susc. Av. larv.	% susc.
X6267	2	9	12	2.3	9	11.2	22.5	.50-.75	Cch-Di	--	4	16.5	100	Ot	15	--	--	0
X6268	1	10	6	2.5	5	13.2	33.8	.75-.90	do	--	4	16.5	100	do	15	--	--	0
X6269	3	22	19	4.3	11	14.4	21.1	.50-.75	ot	15	--	--	0	Cch-Di	--	10	10.2	100
X6270	1	6	3	2.6	2	11.5	18.1	.50-.75	do	17	--	--	0	do	--	8	6.5	100
X6271	6	55	50	3.3	23	9.3	18.0	.05-.10	do	23	--	--	0	do	--	14	8.1	100
X6273	2	7	8	2.8	8	7.6	34.7	.25-.50	Bsn-Di	--	16	7.0	100	Ot	22	--	--	0
X6274	3	23	25	2.4	12	9.4	20.0	.25-.50	do	--	16	7.0	100	do	14	--	--	0
X6275	3	21	20	2.9	15	8.2	26.7	.75-.90	ot	16	--	--	0	Pn-Di	--	16	7.7	100
X6276	2	13	12	1.6	7	3.9	21.9	.50-.75	do	12	--	--	0	do	--	16	7.7	100
X6277	4	21	23	2.4	20	7.3	31.2	.10-.25	do	18	--	--	0	do	--	19	6.5	100
X6278	1	5	8	2.8	4	7.5	23.5	.75-.90	Pn-Di	--	19	8.9	100	Ot	16	--	--	0
X6279	9	53	57	2.6	41	5.1	27.1	.50-.75	do	--	15	10.9	100	do	16	--	--	0
Total	37	245	243	2.4	156	9.0	24.3	--										
pooled								.50-.75										
Heter.								.50-.75										

Table 5. Distribution of F_2 plants for reaction to hessian fly infestation, the average number of larvae per plant and the reaction of the parents to hessian fly in crosses involving Ponca.

Cross. No.	No. of families	F_2 reaction res. No. Plts.	No. Plts.	Av. Larv.	No. Plts.	Av. Larv.	% susc.	X^2 / P	Female	parental reaction res. No. Plts.	inter. No. Plts.	Av. Larv.	susc. No. Plts.	Av. Larv.	% susc.	Male	res. No. Plts.	inter. No. Plts.	Av. Larv.	susc. No. Plts.	Av. Larv.	% susc.
X6280	2	3	9	2.9	14	6.2	53.8	.01-.02	Cch-Di	--	--	--	12	9.0	100	Ponca	13	1	4	2	4	18
X6281	2	3	10	3.1	22	4.1	62.8	.10-.25	Ponca	10	4	2.0	2	4.2	12	Cch-Di	--	--	--	15	9	100
X6282	2	-	1	2.0	31	3.3	97.0	$<$ .005	Bsn-Di	--	--	--	10	5.4	100	Ponca	9	4	2.2	8	3.2	38
X6284	1	3	1	1.0	8	2.8	66.6	.50-.75	Ponca	6	5	2.2	5	3.4	31	Pn-Di	--	--	--	12	8.5	100
Total	5	9	20	2.4	44	4.4	60.6			no. larvae on sus. = 8 no. larvae on res. = 3.9												
pooled								.005														
Heter.								.25-.50														

plants were very few. All these factors limited the amount of data and prevented an analysis of the inheritance to hessian fly resistance in Ponca.

Crosses With Comanche-Ottawa, CI 13548. Table 6 lists the reaction of F_2 plants and their parents. Comanche-Ottawa possessed the H_3 factor and averaged 2.42 percent susceptible plants with average number of 2.2 larvae per plant. The susceptible parents were 100 percent infested and averaged 7.7 larvae per plant. The F_2 plants averaged 34 percent susceptibility and had 6.1 larvae per plant. The resistant parent plants used apparently were not all homozygous for resistance, as some of the progeny of the actual parents were susceptible to hessian fly.

In the crosses X6291 and X6294, the Comanche-Ottawa parent progeny segregated for resistance to hessian fly which suggested that the plant used for crossing had the genotype H_3h_3. There was only one F_1 plant tested and it apparently carried the H_3 gene from Comanche-Ottawa. X6294 was found to be completely susceptible as in F_1 test. Apparently it carried the h_3 gene from Comanche-Ottawa.

Excluding the cross X6294, the pooled data showed a good fit to the ratio of 3 resistant: 1 susceptible. This indicated a single partially dominant factor H_3H_3 for fly resistance was possessed by Comanche x Ottawa. The source of resistance in Comanche x Ottawa was derived from Ottawa.

Table 6. Distribution of F_2 plants for reaction to hessian fly infestation, the average number of larvae per plant and the reaction of the parents to hessian fly in crosses involving Comanche-Ottawa CI 13548.

Cross No.	No. of families	F_2 reaction						X^2	parental reaction													
		res.	inter.		susc.		% susc.		Female	res.	inter.		susc.		% susc.	Male	res.	inter.		susc.		% susc.
		No. plts.	No. plts.	Av. larv.	No. plts.	Av. larv.		P		No. plts.	No. plts.	Av. larv.	No. plts.	Av. larv.			No. plts.	No. plts.	Av. larv.	No. plts.	Av. larv.	
X6286	4	26	15	3.2	15	5.2	26.7	.75-.90	Com-Ot	16	--	--	--	--	0	Cch-Di	--	1	4	12	10.0	92.3
X6287	1	18	7	2.5	16	6.6	39.0	.10-.25	do	15	2	1.5	--	--	0	do	--	--	--	18	7.5	100
X6288	1	5	4	2.2	7	5.5	43.0	.05-.10	do	20	--	--	--	--	0	do	--	--	--	12	6.2	100
X6289	2	15	5	2.2	7	3.4	25.9	$>$ .90	do	20	--	--	--	--	0	do	--	--	--	12	6.2	100
X6290	8	50	32	1.7	54	4.6	39.7	$<$ .005	Cch-Di	--	--	--	16	6.8	100	Com-Ot	12	1	3	--	--	0
X6291	1	2	4	3.2	6	4.2	50.0	.025-.05	Bsn-Di	--	--	--	12	7.2	100	Com-Ot	13	4	2.7	1	2	5.5
X6292	3	60	13	3.1	21	7.4	22.3	.25-.50	Com-Ot	13	--	--	--	--	0	Pn-Di	--	--	--	15	7.6	100
X6293	2	20	11	3.0	22	6.6	41.5	$<$ .005	do	17	--	--	--	--	0	do	--	--	--	16	8.0	100
X6294	2	--	--	--	51	10.0	100	---	Pn-Di	--	--	--	12	10.	100	Com-Ot	13	3	3	1	4	5.8
X6295	2	14	4	3.0	14	7.8	43.76	.01-.025	do	--	--	--	17	9.8	100	do	18	2	2.5	--	--	0
Total	24	210	95	2.6	162	6.1	34.4			no. larvae no. larvae	on susc. = 7.7 on res. = 0.22											
pooled																						
Heter.								.05-.10														

Greenbug Inheritance Studies

F_1 Generation

Table 7 lists the number of greenbugs per leaf and average damage per leaf of F_1 plants and their parents. The F_1 plants infested with 1 aphid averaged 10.96 nymphs per leaf and 54.16 nymphs per leaf when 5 aphids were used. The average damage per leaf for each infestation was 1.788 cm^2.

When one aphid was placed on the leaf of the resistant parent an average of 11.56 nymphs were produced. There were 49.48 nymphs produced on each leaf when 5 aphids were used. The average damage per leaf was .973 cm^2.

The susceptible parents averaged 13.32 nymphs for each single aphid placed on the leaf and 62.32 nymphs were produced when 5 aphids were used. The average leaf area damaged was 2.63 cm^2.

When one aphid was placed on each leaf the rate of aphid reproduction was much more variable than when five aphids were used. Use of five aphids gave a better picture of the reproduction of aphids on the F_1 plants and parents than one aphid. In either case the average number of nymphs per leaf indicated that the F_1 could probably be identified from the parents. The number of progeny of one aphid was 11.0, 11.6, 13.3 on the F_1, resistant parent and susceptible parent respectively. For 5 aphids, in the same order, it was 54, 49, and 62. The rate of increase of nymphs per day on F_1 plants was 1.45, on the resistant parents 1.16 and on the susceptible parents 1.77.

Table 7. Response of 15 F_1 hybrids and their parents for number of nymphs from 1 and 5 aphids on the third leaf produced within one week, increase per female per day and average rating when infested with greenbugs.

Cross No.	No. of families	F_1 reaction: Total No. of nymphs/leaf (1)	(5)	Av. damage per leaf (cm^2)	%	Av. rating	res. parents: Kind of name	Total No. of nymphs/leaf (1)	(5)	Av. damage per leaf (cm^2)	%	Av. rating	sus. parents: Kind of name	Total No. of nymphs/leaf (1)	(5)	Av. Damage per leaf (cm^2)	%	Av. rating
X6267	2	32	79	1.61	35.77	2.5	♀ Cch-Di	29	82	0.88	19.55	1.5	♂ Ot	54	133	2.65	58.88	1.5
X6269	1	11	58	0.50	11.11	1	♂ do	15	60	0.40	8.88	1	♀ do	17	39	.75	16.66	4
X6271	1	7	37	1.13	25.11	2	do	14	40	0.13	2.08	1	do	4	54	2.50	55.55	3
X6274	1	6	41	2.40	53.33	3	♀ Bsn-Di	11	42	0.60	13.33	1	♂ Ot	11	39	1.80	40.00	3
X6276	1	17	54	1.50	33.33	2	♂ Pn-Di	11	44	0.30	6.66	1	♀ Ot	11	63	1.25	27.77	2
X6277	2	29	135	0.90	20.00	1.5	do	40	54	0.30	6.66	1	do	32	134	2.36	52.44	3.5
X6279	5	45	332	1.88	41.77	2.8	♀ do	45	250	0.41	9.11	1	♂ do	90	295	2.31	51.33	3.3
X6281	1	2	65	0.80	17.77	1	♂ Cch-Di	3	18	0.10	2.22	1	♀ Ponca	14	67	1.60	35.55	2
X6286	1	14	65	2.40	53.33	3	do	15	94	1.60	35.55	2	♀ Com-Ot	4	94	3.75	83.33	5
X6287	1	7	40	3.20	71.11	4	do	14	53	1.50	33.33	2	do	11	100	4.00	88.88	5
X6289	2	29	90	3.75	83.33	4	do	20	67	3.75	83.33	3.5	do	23	68	4.25	94.44	3.5
X6290	4	50	235	3.00	66.68	2.25	♀ do	39	237	2.47	54.88	1	♂ do	20	305	2.87	63.77	3.25
X6292	1	7	48	1.36	30.22	2	♂ Pn-Di	4	63	0.57	12.66	1	♀ Com-Ot	13	61	2.46	54.66	4
X6293	1	4	30	1.50	33.33	1	do	6	58	1.00	2.22	1	do	8	52	2.50	55.55	4
X6294	1	14	45	0.90	20.00	1	♀ do	23	75	0.60	13.33	1	♂ do	21	54	4.50	100.00	4
Total	25	274	1354	26.83	--	33.05		289	1237	14.60	—	2.0		333	1558	39.55	--	51.05
Average		10.96	54.16	1.788	39.74	2.2		11.56	49.48	0.973	21.62	1.33		13.32	62.32	12.63	58.59	3.4
Av. Increase per female per day		1.45						1.16						1.77				

Although the effect on the reproduction of the aphids was different on the parents and F_1 plants, the amount of damage to the host was the best indication to differentiate the resistance to greenbugs. Figure 3 illustrates the damage on one cross, X6279 Pawnee-Dickinson x Ottawa. In all five comparisons the middle leaf is from the F_1 plant and was intermediate in reaction in comparison to the susceptible parent, and the resistant parent.

Further studies on the response of F_1 plants to greenbugs was made by studying 23 F_1 plants and their parents sown in flats. Table 8 gives the results.

Table 8. Distribution of plants for greenbug resistance ratings of F_1 plants and parents on one week old plants.

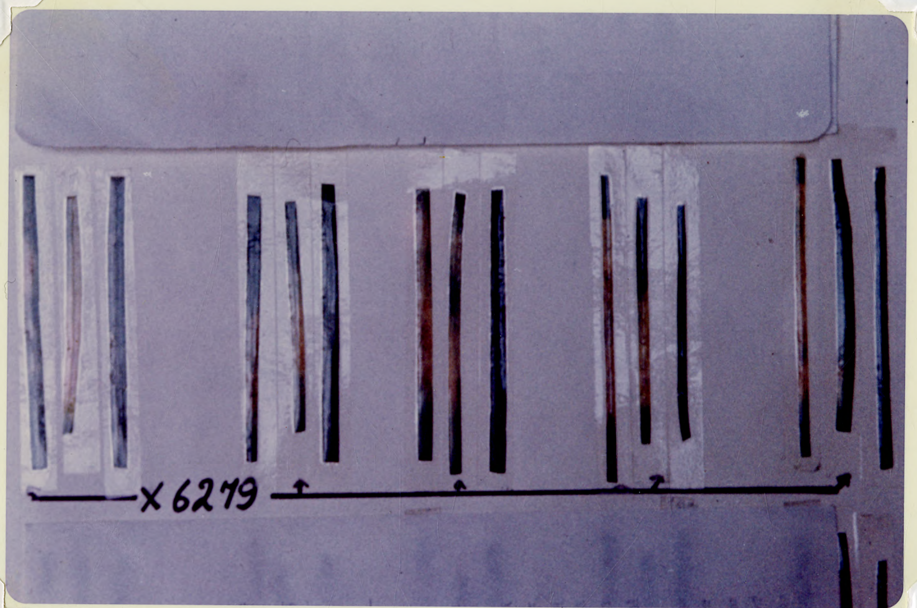
	Class					Total	Average
	1	2	3	4	5	No.	rating
F_1	—	11	7	2	—	20	2.55
res. parent	27	20	—	—	—	47	1.42
susc. parent	—	—	—	34	10	44	4.22

Ratings were made using the scale 1-5 as described in material and methods. The F_1 plants gave an intermediate reaction compared to the parents. Figure 4 shows the reaction of F_1 and parents to greenbug.

EXPLANATION OF PLATE III

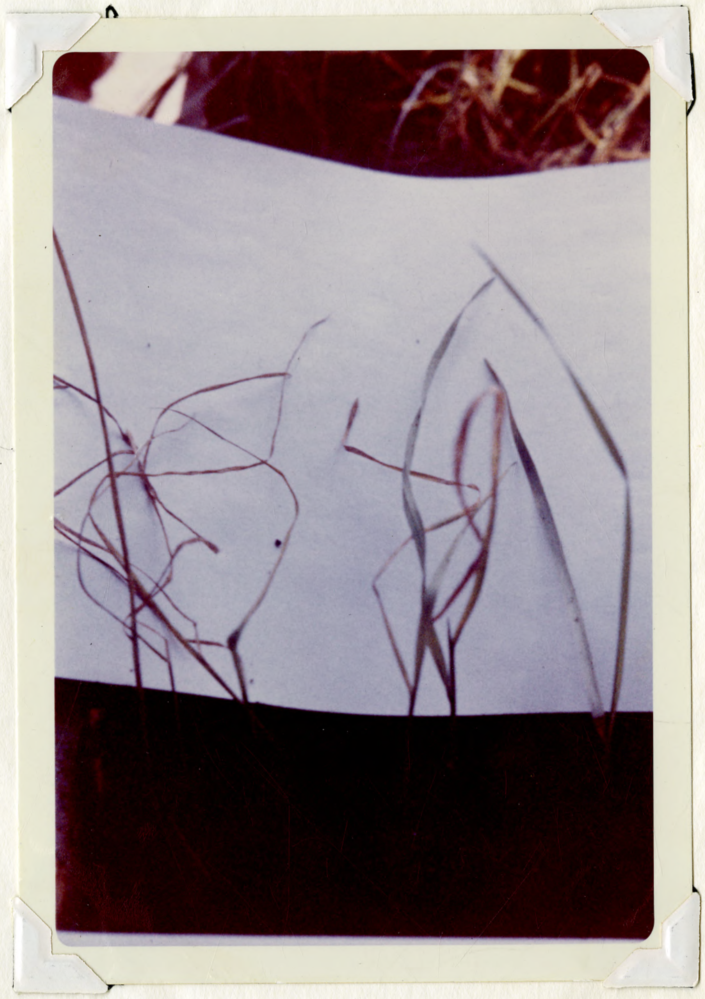
Reaction of F_1 and parent plants to greenbug infestation. The leaf on the left in each group of three is from the susceptible parent, the F_1 leaf is in the middle, and the leaf from the resistant parent on the right.

These leaves came from F_1 plants and parents of the cross X6279, Pawnee-Dickinson x Ottawa.


X 6279

EXPLANATION OF PLATE IV

Reaction of F_1 and parents plants to greenbugs grown in flats and infested with a large number of aphids. The plants were three weeks old from the cross X6288, Comanche-Ottawa x Concho-Dickinson with four plants from the susceptible parents on the left, the two plants in the middle are F_1's, and the plant on the right from the resistant parent. The F_1 plants show intermediate damage between the two parents.



F_2 Generation:

Crosses With Ottawa. Table 9 lists the data from 12 crosses and their parents for reaction to greenbugs. F_2 plants of cross X6268 were all susceptible to greenbugs. No seeds of the resistant parent were available for this test. It was assumed that the parent was an off-type, that is, susceptible to greenbugs.

For analysis, the class zero, 1, and 2 were considered as resistant and classes 3, 4, and 5 as susceptible. With this classification, all 11 families segregated 1 resistant to 3 susceptible plants and fit the hypothesis as tested by Chi square. The pooled data also fit the 1:3 ratio and the test for heterogenity indicated the families were from the same population.

Crosses With Ponca. Table 10 gives the data from 5 crosses and their parents for reaction to greenbugs. F_2 plants of cross X6284 were all susceptible to greenbugs. It was assumed that the parent was an off-type, that is, susceptible to greenbugs.

With the classification previously mentioned, 2 families segregated 1 resistant to 3 susceptible plants and fit the hypothesis as tested by Chi square. In one family, X6281 the X^2 was highly significant with P = .005 _ .01 in which the susceptible parent was used as a female, but more F_2 plants were classified in the resistant group than was expected. However, the pooled data and the test for heterogenity fit the ratio 1:3 indicated the families were from the same population.

Table 9. Distribution of F_2 plants and their parents to greenbug infestation in crosses involving Ottawa.

Cross No.	No. of families	F_2 reaction 0,1,2	3,4,5	Total	X^2 P value	parental reaction female name	0,1,2	3,4,5	Total	male name	0,1,2	3,4,5	Total
X6267	3	16	39	55	.25-.50	Cch-Di	22	---	22	Ot	---	21	21
X6268	1	---	13	13	---								
X6269	4	25	62	87	.25-.50	Ot	---	21	21	Cch-Di	20	---	20
X6270	1	3	5	8	.25-.50								
X6271	7	48	151	199	.90	Ot	---	21	21	Cch-Di	21	---	21
X6273	2	6	37	43	.05-.10	Bsn-Di	---	---	---	Ot	---	10	10
X6274	2	23	50	73	.10-.25	Bsn-Di	18	3	21	Ot	---	10	10
X6275	4	26	79	105	.75-.90	Ot	---	31	31	Pn-Di	20	---	20
X6276	2	11	30	41	.75-.90	Ot	---	20	21	Pn-Di	20	---	20
X6277	5	35	91	126	.25-.50	Ot	---	12	12	Pn-Di	22	---	22
X6278	1	8	22	30	.75-.90	Pn-Di	25	---	25	Ot	---	19	19
X6279	10	51	189	240	.25-.50								
Total	41	252	755	1007									
pooled					7.99								
Heter.					.50-.75								

Table 10. Distribution of F_2 plants and their parents to greenbug infestation in crosses involving Ponca.

Cross No.	No. of families	F_2 reaction 0,1,2,	3,4,5	Total	X_2 P value	parental reaction female name	0,1,2	3,4,5	Total	male name	0,1,2	3,4,5	Total
X6280	2	16	38	54	.25-.50	Cch-Di	20	---	20	Ponca	---	22	22
X6281	3	25	37	62	.005-.01	Ponca	---	6	6	Cch-Di	21	---	21
X6282	3	16	54	70	.50-.75	Bsn-Di	---	---	---	Ponca	---	18	18
X6284	1	---	32	32	----	Ponca	---	19	19	Pn-Di	26	---	26
X6285	1	4	13	17	.90								
Total	9	61	142	203									
pooled					.05-.10								
Heter.					.10-.25								

Crosses With Comanche-Ottawa, CI 13548. Table 11 gives the data from 9 crosses and their parents for reaction to greenbugs. F_2 plants of cross X6289 were all susceptible. In the same test its parent revealed 100 percent susceptibility. Data from this cross was eliminated from the analysis. Progeny of the cross X6292 was classified as susceptible. It was not a self as the F_2 generation segregated for reaction to hessian fly. As the male parent was resistant to greenbugs the F_1 probably was an outcross.

The other 7 crosses segregated for reaction to greenbugs and gave a good fit to a 1 resistant: 3 susceptible. Also reciprocal crosses responded similarly, indicating an absence of cytoplasmic influence on the hereditary mechanism.

Data of the three types of crosses were grouped and analysed and data are shown at the bottom of Table 11. Heterogeneity X^2 was not significant, confirming the hypothesis of one single recessive factor involved in the resistance to greenbugs originally derived from Dickinson spring wheat.

DISCUSSION

Genetic Studies On Hessian Fly

From these studies, it appears that, for the most part, the inheritance of resistance to hessian fly was simple. It should not be difficult to obtain selections of wheat resistant to this insect. Selections can be conveniently tested in the greenhouse for their reaction to hessian fly.

Table 11. Distribution of F_2 plants and their parents to greenbug infestation in crosses involving Comanche-Ottawa, CI 13548.

Cross No.	No. of families	F_2 reaction 0,1,2	3,4,5	Total	X_2 P value	parental reaction female name	0,1,2	3,4,5	Total	male name	0,1,2	3,4,5	Total
X6286	3	28	76	104	.50-.75	Com-Ot	---	21	21	Cch-Di	8	6	14
X6287	1	12	30	42	.50-.75								
X6288	3	14	46	60	.75-.90								
X6289	4	---	145	145	----	Com-Ot	---	13	13	Cch-Di	---	17	17
X6290	8	52	160	212	.75-.90	Cch-Di	14	---	14	Com-Ot	---	26	26
X6292	2	1	57	58	----	Com-Ot	---	22	22	Pn-Di	18	---	18
X6293	1	3	13	16	.50-.75	Com-Ot	---	21	21	Pn-Di	23	---	23
X6294	2	11	30	41	.75-.90	Pn-Di	22	---	22	Com-Ot	---	21	21
X6295	1	10	25	35	.50-.75	Pn-Di	26	---	26	Com-Ot	---	21	21
Total	19	130	380	510									
pooled					.75-.90								
Heter.					.90-.95								
*Total	69	443	1277	1720									
*pooled					.25-.50								
*Heter.					.50-.75								

*Grand Total for all the three crosses.

A single partially dominant factor H_3H_3 appears to separate the resistant variety, Ottawa, CI 12804, from the susceptible varieties, Concho-Dickinson, K61293; Bison-Dickinson, K61296; and Pawnee-Dickinson, K61299.

The F_1 plants showed an intermediate reaction compared with both parents. Painter et al (1931) found that in the crosses of Illini Chief, sel. No. 223415, with Tenmarq and Kanred the F_1 was nearly as heavily infested as the susceptible parents. Painter et al (1940) tested F_1 plants of Marquillo hybrids x susceptible varieties and found them to vary from 50 to 100 percent infested. The susceptible parents varied from 67 to 100 percent infestation and the resistant parents varied from 0 to 46 percent. Hybrids of W38 and B 36162A13-12, resistant crossed with Wabash, CI 12017 and other susceptible types had been tested in the field and greenhouse. Infestation varied from 20 to 100 percent (Caldwell et al 1946).

The reaction of F_1 plants to hessian fly gave an intermediate reaction compared with both parents. X6294 was found to be completely susceptible and no selfing was involved, because it segregated in greenbug test. Yet the parent Comanche-Ottawa in this cross behaved as F_1 plants and it was believed that this parent was heterozygous in this respect.

Some of F_1 plants and the susceptible parents were described as resistant, as they were found to be free of larvae, but they may have escaped infestation. There was no significant difference between the average number of tillers probably because infestation tests were made on plants that were 8 weeks old.

Data from the F_2 crosses involving Ottawa gave a good fit to a 3:1 ratio of resistant to susceptible plants. This agreed with information given by Allan et al (1959), and it is assumed Ottawa has the gene pair H_3H_3 for resistance to hessian fly.

The F_2 data from the crosses involving Ponca showed great variability. Allan et al (1959) were unable to determine the factors carried by Ponca for resistance to hessian fly but suggested there may be three factors. Ponca in one test ranged from 12-38 percent infestation. The analysis of the F_2 data of crosses involving Ponca indicated that some families segregated in the ratio 1 resistant to 3 susceptible, other 27 resistant to 37 susceptible, and in one case 1 resistant to 15 susceptible.

Ponca apparently is a mixture of different genotypes derived from its parents Kawvale-Marquillo x Kawvale-Tenmarq.

F_2 data of the crosses involving Comanche-Ottawa, CI 13548 indicated the resistant parent was not homozygous for resistance to hessian fly. It appears that Comanche-Ottawa carries the H_3H_3 gene pair for resistance to hessian fly in most plants but some plants had the genotype H_3h_3.

Genetic Studies On Greenbugs

A single recessive gene pair, gb gb, appears to govern the resistance to greenbugs. Dickinson was the original resistant parent and had been crossed with Bison, Pawnee, and Concho. Selections from these three crosses were crossed to the hessian fly resistant varieties.

The reaction of the F_1 hybrids to greenbugs showed that these plants had some resistance to greenbugs. That there was a lack of dominance for susceptibility, is further supported by Daniels and Porter (1958). They found that F_1 plants were intermediate between the parents, and suggested that modifying genes may be involved in addition to the gene gb gb.

F_2 data confirm the single gene hypothesis and that the heterozygous plants have an intermediate reaction. This, however, does not prove that only one factor was responsible as Porter et al (1963), using heretability analysis, found the inheritance more complex than monogenic, and suggested that environmental factors precluded a conclusion of the mode of inheritance.

These conflicting results may be due to difference in testing methods. It is possible that different biotypes of the greenbug, and genotypes of the varieties may also contribute to these differences.

Breeding For Hessian Fly And Greenbug Resistance

In breeding for resistance to these two insects, it seems desirable to screen the F_2 population for both insects and grow the resistant plants to maturity. Tests of F_2 plants would eliminate 13/16 of the population. Because of escapes the progeny would be tested in F_3. Another procedure would be to test only F_3 lines. This would require only one test for each insect as the homozygous resistant lines could be easily identified. This procedure would require more space and plants for testing, but would eliminate the factor of escapes. An advantage, is that selection could be practiced in segregating F_3 lines if desired.

Breeding for insect resistance may become more difficult as biotypes of these two insects are known to occur.

It appears that resistance to both greenbugs and hessian fly can be combined into one variety and that there are no associations with resistance that would prevent this being done in an adapted wheat variety.

SUMMARY

The inheritance of hessian fly and greenbugs was studied in the F_1 and F_2 generations, at Manhattan, Kansas during 1962, and 1963. This study was an attempt to combine the resistance for both insects in adapted improved varieties for Kansas. Two different sources for fly resistance were used. The H_3H_3 gene in Ottawa and Comanche-Ottawa, and the resistance from Ponca that may be due to three factors. The source for greenbug resistance was from Dickinson in crosses with Bison, Pawnee, and Concho.

From this study, it appears that Ottawa was a pure line in respect to hessian fly resistance and possessed the H_3H_3 factor. Ponca gave conflicting results and gave an infestation ranging from 12-38 percent. The data in this study should be adjusted on the basis of F_3 lines and the backcrosses so as to find a solution for Ponca's factors.

A single recessive gene pair, gb gb, appeared to govern resistance to greenbugs and heterozygous plants have an intermediate reaction. Responses from reciprocal crosses were the same.

It appeared that resistance to both greenbugs and hessian fly was different, simply inherited, and could be combined into one adapted wheat variety.

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RELATIONSHIP OF RESISTANCE TO GREENBUGS AND HESSIAN FLY IN SEGREGATING POPULATIONS OF HARD RED WINTER WHEAT

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Greenbugs, /*Shizaphis graminum*, (Rondani)7 and hessian fly, /*Phytophaga destructor*, (Say)7 are two damaging insects of wheat in the United States. Losses in wheat production in a single season in the United States was estimated at $84,400,000 due to hessian fly, and $50,000,000 due to greenbugs.

The relationship of resistance to greenbugs and hessian fly, in early segregating populations of hard red winter wheat, was studied at Manhattan, Kansas during 1962, and 1963.

This study was an attempt to combine the resistance to both insects in one variety for Kansas. Two different sources for fly resistance were utilized. The H_3H_3 factor, found in Ottawa and Comanche-Ottawa, and the probability of three factors found in Ponca. One source for greenbug resistance found in Dickinson spring wheat in crosses with Bison, Concho, and Pawnee was designated as gb gb. These lines were crossed with each other and the study was carried through the second generation.

Results in F_1 showed an intermediate reaction compared with both parents in hessian fly tests. No significant difference between the average number of tillers among the F_1 plants and the parents apparently because the plants were 8 weeks old when infested by fly. The F_1 plants had nearly as many larvae per plant as the susceptible parents. The F_1 plants averaged 3.56 larvae per plant; the susceptible parents 4.16; and the resistant parents 0.6.

In greenbug tests, F_1 plants also showed an intermediate reaction. The number of progeny of one aphid placed on the third leaf was 11.0, 11.6, 13.3 on the F_1, resistant parent and susceptible parent respectively. For 5 aphids, in the same order, it was 54, 49, and 62. The rate of increase of nymphs per day on F_1 plants was 1.45, on the resistant parents 1.16 and on the susceptible parents 1.77. Although the effect on the reproduction of the aphids was different on the parents and F_1 plants, the amount of damage to the host was the best indication to differentiate the resistance to greenbugs. The average damage per leaf within each cage was found to be 1.788 cm^2, .973 cm^2, and 2.63 cm^2 in the same order.

Results for F_2 plants in hessian fly tests showed that all crosses involving Ottawa segregated in the ratio 3 resistant to 1 susceptible and that Ottawa was a pure line and its factor for fly resistance was accepted as H_3H_3. Crosses involving Comanche-Ottawa also segreated in the same ratio as expected, as CI 13548 derived its resistance from Ottawa. In some crosses involving Comanche-Ottawa it was found that some plants of this parent were heterozygous for resistance to hessian fly. Crosses involving Ponca gave conflicting results and showed an infestation ranging from 12 to 38 percent. Ponca apparently is a mixture of a different genotypes.

In greenbug studies heterogeneity X^2 gave a good fit to the ratio 1 resistant to 3 susceptible confirming the hypothesis of one single recessive gene independent of the factors for hessian fly resistance.

From this study it was concluded that the genetic factors for hessian fly and greenbugs are different, and simply inherited.