A GENETIC STUDY OF GREENBUG RESISTANCE IN BARLEY

By

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A GENETIC STUDY OF GREENBUG

RESISTANCE IN BARLEY

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CHAPTER I

INTRODUCTION

The greenbug, Schizaphis graminum (Rondani), is a traditional pest of small grains and sorghum in the United States. This small, green aphid has caused periodic crop failures.

Methods developed for controlling this aphid are not always practical. High cost coupled with ineffectiveness in cold weather when greenbugs are feeding and reproducing limits the use of insecticides in much of the small grain growing areas of the southwest (6). Control by parasites or predators, or by cultural means, has not been effective in reducing greenbug damage. Consequently, new more effective methods of control were sought. The development of greenbug resistant varieties offers the best approach to this problem.

Tolerance as a major resistance mechanism provides several advantages: 1) it does not exert excessive selection pressure favoring the evolvement of a new biotype possessing immunity to prior resistance; 2) it tends to be less disturbing to the ecosystem since pest populations are maintained at levels sufficient to support moderate populations of beneficial species; and 3) tolerance may be integrated with other natural control measures.

In many cases, the greenbug population peaks at a level at or slightly higher than the level of economic injury of the susceptible varieties presently being grown. If tolerant hybrids were grown, the economic injury level would be raised, thereby increasing the probability that

natural decline of the greenbug population would occur before the level of economic injury was attained.

Several sources of barley resistant to greenbugs have been tested and utilized in producing greenbug resistant varieties.

The purpose of this study was to determine the nature of inheritance of greenbug resistance in barley and to determine if any observable agronomic characters are associated with resistance or susceptibility.

CHAPTER II

REVIEW OF LITERATURE

The greenbug, Schizaphis graminum (Rondani), is a major pest of small grains and sorghum in the United States. The first reported infestation of this insect in this country was in Virginia in 1882 (25). Some damage is incurred annually and at least 19 extensive outbreaks have occurred producing losses of millions of bushels of grain amounting to millions of dollars (5, 6, 17, 24). Near total crop failures have resulted from severe greenbug infestation.

Biotypes of the Greenbug

This pest, being an aphid, has a high parthenogenetic reproductive rate with many generations being produced in a single year under favorable conditions (6). This method of reproduction is conducive to the development of biotypes. In 1961 Wood (26) discovered a new greenbug biotype in the greenhouse. This biotype was able to overcome the resistance in Dickinson Sel. 28A and C.I. 9058 wheats. Since it was only found in cultures maintained in the greenhouse, he called it the "greenhouse strain" while the greenbug prevailing in the field was termed the "field strain." The greenhouse strain was later specified biotype B and the field strain biotype A (27, 28). A new biotype of greenbug appeared in the 1968 outbreak on grain sorghum. This biotype C, acknowledged by Harvey and Hackerott (12), was found to prefer sorghum and sudangrass while barley,

wheat, and rye were preferred by biotype B. Comparisons of the three biotypes were made by Wood et al. (28) in 1969. Biotypes A and B were found to have similar ecological and morphological characteristics while biotype C differed from the other two in these traits. It was observed that biotypes A and C feed in the phloem sieve-tube of the leaf vascular bundles of the plant and that biotype B prefers to feed in the mesophyll parenchyma of the leaf. This verifies the original findings of Chatters and Schlehuber (3) that the primary feeding site of the original greenbug, biotype A, is the phloem. The feeding habits of biotypes A and B were confirmed by Saxena and Chada (18). Plant tissue damaged by biotype A was found mainly in the phloem where phloem cells appeared completely collapsed. No distinction could be made between sieve tube elements and the phloem parenchyma. Biotype B produced damage in the mesophyll leaf cells. Saxena and Chada initiated studies of the greenbug's salivary gland complex (19), digestive system (20), plus the central and stomatogastric nervous systems (21) with respect to plant resistance and susceptibility. Results were inconclusive and indicated a need for additional studies.

In 1972, Wood and Starks (30) studied the effect of temperature and host plant interaction of the three greenbug biotypes: A, B, and C. Their data indicated that the greenbug survived temperatures ranging from -6.7 to 40.6° C. Optimum reproduction temperature was 21 to 24° C. Plant resistance decreased fecundity at nearly all temperatures. At extreme temperatures biotype C was better adapted than A or B and produced larger numbers of progeny at all temperatures. This may explain why biotype C is presently the most damaging greenbug biotype in the Midwest and the only biotype considered to be important on sorghum. They noted that the results of their laboratory tests may not be comparable to field conditions

where climatic factors interact.

Starks and Burton (23) in 1977 divided greenbugs into four biotypes: A, B, C, and D, on field crops. Biotypes A and B were alike in appearance and preferred the same host species in the field; wheat, barley, oats, and rye. Biotypes C and D had the same appearance but differed in appearance from A and B. Biotypes C and D differed from A and B in that they attacked and readily reproduced on sorghum where biotypes A and B did not. Biotype D apparently produces the same reaction on plants as biotype C but a more thorough study is needed. Biotype D had as much as a thirtyfold resistance to some organophosphorous insecticides compared with biotype C. "Will" barley was found to have resistance to all known biotypes.

Greenbug Resistance in Small Grains

After screening the domestic and U.S. Department of Agriculture world collections of small grains, more than 18,860 varieties and lines for greenbug resistance, Chada et al. (2) in 1951 found Dickinson Sel. 28A and C.I. 9058 wheats to be the only two resistant to greenbugs. Omugi, Kearney, and Dobaku barley survived and yielded grain while the remainder of the 1,230 barley varieties tested did not survive. Oat varieties Andrew, New Nortex, Russian No. 77 (C.I. 2898) and P.I. 183990 appeared to be resistant.

Painter and Peters (15) screened better than 2,000 wheat introductions using "Pawnee" as a susceptible check for greenbug resistance. They reported that only 4% of the strains carried some resistance and most strains were more susceptible than Pawnee. The F_1 and F_2 populations of Dickinson Sel. crossed with three susceptible wheats (Pawnee/Dickinson Sel., Chiefkan-Oro-Tenmarq/Dickinson Sel., and Concho/Dickinson Sel.) were also screened.

Out of the 872 F_2 plants screened, 207 plants survived the infestation. This was very close to a 3:1 ratio. From these results they suggested that a single major genetic factor was responsible for this type of greenbug reaction in wheat. Daniels and Porter (7) also submitted F_2 data which suggested that a single recessive gene controlled resistance in selection Dickinson 28A. They reported that modifiers or minor genes may also be involved since the F_1 plants were slightly more tolerant than the susceptible parents. Curtis et al. (4) in 1960 crossed DS28A and C.I. 9058 resistant wheats with each of the susceptible varieties Ponca, Concho and Crocket. A single recessive gene pair, gb gb, was found to condition resistance. They also concluded that resistance could be quickly transferred from DS28A and C.I. 9058 to other strains of wheat.

In 1964 Gardenhire (8) reported the results of a study he made on the mode of inheritance of greenbug resistance in oats. He crossed "Russian 77" (Avena sativa L.), the resistant parent, with "New Nortex" (Avena byzantina C. Koch), and Texas Sel. 2. Data from the segregating populations in the F_2 and F_3 generations indicated that the inheritance of greenbug resistance in the oat variety Russian 77 was conditioned by a single dominant gene pair.

Arriaga and Ree (1) in 1963 reported that a single dominant gene controlled greenbug resistance in an Argentine rye, Insave F.A., which is the only greenbug resistant rye known at the present time. Wood et al. (29) found "Gaucho" (C.I. 15323) triticale, developed from a cross between susceptible "Chinese Spring" wheat and the Insave F.A. rye, to be resistant to the biotype C greenbug. Insave F.A. rye was found to possess all three of the mechanisms of resistance discribed by Painter (14); tolerance, antibiosis, and nonpreference. Gaucho triticale exhibited the tolerance

and antibiosis mechanisms of resistance.

Peiretti (16) studied greenbug resistance in sorghum with respect to the bloomless character since greenbugs were observed to have a high degree of nonpreference for bloomless sorghums. Using a bloomless line, RWD3-Weskan, a normal resistant line, Shallu Grain, the F_1, F_2, and susceptible check, RS 610, he found that the bloomless character was controlled by a single recessive pair of genes with the character for bloom being dominant to bloomless. The bloomless trait from RWD3-Weskan (nonpreference) was independently inherited from the alleles which regulate the expression of tolerance to damage from Shallu Grain. Tolerance to damage was governed by a single pair of alleles with partial or no dominance.

Greenbug Resistance in Barley

Chatters and Schlehuber (3) studied the mechanics of greenbug feeding and injury to plant cells of barley, oats, and wheat. They found some evidence that greenbug resistance in barley was correlated with the leaf thickness and the length of the extended stylet. Their conclusions were that the evidence obtained was insufficient to substantiate such an hypothesis and that greenbug resistance is probably physiological rather than morphological.

Dahms et al. (5) used greenhouse testing techniques to demonstrate that Omugi, Kearney, and several other barleys were resistant. They concluded from data on the F_1 and F_2 populations of crosses involving greenbug resistant parents that resistance in barley was governed by two or more pairs of genes. Gardenhire and Chada (10) studied the inheritance of resistance in Omugi by crossing it with six greenbug susceptible varieties

carrying tester genes for all the barley chromosomes except chromosomes 3 and 6. F_1, F_2, and F_3 data showed that resistance in Omugi was governed by a single dominant gene. Evidence from data on the F_2 and F_3 hybrids involving Omugi, Kearney, and Derbent indicated that the same gene or closely linked genes controlled resistance. No associations were found between the gene for greenbug resistance and the genes conditioning kernel row number, stem rust resistance, covered seed, black pericarp, hooded, and rough awns. Smith et al. (22) reported that inheritance studies on greenbug resistance in the four winter barley varieties, Omugi, Dobaku, Kearney, and C.I. 5087 showed that these varieties contain a common dominant gene for resistance. F_1 and F_2 hybrids from all combinations of crosses, including reciprocals, of the resistant varieties were tested with parents and checks for greenbug reaction. Hybrids and parents showed no measurable differences in their degree of resistance. They also concluded that a single dominant gene controls resistance in Omugi and Dobaku.

Gardenhire (9) crossed four greenbug susceptible strains of barley, R244-1, R431, "Cebada Capa," and "Rogers" to the resistant strains Omugi or a selection from Cordova/Omugi to determine the mode of inheritance of greenbug resistance in Omugi barley. He also studied the possible linkages between the locus conditioning greenbug resistance and the loci conditioning green seedling, powdery mildew resistance, leaf rust resistance, and orange lemma. He found that resistance in the Omugi variety and the Cordova/Omugi selection was governed by a single dominant gene. No associations were found between the greenbug resistance and the other characters studied.

Gardenhire et al. (11) using primary trisomics and tertiary trisomic homozygous translocations studied the linkage group of the gene for green-

bug resistance in the barley cultivar "Will." They determined that the gene for greenbug resistance in the Will cultivar was on linkage group 1 located on the centromere segment of chromosome 1 in the T1-6a translocation.

Juneja et al. (13) used isogenic lines of barley to determine the chemical basis for greenbug resistance. The isogenic lines were developed from a cross of "Omugi," greenbug resistant, and "Rogers," greenbug susceptible. Extracts of both barley types were made. A gas chromatographic analysis was made of each extract and compared with that of chemically pure benzyl alcohol. The same analytical procedure was used with the parent strains. Benzyl alcohol was found to be present in the resistant strains of barley but was absent from the susceptible strains. Isogenic susceptible plants were treated with 100 ppm of benzyl alcohol and artificially infested with biotype C greenbugs. After four days the reproduction rate on the treated isogenic susceptible plants was reduced to the level of reproduction observed on the naturally resistant isogenic plants. Results indicated that greenbug resistant barley plants contain larger amounts of benzyl alcohol than greenbug susceptible ones. A single chemical resistance factor is consistent with prior genetic studies that have shown that a single dominant gene controls resistance in Omugi barley.

The present knowledge of the mechanisms of inheritance of greenbug resistance in host plants is lacking in many areas as the literature reviewed indicates. Future studies will, hopefully, give us further insight into such areas as the mode of resistance inheritance, the chemical basis of resistance, physiological and morphological characters associated with resistance, and the genetic constitution of resistance. Additional research is the key to solving these mysteries.

CHAPTER III

MATERIALS AND METHODS

F_2 Greenhouse Study

Omugi was crossed with Rogers. Resistant selections were backcrossed to Rogers. Plants were selfed for five generations. The gene for greenbug reaction was maintained in the heterozygous condition while all other genes were becoming homozygous. After five generations of selfing, resistant and susceptible isogenic lines were selected from this population. Eighteen pairs of these 2* Rogers/Omugi isogenic lines for greenbug resistance were crossed to produce twenty-one F_2 populations for this study. One parent of each cross was the resistant and the other parent was the susceptible member of a pair of isogenic lines. Two F_2 populations derived from the cross of Omugi/Rogers and one F_2 population resulting from one reciprocal cross were also used.

Omugi (C.I. 5144), one of the most greenbug-resistant varieties known, is a 6-rowed variety which was introduced from Korea. It is a winter barley variety with moderately weak straw. Rogers (C.I. 9174), a winter barley variety susceptible to greenbugs, was developed in the small grain breeding program at the Oklahoma Agricultural Experiment Station in Stillwater, Oklahoma and released in 1956. It is a 6-rowed strain that is high yielding, stiff strawed, and mildew resistant.

Greenbug reaction tests were conducted in the greenhouse insectary. Galvanized iron flats having inside measurements of approximately 13 x 20 x

3 1/2 inches were filled with a soil mixture of 3 parts Norge Loam, 1 part peat moss, and 1 part washed river sand. Each flat was marked off into 10 rows, 13 inches long, 2 inches apart and 1/2 inch deep with a corrugated row marker. Seed was treated with "Arasan 50 Red" prior to planting. Rows were seeded with a variable number of seed of each F_2 population. Depending upon the amount of seed available, a minimum of 2 rows and a maximum of 16 rows were sown with seed of each F_2 population. One row per flat was divided in half and seeded with 10 seed from the resistant isogenic check, OK654833-7R, and 10 seed from the susceptible isogenic check, OK654833-2S. These two checks represented one pair of isogenic lines. Twenty seeds from each parent were planted adjacent to the F_2 populations as an additional check. The flats were then filled to the top with sand and watered. Automatic room temperature controls were set for 70° F and temperatures were maintained between 65 and 80° F. Biotype C greenbugs which had been increased on Rogers barley were applied as uniformly as possible on the plants soon after emergence. During the succeeding few days as the seedlings continued to develop, additional aphids were added to the flats. Clippings were made on three occasions to trim 6 inch seedlings back to 4 inches. No ill effects were observed from these clippings.

This greenbug screening test was seeded on December 1, 1978. Emergence began on December 5, 1978 and was complete on December 7, 1978 with approximately 92% germination. Susceptible checks began to show signs of chlorosis and stunting on December 13, 1978. Final readings of resistant and susceptible plants per population were made on December 18, 1978.

F_3 Greenhouse Study

Ten pairs of 2* Rogers/Omugi isogenic lines, consisting of one

resistant and one susceptible line, were crossed to produce twelve F_3 populations used for this study. Two F_3 populations derived from crosses of Omugi/Rogers plus two F_3 populations resulting from reciprocal crosses were also used.

Greenbug reaction tests were conducted in the greenhouse insectary. Test conditions were the same as those used in the F_2 greenhouse study. Rows were divided in half and seeded with 10 seed per half-row. These 10 seeds came from one F_2 plant. The remaining seeds from each F_2 plant were used to plant one row in the F_3 field study. Several half-rows were sown with seed from each F_3 population with a minimum of 56 and a maximum of 133 half-rows being planted with seed from a particular F_3 population. One row per flat was equally divided with 10 seed of OK654833-7R, the resistant isogenic check, planted in one half of the row and 10 seed of OK654833-2S, the susceptible isogenic check, planted in the other half. Ten seeds of each parent were planted per half-row adjacent to each F_3 population as an additional check. The flats were then filled to the top with sand and watered. Greenhouse temperatures and other test conditions were similar to those used in the F_2 study. This greenbug screening test was seeded on November 10, 1978. Emergence began on November 14, 1978, and was complete on November 17, 1978, with approximately 90% germination. Susceptible checks began to show signs of chlorosis and stunting on November 23, 1978. Twenty plants were chosen at random from various flats and the number of greenbugs per plant were counted and averaged. The average number of greenbugs per plant was 43.6 per 4 inch seedling. According to Dr. Richard L. Wilson, USDA Entomologist who provided the greenbug cultures and supervised the infesting of the tests, the Greenbug Economic Injury Level is equal to 300 or more greenbugs per row foot.

This is approximately 20 greenbugs per plant under field conditions. The average number of greenbugs per seedling was therefore ample. Final readings were made on November 27, 1978. The expressions of resistant, susceptible, and segregating characteristics were read on a per row basis. Homozygous resistant F_2 plants should have produced F_3 rows containing all resistant plants; homozygous susceptible F_2 plants should have produced F_3 rows containing all susceptible plants; heterozygous F_2 plants should have produced F_3 rows containing both resistant and susceptible plants. Therefore, the F_3 row segregation should have been 1 with all plants resistant : 2 segregating : 1 with all plants susceptible if greenbug resistance in these populations was controlled by a single dominant gene.

F_3 Field Study

The F_3 seed not allocated to the F_3 greenbug screening test was field planted on October 18, 1978, in an unreplicated test at the Agronomy Research Station, Stillwater, Oklahoma. One hundred pounds per acre of 18-46-0 fertilizer had been applied prior to planting. Forty pounds of ammonium nitrate was top-dressed at planting time. More than one row was sown with variable amounts of seed from each F_3 population. A minimum of 56 and a maximum of 133 rows were planted with seed from a particular F_3 population. Seed for each row was produced from one F_2 plant and corresponded to a particular half-row in the F_3 greenhouse study. Seeds of each parent were seeded adjacent to each F_3 population. Rows were 4 1/2 feet long and spaced 1 foot apart. A total of 1,654 rows were planted in 15 ranges. The first 14 ranges were composed of 116 rows per range with the fifteenth partial range consisting of 30 rows. The purpose of this field study was to determine if any observable agronomic and/or morphological

character of the F_3 lines might be associated with greenbug resistance or susceptibility.

Samples of 10 resistant and 10 susceptible plants were collected at random from respective resistant and susceptible rows on May 15, May 24, and May 31, 1979. Resistant and susceptible rows were determined from the prior results of the F_3 greenbug reaction test. Observations and comparisons were made between the collected resistant and susceptible plants on the following plant characters:

Awns - length, rough or smooth

Glume awns - length

Hairiness - long or short hairs on rachis edges, long or short rachilla hairs, ligule hair length

Kernels - color, hull wrinkling, aleurone color, covered or naked

Leaves - length, width, shade of green, bloom, rough or smooth, margin differences, color of midrib, auricle length, collar shape, ligule shape

Lemma - teeth number

Spike - length, basal node length and width.

The nursery was harvested on June 15, 1979. Ten resistant, ten susceptible, and ten progenies classified as segregating in the F_3 greenbug reaction test were harvested from each F_3 population. Progenies were chosen at random. Plants from each progeny were harvested in bulk and threshed. In addition, all parental rows were harvested and threshed separately.

F_4 Greenhouse Study

Seeds from the harvested F_3 field grown populations which were segregating for greenbug resistance were used in this study. Segregating lines were identified by the results of the F_3 greenbug screening test.

Conditions for this greenbug test were identical to those mentioned previously. Ten rows in each flat were seeded with 25 seed per row from one segregating F_4 population. Ten seed of each parent were planted per half row adjacent to each F_4 population. Parental seed in each flat served as the resistant and susceptible checks. The flats were then filled to the top with sand and watered. Biotype C greenbugs were applied as uniformly as possible on the plants soon after emergence. During the succeeding few days as the seedlings continued to develop, additional aphids were added to the flats.

This greenbug screening test was seeded on January 18, 1980. Emergence began on January 22, 1980, and was complete on January 25, 1980, with approximately 90% germination. Susceptible checks began to show signs of chlorosis and stunting on January 29, 1980. Final readings were made on February 1, 1980. The number of resistant and susceptible plants were counted per row. Since these progenies were not selected in the F_3 generation, they should have segregated 5 resistant : 3 susceptible if one dominant gene conditions resistance. Numerous rows in each flat had signs of damping off. Severe damping off of seedlings was evident in 58% of the flats tested.

Statistical Analysis

The Chi-square (X^2) goodness of fit test was used to evaluate the fit of the observed segregation ratios to expected ratios for each of the three generations tested. The Chi-square (X^2) test for heterogeneity was also used as a statistical tool to test data from the various populations for homogeneity. The 0.05 level was used as the significance level.

CHAPTER IV

RESULTS AND DISCUSSION

General Observations

The difference in tolerance between resistant and susceptible parents and checks was easily observed. The F_2, F_3, and F_4 resistant plants from all resistant X susceptible crosses were as tolerant as the resistant parents. All susceptible plants in the three generations tested were as susceptible as the susceptible parents. There was practically no stunting nor chlorosis in the resistant isogenic check, OK654833-7R; but there was severe stunting and complete chlorosis of the susceptible isogenic check, OK654833-2S.

Clipping the plants back to a maximum height of 4 inches at 6 to 12 days of age apparently did not affect their greenbug resistance. Resistant parents and hybrids recuperated rapidly as compared to the susceptible parents and checks.

F_2 Generation

A total of 7,766 F_2 plants from 24 resistant X susceptible crosses were tested for their reaction to greenbugs. The F_2 populations were classified into two categories on the basis of plant resistance or plant susceptibility. A chi-square test for goodness of fit to a 3:1 one-gene segregation ratio was calculated for each of the twenty-four F_2 populations tested. A good fit was obtained in each instance as shown in Table I.

TABLE I

CHI-SQUARE TESTS FOR GOODNESS OF FIT TO A 3:1 RATIO AND HETEROGENEITY FOR F_2 BARLEY POPULATIONS RESULTING FROM CROSSING ISOGENIC LINES FOR GREENBUG REACTION

Cross Number	Number of Plants		χ^2	df	P
	Res.	Susc.			
St654832-2S/St654832-3R	303	106	0.183375	1	0.75-0.50
St654832-2S/St654832-3R	292	119	3.426601	1	0.10-0.05
St654832-3R/St654832-2S	217	82	0.937569	1	0.50-0.25
St654833-2S/St654833-7R	371	118	0.197001	1	0.75-0.50
St654833-7R/St654833-2S	176	60	0.022599	1	0.95-0.80
St654833-7R/St654833-2S	224	94	3.526205	1	0.10-0.05
St654835-3S/St654835-4R	234	82	0.151899	1	0.75-0.05
St654835-3S/St654835-4R	220	74	0.004535	1	0.95-0.80
St654835-4R/St654835-3S	418	141	0.014908	1	0.95-0.80
St654835-4R/St654835-3S	231	85	0.607595	1	0.50-0.25
St654835-4R/St654835-3S	146	51	0.082911	1	0.90-0.75
St654843-3S/St654843-9R	263	79	0.658869	1	0.50-0.25
St654843-3S/St654843-9R	209	73	0.118203	1	0.75-0.50
St654843-3S/St654843-9R	55	19	0.018019	1	0.95-0.80
St654843-9R/St654843-3S	33	14	0.574468	1	0.50-0.25
St654843-9R/St654843-3S	192	64	0.00	1	1.00
St654844-1S/St654844-8R	458	146	0.220751	1	0.75-0.50
St654844-1S/St654844-8R	118	37	0.105376	1	0.75-0.50
St654844-8R/St654844-1S	257	77	0.674651	1	0.50-0.25
St654844-8R/St654844-1S	309	98	0.184275	1	0.75-0.50
St654844-8R/St654844-1S	279	84	0.669421	1	0.50-0.25
Rogers/Omugi	294	113	1.658476	1	0.25-0.10
Omugi/Rogers	339	94	2.501155	1	0.25-0.10
Omugi/Rogers	159	59	0.495413	1	0.50-0.25
Total			17.034275	24	0.90-0.75
Pooled	5797	1969	0.519357	1	0.50-0.25
Heterogeneity			16.514918	23	0.90-0.75

A heterogeneity test was calculated for the twenty-four populations and a P value of 0.75-0.90 was obtained. The high P value indicated that the data were homogeneous and could be pooled. A chi-square test for goodness of fit on the pooled data gave a P value of 0.25-0.50 and showed a good fit to a 3:1 ratio. The 0.05 level was the significance level under which the hypothesis was rejected or not rejected. The F_2 data support the hypothesis of monogenic inheritance of greenbug resistance with resistance being dominant.

F_3 Families

A total of 1,630 rows of F_3 material from sixteen resistant X susceptible crosses were tested for their reaction to greenbugs. Individual rows were read as resistant, segregating or susceptible. Data could not be ascertained for four of the sixteen F_3 populations tested due to excessive damping off. Therefore, two populations from each of the two F_3 families, St654843-3S/St654843-9R and St654844-1S/St654844-8R, were eliminated. Since observed plant data from the F_2 generation fit a 3:1 ratio, F_3 progeny data was expected to fit a 1:2:1 ratio.

St654843-3S/St654843-9R

A chi-square test for goodness of fit to a 1:2:1 one-gene segregation ratio was calculated for each of the four populations in the F_3 family St654843-3S/St654843-9R as shown in Table II. Observed data from one population fit the expected 1 resistant : 2 segregating : 1 susceptible ratio with a probability value of 0.25-0.50 indicating a good fit. The remaining three populations did not fit the expected 1:2:1 ratio as shown by

TABLE II

CHI-SQUARE TESTS FOR GOODNESS OF FIT TO A 1:2:1 RATIO AND HETEROGENEITY FOR THE F_3 FAMILY St654843-3S/St654843-9R

Cross Number	Number of Progenies Res.	Seg.	Susc.	χ^2	df	P
St654843-3S/St654843-9R	17	30	10	1.877193	2	0.500-0.250
St654843-3S/St654843-9R	30	74	18	7.901640	2	0.025-0.010[1]
St654843-9R/St654843-3S	35	61	15	8.297297	2	0.025-0.010[1]
St654843-9R/St654843-3S	26	50	11	7.114942	2	0.050-0.025[1]
Total				25.191072	8	P<0.005[1]
Pooled	108	215	54	22.920424	2	P<0.005[1]
Heterogeneity				2.270648	6	0.900-0.750[2]

[1]Hypothesis that the observed data fit a 1:2:1 ratio is rejected.

[2]Hypothesis that the observed data is homogeneous is not rejected.

probability values of 0.01 to 0.05. The 0.05 level was used as the level of significance. The chi-square test for heterogeneity gave a P value of 0.75-0.90 for the four populations. This high P value indicated that the data were homogeneous and could be pooled. A chi-square test for goodness of fit calculated on the pooled data gave a $P<0.005$. This low P value reveals that data from this F_3 family do not fit a 1:2:1 ratio.

In instances where data from this family did not fit a 1 resistant: 2 segregating : 1 susceptible ratio, insufficient numbers of susceptible individuals were observed. A chi-square test for goodness of fit to a 1 resistant : 2 segregating ratio was calculated for each of the four populations in this family as shown in Table III. A good fit was obtained in each instance. A heterogeneity test was calculated and a high P value was obtained. The high probability level indicated that the data were homogeneous and could be pooled. A chi-square test for goodness of fit was calculated for the pooled data, and a P value of 0.950-0.975 was obtained. This indicated a very good fit to a 1:2 ratio which supports a one-gene hypothesis with resistance being dominant. We thought that the F_2 plants which produced these F_3 progenies were selected completely at random; however, there must have been a deficiency of susceptible F_2 plants among our selections. This resulted in the deficiency in susceptible F_3 progenies. The reasons for these deficiencies are not known.

St654844-1S/St654844-8R

A chi-square test for goodness of fit to a 1:2:1 one-gene segregation ratio was calculated for each of the four populations in the F_3 family St654844-1S/St654844-8R as shown in Table IV. Observed data from one population did not fit the expected 1 resistant : 2 segregating : 1 sus-

TABLE III

CHI-SQUARE TESTS FOR GOODNESS OF FIT TO A 1:2 RATIO (RESISTANT ROWS : SEGREGATING ROWS) AND HETEROGENEITY FOR THE F_3 FAMILY St654843-3S/St654843-9R

Cross Number	Number of Progenies		χ^2	df	P
	Res.	Seg.			
St654843-3S/St654843-9R	17	30	0.1616369	1	0.75-0.50[1]
St654843-3S/St654843-9R	30	74	0.9553584	1	0.50-0.25[1]
St654843-9R/St654843-3S	35	61	0.4218750	1	0.75-0.50[1]
St654843-9R/St654843-3S	26	50	0.0496647	1	0.90-0.75[1]
Total			1.5885351	4	0.900-0.750[1]
Pooled	108	215	0.0012537	1	0.975-0.950[1]
Heterogeneity			1.5872814	3	0.750-0.500[2]

[1]Hypothesis that the observed data fit a 1:2 ratio is not rejected.

[2]Hypothesis that the observed data is homogeneous is not rejected.

TABLE IV

CHI-SQUARE TESTS FOR GOODNESS OF FIT TO A 1:2:1 RATIO AND HETEROGENEITY FOR THE F_3 FAMILY St654844-1S/St654844-8R

Cross Number	Number of Progenies			χ^2	df	P
	Res.	Seg.	Susc.			
St654844-1S/St654844-8R	22	39	10	4.746479	2	0.100-0.050
St654844-1S/St654844-8R	20	60	19	4.474748	2	0.250-0.100
St654844-8R/St654844-1S	38	73	22	5.120300	2	0.100-0.050
St654844-8R/St654844-1S	26	73	16	10.095652	2	0.010-0.005[1]
Total				24.437179	8	P<0.005[1]
Pooled	106	245	67	19.679426	2	P<0.005[1]
Heterogeneity				4.757753	6	0.750-0.500[2]

[1]Hypothesis that the observed data fit a 1:2:1 ratio is rejected.

[2]Hypothesis that the observed data is homogeneous is not rejected.

ceptible ratio as indicated by the low probability level of 0.005-0.010. The remaining three populations did fit the 1:2:1 ratio as shown by probability levels of 0.05 to 0.25. The chi-square test for heterogeneity gave a P value of 0.50-0.75 for the four populations. This P value indicated that the data were homogeneous and could be pooled. A chi-square test for goodness of fit calculated on the pooled data gave a $P<0.005$. This low P value indicates that data from this family do not fit a 1:2:1 ratio.

In instances where data from this family did not fit a 1 resistant : 2 segregating : 1 susceptible ratio, insufficient numbers of susceptible individuals were observed. A chi-square test for goodness of fit to a 1 resistant : 2 segregating ratio was calculated for each of the four populations in this family as shown in Table V. A good fit was obtained in each instance. A heterogeneity test was calculated and a good P value was obtained indicating that the data were homogeneous and could be pooled. A chi-square test for goodness of fit was calculated for the pooled data, and a P value of 0.10-0.25 was obtained. This indicated a good fit to a 1:2 ratio supporting the hypothesis that a single gene conditions resistance. Again, we do not know what caused the deficiency in susceptible F_2 plants which resulted in the deficiency in F_3 progenies.

Rogers/Omugi

A chi-square test for goodness of fit to a 1:2:1 one-gene segregation ratio was calculated for each of the four populations in the F_3 family Rogers/Omugi as shown in Table VI. Observed data from one population did not fit the expected 1 resistant : 2 segregating : 1 susceptible ratio as indicated by the low probability level of 0.010-0.025. The remaining

TABLE V

CHI-SQUARE TESTS FOR GOODNESS OF FIT TO A 1:2 RATIO (RESISTANT ROWS : SEGREGATING ROWS) AND HETEROGENEITY FOR THE F_3 FAMILY St654844-1S/St654844-8R

Cross Number	Number of Progenies		χ^2	df	P
	Res.	Seg.			
St654844-1S/St654844-8R	22	39	0.2133719	1	0.75-0.50[1]
St654844-1S/St654844-8R	20	60	2.5234873	1	0.25-0.10[1]
St654844-8R/St654844-1S	38	73	0.0405405	1	0.90-0.75[1]
St654844-8R/St654844-1S	26	73	2.2272727	1	0.25-0.10[1]
Total			5.0046724	4	0.50-0.25[1]
Pooled	106	245	1.5512821	1	0.25-0.10[1]
Heterogeneity			3.4533903	3	0.50-0.25[2]

[1]Hypothesis that the observed data fit a 1:2 ratio is not rejected.

[2]Hypothesis that the observed data is homogeneous is not rejected.

TABLE VI

CHI-SQUARE TESTS FOR GOODNESS OF FIT TO A 1:2:1 RATIO AND HETEROGENEITY FOR THE F_3 FAMILY ROGERS/OMUGI

Cross Number	Number of Progenies			χ^2	df	P
	Res.	Seg.	Susc.			
Rogers/Omugi	22	65	16	7.776700	2	0.025-0.010[1]
Rogers/Omugi	28	59	24	0.729730	2	0.750-0.500
Omugi/Rogers	30	59	20	2.577982	2	0.500-0.250
Omugi/Rogers	24	54	19	1.762886	2	0.500-0.250
Total				12.847298	8	0.250-0.100
Pooled	104	237	79	9.9190476	2	0.010-0.005[1]
Heterogeneity				2.9282504	6	0.900-0.750[2]

[1]Hypothesis that the observed data fit a 1:2:1 ratio is rejected.

[2]Hypothesis that the observed data is homogeneous is not rejected.

three populations did fit the 1:2:1 ratio as shown by the probability levels of 0.25 to 0.75. The chi-square test for heterogeneity gave a P value of 0.75-0.90 for the four populations. This high P value indicated that the data were homogeneous and could be pooled. A chi-square test for goodness of fit calculated on the pooled data gave a P value of 0.005-0.010. This low P value indicates that pooled data from this family do not fit a 1:2:1 ratio.

In instances where data from this family did not fit a 1 resistant : 2 segregating : 1 susceptible ratio, insufficient numbers of susceptible individuals were observed. A chi-square test for goodness of fit to a 1 resistant : 2 segregating ratio was calculated for each of the four populations in this family as shown in Table VII. A good fit was obtained in each instance. A heterogeneity test was calculated and a high P value was obtained. The high probability level indicated that the data were homogeneous and could be pooled. A chi-square test for goodness of fit was calculated for the pooled data, and a P value 0.25-0.50 was obtained. This indicated a good fit to a 1:2 ratio. The data from this cross also supports the one-gene hypothesis. Again, the reason for the deficiency in susceptible F_2 plants and F_3 progenies is not known.

Combining F_3 Populations

Observed data from five of the twelve F_3 populations did not fit the expected 1:2:1 segregation ratio. A deficient number of susceptible individuals was noted in each instance. The chi-square test for goodness of fit to a 1 resistant : 2 segregating ratio was calculated for each of the twelve F_3 populations tested. A good fit was obtained in each instance as shown in Table VIII. A heterogeneity test was calculated

TABLE VII

CHI-SQUARE TESTS FOR GOODNESS OF FIT TO A 1:2 RATIO (RESISTANT ROWS : SEGREGATING ROWS) AND HETEROGENEITY FOR THE F_3 FAMILY ROGERS/OMUGI

Cross Number	Number of Progenies		χ^2	df	P
	Res.	Seg.			
Rogers/Omugi	22	65	2.5344828	1	0.25-0.10[1]
Rogers/Omugi	28	59	0.0517241	1	0.90-0.75[1]
Omugi/Rogers	30	59	0.0045480	1	0.95-0.90[1]
Omugi/Rogers	24	54	0.2307692	1	0.75-0.50[1]
Total			2.8215243	4	0.75-0.50[1]
Pooled	104	237	1.2414749	1	0.50-0.25[1]
Heterogeneity			1.5800494	3	0.75-0.50[2]

[1]Hypothesis that the observed data fit a 1:2 ratio is not rejected.

[2]Hypothesis that the observed data is homogeneous is not rejected.

TABLE VIII

CHI-SQUARE TESTS FOR GOODNESS OF FIT TO A 1:2 RATIO (RESISTANT ROWS : SEGREGATING ROWS) AND HETEROGENEITY FOR F_3 BARLEY POPULATIONS RESULTING FROM CROSSING ISOGENIC LINES FOR GREENBUG REACTION

Cross Number	Number of Progenies		χ^2	df	P
	Res.	Seg.			
St654843-3S/St654843-9R	17	30	0.1616369	1	0.75-0.50
St654843-3S/St654843-9R	30	74	0.9553584	1	0.50-0.25
St654843-9R/St654843-3S	35	61	0.4218750	1	0.75-0.50
St654843-9R/St654843-3S	26	50	0.0496647	1	0.90-0.75
St654844-1S/St654844-8R	22	39	0.2133719	1	0.75-0.50
St654844-1S/St654844-8R	20	60	2.5234873	1	0.25-0.10
St654844-8R/St654844-1S	38	73	0.0405405	1	0.90-0.75
St654844-8R/St654844-1S	26	73	2.2272727	1	0.25-0.10
Rogers/Omugi	22	65	2.5344828	1	0.25-0.10
Rogers/Omugi	28	59	0.0517241	1	0.90-0.75
Omugi/Rogers	30	59	0.0045480	1	0.95-0.90
Omugi/Rogers	24	54	0.2307692	1	0.75-0.50
Total			9.4147315	12	0.75-0.50
Pooled	318	697	1.8270900	1	0.25-0.10
Heterogeneity			7.5876415	11	0.75-0.50

for the twelve populations and a high P value was obtained. The high P value indicated that the data were homogeneous and could be pooled. A chi-square test for goodness of fit was calculated for the pooled data, and a P value of 0.10-0.25 was obtained. This indicated a good fit to a 1:2 ratio and supported the hypothesis that greenbug resistance is controlled by a single dominant gene. A deficient number of susceptible individuals is the reason the observed F_3 data do not fit the expected 1:2:1 segregation ratio.

The chi-square goodness of fit test was used with additional three class ratios to test the F_3 data for segregating characteristics. The ratios tested were: 675:225:124, 45:15:4, 12:3:1, 9:6:1, 9:4:3, 9:3:4, 7:6:3, 6:1:1, 4:3:1, 3:3:2, and 2:1:1. The F_3 data best fit a 1:2:1 segregation ratio of all the three class ratios evaluated.

Several reasons for the significantly low number of recessive individuals are possible. The F_2 parent plants for the F_3 generation were thinly planted late in the planting season. These plants were grown in the field under abnormally dry conditions in competition with a heavy weed infestation. A possible light infestation of greenbugs coupled with the severe growing conditions could have resulted in fewer than the normal number of seeds being produced on the susceptible plants. In addition, seed was not saved from those plants that produced small numbers of seed. Consequently, selection pressure may have led to fewer than the expected number of susceptible plants being harvested thereby producing a deficiency of recessive plants in the F_3 generation.

F_3 Field Study

There was no apparent correlation between readily visible morpho-

logical characteristics of the barley plant and greenbug resistance or susceptibility. No associations could be found between awn length and texture; glume awn length; rachis, rachilla, and ligule hair length; kernel color, hull wrinkling, aleurone color, and covered seed; leaf length, width, shade of green, bloom, texture, color of midrib, auricle length, collar shape, and ligule shape; number of lemma teeth; spike basal node length and width, and spike length with either greenbug resistance or susceptibility.

F_4 Generation

Due to the inconclusive results from the F_3 greenbug screening test, 2,299 F_4 seedlings from 12 segregating F_3 populations were grown and tested for their reaction to greenbugs to ascertain their segregation ratio. The anticipated segregation ratio was 5 resistant : 3 susceptible. Segregating F_3 populations were determined from the results of the F_3 greenbug screening test.

A chi-square test for goodness of fit to a 5:3 segregation ratio was calculated for each of the twelve F_4 populations tested as shown in Table IX. Observed data from six populations fit the expected 5:3 ratio as shown by probability values of 0.10 to 0.95. The remaining six populations did not fit the expected 5 resistant : 3 susceptible ratio as indicated by probability values of $P<0.005$ to 0.050. The 0.05 level was used as the critical level of significance. The chi-square test for heterogeneity gave a P value of $P<0.005$ for the twelve populations. This low P value indicated that the data were not homogeneous.

In each instance where data from this generation did not fit the expected 5:3 ratio, there were too many susceptible plants. The most

TABLE IX

CHI-SQUARE TESTS FOR GOODNESS OF FIT TO A 5:3 RATIO AND HETEROGENEITY FOR F_4 BARLEY POPULATIONS DERIVED FROM SEGREGATING F_3 ROWS

Cross Number	Number of Plants		χ^2	df	P
	Res.	Susc.			
St654843-3S/St654843-9R	112	99	7.9876777	1	P<0.005[1]
St654843-3S/St654843-9R	143	70	1.9533646	1	0.250-0.100
St654843-3S/St654843-9R	125	89	1.5264798	1	0.250-0.100
St654843-9R/St654843-3S	118	96	4.9457944	1	0.050-0.025[1]
St654844-1S/St654844-8R	115	97	6.1635220	1	0.025-0.010[1]
St654844-1S/St654844-8R	95	92	10.9180040	1	P<0.005[1]
St654844-1S/St654844-8R	108	52	1.7066667	1	0.250-0.100
St654844-8R/St654844-1S	96	72	2.0571429	1	0.250-0.100
St654844-8R/St654844-1S	105	64	0.0098619	1	0.950-0.900
St654844-8R/St654844-1S	96	82	5.5745318	1	0.025-0.010[1]
Rogers/Omugi	117	84	1.5791045	1	0.250-0.100
Omugi/Rogers	89	83	8.4899225	1	P<0.005[1]
Total			52.9120680	12	P<0.005[1]
Pooled	1319	980	25.7865420	1	P<0.005[1]
Heterogeneity			27.1255260	11	P<0.005[2]

[1]Hypothesis that the observed data fit a 5:3 ratio is rejected.

[2]Hypothesis that the observed data is homogeneous is rejected.

plausible reason for having an excessive amount of susceptible individuals during this test is that many plants classified as susceptible were actually victims of severe damping off. The results of this test were inconclusive. They did not add nor detract from our one-gene hypothesis.

CHAPTER V

SUMMARY AND CONCLUSIONS

The purpose of this genetic study on greenbug resistance in barley was to determine the number of genes involved. Parents for the F_2, F_3, and F_4 generations tested were 2* Rogers/Omugi resistant crossed with 2* Rogers/Omugi susceptible and Omugi/Rogers with reciprocal crosses. Inheritance studies were conducted in the greenhouse insectary during the period 1978-1980. Statistical analyses were accomplished using the chi-square tests for goodness of fit and heterogeneity. In addition, observable agronomic and morphological characters were examined in F_3 field grown material for evidence of association with resistance or susceptibility.

Evidence from the F_2 data indicated a monogenic inheritance of greenbug resistance with resistance being dominant.

Observed data from the F_3 families tested best fit a 1 resistant : 2 segregating one-gene segregation ratio. Due to a deficiency in susceptible individuals, the data did not always fit the expected 1:2:1 segregation ratio. However, the results from the F_3 study appear to support a monogenic inheritance for greenbug reaction.

An excess of susceptible individuals was encountered in data from six of the twelve F_4 populations tested. Severe damping off may have caused too many individuals to be classified as susceptible effecting a very poor fit to the expected ratio of 5 resistant : 3 susceptible.

The results of this test were inconclusive, but do not support any alternate hypothesis. The hypothesis of monogenic control still appears to be the most feasible.

No correlations could be found between the following observable morphological plant characters and greenbug resistance or susceptibility:

Awns - length, rough or smooth

Glume awns - length

Hairiness - long or short hairs on rachis edges, long or short rachilla hairs, ligule hair length

Kernels - color, hull wrinkling, aleurone color, covered or naked

Leaves - length, width, shade of green, bloom, rough or smooth, margin differences, color of midrib, auricle length, collar shape, ligule shape

Lemma - teeth number

Spike - length, basal node length and width.

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