INHERITANCE OF RESISTANCE IN OATS TO TWO BIOTYPES OF THE GREENBUG

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CHAPTER I

INTRODUCTION

Presently, the use of genetic resistance in crop varieties to insect infestation plays an important role in integrated pest management. Plant resistance offers the unique advantage of protecting the crop against insect economically, without causing environmental problems for any level of farming. Utilization of genetic resistance could limit the build-up of insect pests and reduce the damage done by them.

In small grains, the greenbug, Schizaphis graminum (Rondani), is one of the most destructive insects, especially in the Southwestern Great Plains of the United States. Chemical control using organophosphorus insecticides such as disulfoton, was once highly effective; but now an insecticide-resistant strain designated as biotype D makes chemical control on sorghum, Sorghum bicolor L. Moench., more difficult in some areas of the United States (Peters et al., 1975; Teetes et al., 1975). Thus, there is a need for greenbug resistant cultivars as an adjunct to present control methods. Breeding for greenbug resistance in addition to high yield and quality has been successful in barley, Hordeum vulgare L., and grain sorghum. Resistant rye, Secale cereale L., and triticale are also available commercially, though the yield and quality are low. High

yielding, good quality wheat with greenbug resistance should be available commercially in 1981. This leaves oats, Avena sativa L., as the only important host without greenbug resistance available to growers.

Resistance mechanisms to greenbug biotypes B and C have been studied in oats in the greenhouse (Wilson et al., 1978). In order to make the most efficient progress in adding resistance to otherwise adapted oat varieties in breeding program, it will be useful if knowledge of the genetic mechanism of greenbug resistance be expanded. Hence, the need for the present research.

The objectives of these studies were: (1) to determine the inheritance of greenbug resistance in biotypes B and C and the number of genes involved, (2) to investigate whether greenbug resistance of all resistant oat varieties is due to the same or different genes, and (3) to determine the feasibility of transferring the resistance to the two biotypes to adapted varieties.

CHAPTER II

REVIEW OF LITERATURE

The greenbug, Schizaphis graminum (Rondani), is a destructive pest of wheat, barley, oats, rye, sorghum and also many types of grasses in the Great Plains area of the United States. It was first described by Rondani of Italy, who observed the aphid infesting grasses in 1847 (Hunter, 1909). Webster and Phillips (1912) stated that the greenbug was first found in the United States in Virginia in 1882. The first damage to wheat in Texas occurred in 1890 in Denton and nearby counties of north-central Texas and was found in oats in North Carolina in the same year. Damage to wheat and oats also was recorded in 1901, 1903, 1904, and 1906. These infestations were followed by the serious, widespread outbreak in 1907, when the insect damaged crops in central Texas, then spread northward through Oklahoma, Kansas, Missouri, Arkansas, and into Illinois. The outbreak in 1942 extended from central Texas to northern Oklahoma, and an estimated 61 million bushels of grain were destroyed with almost total crop losses of oats, barley, and wheat (Daniels et al., 1956).

In the spring of 1950, this insect severely damaged barley, oats, and wheat in northern Texas, western Oklahoma, and in some parts of Colorado, Kansas, and Nebraska. More than 1,500,000 acres were abandoned and the yield on many acres was greatly reduced. In the previous year, there was severe damage in the Great Plains from Nebraska

to southern Canada. Other severe outbreaks happened in 1951, 1959, 1961, and 1976. In 1976, damage and control costs exceeded $80 million in Oklahoma alone (Starks and Burton, 1977b).

In regard to damage, the greenbug has piercing and sucking mouth parts. While feeding on the plant, it also injects toxic substances. The leaves of small grains attacked by greenbugs first turn yellow or orange. In heavy infestations, the leaves soon whiten and the plants die. The aphids then leave these plants and move on to others. Greenbugs also have a high parthenogenetic reproductive rate, so in a short time they can build up a huge population. Portions or whole fields may be severely damaged. In addition to the damage they cause, greenbugs are effective vectors of barley yellow dwarf virus, maize dwarf mosaic virus, and sugar-cane mosaic virus (Gill, 1970; Nault and Bradley, 1969; Komblas and Long, 1972); and may predispose sorghum to charcoal rot (Teetes et al., 1973). Gill (1970) found that young nymphs of Schizaphis graminum transmit an isolate of barley yellow dwarf virus more efficiently than do adults. This study was confirmed by Johnson and Rochow (1972). An isolate of barley yellow dwarf virus designated as "SGV" isolate originated from a spring oat plant (Avena sativa L.) was transmitted specifically by the greenbug.

Greenbug and Biotypes

The greenbug is recorded as having four major biotypes (A, B, C, and D) of importance on field crops. Some morphological characteristics are differentiated. Biotypes A and B have dark green bodies with at least one-fourth of the cornicle black tipped throughout the life. Biotypes C and D have pale green bodies and are slightly more

elongated than A or B. The cornicle is green or else only the extremity is black tipped. But these distinctions may be unreliable because food sources can influence insect color. Morphological characteristics are generally not as reliable as physiological characteristics based on fecundity and survival on host plants, especially in regards to temperature differences and to tolerance to specific insecticides (Starks and Burton, 1977a).

Biotype A, the "original" greenbug, is differentiated from the other three biotypes by the resistance of Dickinson selection 28-A (DS 28-A) and CI 9058 wheat to only this biotype (Starks and Burton, 1977a). Biotype A probably does not occur in southwestern small grain fields now.

Biotype B was discovered by Wood (1961b) in barley cultures maintained in the greenhouse and became predominant and replaced A in the field by 1965. Biotype B is not morphologically and reproductive different from biotype A, but differs in feeding habits. Saxena and Chada (1971) found that biotype A made intercellular penetration of stylets in the plant tissues, and invariably feeds in the phloem tissues of the vascular bundles; whereas biotype B stylets penetrate both intra and intercellularly and it preferentially feeds in the mesophyll parenchyma of the leaf. Biotype C feeds in phloem tissues the same as biotype A (Wood et al., 1969b).

Biotype C was discovered during the summer of 1968 when large numbers of greenbugs made an unprecedented and widespread attack on sorghum. Since this time it has largely replaced B on small grains in much of the Great Plains. Biotype C was able to better reproduce at constant extreme temperatures than A and B (Wood and Starks, 1972).

So biotype C is capable of attacking and injuring small grains during the winter and grain sorghum in the summer. At the present time biotype C has become the most damaging biotype of the greenbugs. Harvey and Hackerott (1969) found that Piper sudangrass (Sorghum sudanese) in the seedling stage was highly resistant to biotype B and susceptible to biotype C. Starks et al. (1972) tested broomcorn cultivar 'Deer' and RS-610 for biotype B and C of the greenbugs. They found that 'Deer' is strongly nonpreferenced by biotype B. So, 'Piper' sudangrass and 'Deer' broomcorn can be used to separate biotypes B and C.

Wilson et al. (1978) studied greenbug resistance in common oats (Avena sativa L.). They reported that CI 4888 showed resistance with three components, antibiosis, nonpreference, and tolerance, to biotype B; whereas PI 186270 indicated resistance with three components to biotype C. Thus, these sources of resistance can also be used to separate two biotypes of the greenbug.

Biotype D, insecticide resistance, was first reported on sorghum in west Texas in the summer of 1974, but it was probably present on wheat in New Mexico prior to this. In 1975, it was reported in Texas, Oklahoma, Kansas, Nebraska, and South Dakota (Starks and Burton, 1977a). It was tested and confirmed by Peters et al. (1975) and Teetes et al. (1975) that the greenbug populations had become organophosphate-resistant and were designated as biotype D. This new biotype probably gives the same reaction on plants as biotype C.

Mechanisms and Nature of Resistance

Painter (1951) divided the phenomena of resistance into three mechanisms. Of these, one or a combination of the three is present in

most cases of resistance that have been studied sufficiently. The three mechanisms are nonpreference or antixenosis, antibiosis, and tolerance. The three are usually the result of separate genetic factors but are interrelated in their final effects on the insect-plant relationship. Gallun (1972) reported that resistance to insects is genetically controlled and expressed as antibiosis, nonpreference, and tolerance. The ability of the insect to attack the plant is also genetically controlled and expresses itself in the form of insect variants called biotypes. Biotypes develop through selection pressure from resistant varieties and are able to survive, interbreed, and develop into epidemic numbers. The inheritance of resistance in crop plants varies from being monogenic, with complete dominance, to polygenic inheritance, involving epistasis or having additive effects. Plants having single genes for resistance are more vulnerable to biotype build-up than are plants with polygenic inheritance.

Allard (1960) indicated that the inheritance of insect resistance differs in no major way from inheritance of disease resistance. He suggested that whether a variety is resistant or susceptible to physiological race or biotype depends on its genotype for resistance and the genotype for virulence or avirulence of the race in question. In the final analysis, therefore, insect reaction involves interaction of genes conditioning resistance in the host with those conditioning virulence in the insect.

Todd et al. (1971) determined the chemical substances that caused resistance to greenbug biotype B in barley by rearing aphids on chemically defined diets containing commercially available phenolic and flavonoid compounds individually incorporated at 3.75×10^{-4}M or less.

These compounds were detrimental to growth, drastically reduced number of progeny, reduced weight gain and the survival of the progeny. These compounds are constituents of resistant barley leaves. It is therefore likely that at least part of the resistance to greenbug biotype B of some barley varieties is attributable to the presence of these phenolic and flavonoid substances in quantities sufficient to retard insect growth and reproduction.

Juneja et al. (1972) studied the biochemical nature of resistance to greenbug biotype C in small grains. They analyzed extracts of the water soluble components of leaves from isogenic selections of barley resistant (R) and susceptible (S) to the greenbug. They found that benzyl alcohol is virtually absent from the S strain, and concluded that benzyl alcohol probably was a chemical resistant factor of plant resistance to greenbug biotype C. They confirmed their discovery by using benzyl alcohol added in nutrition medium on the susceptible barley and susceptible 'Wheatland' sorghum seedlings. The susceptible plants became phenotypically resistant to greenbug biotype C. In a further study, Juneja et al. (1975) strongly suggested that the gene which confers greenbug resistance to barley is involved with the synthesis rather than the subsequent metabolism of benzyl alcohol. Thus, free benzyl alcohol synthesis is at least one of the plant components responsible for greenbug resistance.

In sorghum, one of the characters that indicates resistance to greenbug biotype C is the absence of the waxy material from the surface of the stems and leaves called "bloomless sorghum". Peiretti (1975) concluded from his study on aspects of greenbug resistance in bloomless sorghum that the bloomless plants seem to increase the nonpreference

mechanism of resistance as the plants increased in age. Tolerance did not appear to be a component of resistance in the bloomless sorghum.

Greenbug Resistance and the Mode of Inheritance in Small Grains and Sorghum

Fenton and Fisher (1940) observed the greenbug in Oklahoma: barley was the preferred host and oats and wheat followed. Spring oats were injured seriously. Atkins and Dahms (1945) reported varietal differences in reaction to greenbug among a large collection of barley, wheat, and oats during a 1942 outbreak. High resistance was found among barley varieties, especially certain ones of Oriental origin. A moderate resistance was observed in wheats; among the best were certain 'Marquillo' x 'Oro' strains, which also were resistant to the Hessian fly. Among oat strains, no high degree of resistance was found. Dahms et al. (1955) found high resistance in 'Dickinson' durum wheat (CI 3707) and in 'Dickinson Sel. 28A', a selection which was then used in breeding programs for resistance to biotype A in Texas, Oklahoma, and Kansas. More recently, 'CI 9085' was found to be resistant.

Painter and Peters (1956) screened 2,141 foreign wheat introductions with 'Pawnee', a wheat commonly grown in Kansas at that time, as a susceptible check and 'Dickinson' selection as a resistant check. Most of the varieties tested were more susceptible than 'Pawnee'. About 4% of the strains carried some resistance. They also tested F_1 and F_2 from crosses between three susceptible winter wheats and resistant 'Dickinson Sel. 28A': Pawnee CI 11669 x DS 28A; Chiefkan-Oro-Tenmarq, CI 12518 x DS 28A; Concho, CI 12517 x DS 28A. From data of

F_2 populations, the ratio of susceptible and resistant plants was near 3:1. They suggested the greenbug resistance in wheat 'DS 28A' was controlled by a single recessive factor pair. This result was confirmed by Daniels and Porter (1958), and Curtis et al. (1960). The latter authors designated gbgb as a single recessive gene pair which controlled greenbug resistance in 'DS 28A' as well as 'CI 9058'. However, susceptibility in F_1 hybrids between susceptible and resistant wheats indicated incompletely dominant.

Porter and Daniels (1963) determined the inheritance and heritability of greenbug resistance in 'DS 28A' by using F_1, F_2, F_3, F_4, and backcross generations after crossing to the common wheat 'Concho'. The result appeared to be an absence of dominance of the factor or factors conditioning the expression of greenbug resistance. They pronounced that resistance to greenbugs was highly heritable if the influence of environmental factors were minimized by replication. They concluded that resistance can be transferred to a commercial winter wheat variety by commonly used breeding methods if factors contributing toward greenbug resistance do not in addition contribute toward undesirable agronomic characteristics.

When new biotypes (B and C) appeared, 'DS 28A' became susceptible. Subsequently, when the world wheat collection was screened by using the new biotype of greenbug, no high level of resistance was found. So 'Gaucho', an octoploid triticale, was developed from the cross between susceptible 'Chinese Spring' common wheat and an Argentine rye, 'Insave F.A.', which is highly resistant to the greenbug (Wood et al., 1974).

Sebesta and Wood (1977) developed and released 'Amigo' (CI 17609) wheat with greenbug resistance transferred from Insave F.A. rye via Gaucho. Amigo, a red winter wheat, is resistant to all present biotypes of the greenbug with resistance controlled by a single dominant gene.

Chada et al. (1961), at Denton, Texas from 1951-1959, tested for greenbug resistance in more than 18,860 selections of barley, oats, and wheat of domestic and local origin from collections of the United States Department of Agriculture. High resistance was found in 'Omugi', 'Kearney', and 'Dobaku' barleys. It was then transferred to desirable domestic varieties by crossing.

Gardenhire and Chada (1961) studied the inheritance of biotype A greenbug resistance in barley by using crosses among six susceptible varieties carrying tester genes and the resistant parent, Omugi. Their data supported the hypothesis that resistance to the greenbug in the variety Omugi is conditioned by a single dominant gene GrbGrb. Resistance appeared completely dominant. In addition to Omugi, the varieties 'Derbent' and 'Kearney' were resistant to the greenbug. Evidence from the resistant x resistant crosses (lack of segregation in F_2 and F_3) indicated that the three varieties derived their resistance from the same gene or closely linked genes. They also found that the gene for greenbug resistance was not associated with genes conditioning kernel row number, rough awns, hooded, black pericarp, covered seed, and stem rust resistance. Gardenhire (1965) later found no associations between the gene for greenbug resistance and the genes conditioning green-seedling powdery mildew resistance, leaf rust resistance, and orange lemma.

Smith et al. (1962) also studied the inheritance of greenbug resistance in barley. The result of their experiment showed that the barley resistant varieties Omugi, Dobaku, Kearney, and CI 5087 had one common dominant factor controlling greenbug resistance. No measurable differences in the degree of resistance were observed among the hybrids of resistant varieties and parents. The results of hybrids between susceptible and resistant varieties, indicated a single dominant gene produced the major effect in controlling resistance in Omugi and Dobaku.

Wood et al. (1969b) studied the preference of three greenbug biotypes (A, B, and C) on small grains and sorghum in the laboratory. All three biotypes showed a definite nonpreference for 'Will' barley and there was less injury on this variety. Gardenhire et al. (1973) determined the linkage group of the gene for greenbug resistance in Will. They used primary trisomics and tertiary trisomic homozygous translocation in locating genes and found that the gene for greenbug resistance was on linkage group 1 and on the centromerebearing segment of chromosome 1 in the TI-6a translocation.

Wood et al. (1969a) screened 263 sorghums for greenbug tolerance. One entry, SA 7536-1 ('Shallu'), was found with an extremely high tolerance to all three greenbug biotypes. Studies on fecundity, preference, and antibiosis showed this variety to be a very poor greenbug host. Fecundity was greatly reduced; there was a definite nonpreference for SA 7536-1; and all three biotypes, when reared on this variety, became stunted with weight losses up to 80% of normal.

Hackerott et al. (1969) observed plant injury of 648 cultivars and breeding lines from diverse sorghum types during a natural heavy

greenbug infestation in the field in 1968. Some tolerant types noted in the field possessed tan plant color so lack of purple pigmentation could have masked greenbug injury. The entries classified as tolerant to greenbug attack in the field were Sudan-grain, 'Shallu', some waxy endosperm types, and derivative of these three groups. They also conducted greenhouse tests without controlled temperatures by mass infestations of seedlings. Surviving seedlings indicated that two S. virgatum sources (PI 38108 and TS 1636) and some of their derivatives, and sudan-grain were resistant to greenbugs. Seedling survival of the resistant entries ranged from 50 to 100%. The greenhouse results agreed with the field observations as all entries classified as tolerant in the field were resistant or intermediate in the greenhouse seedling survival trials. For the inheritance study, the seedling survival trial involved the parents, the F_1, and F_2 generations of a resistant x susceptible cross. The F_1 and the resistant parent survived 100% and the susceptible parent was killed. In the F_2 population there was segregation into resistant and susceptible plants in the ratio of 9:7. This indicated resistance was controlled by dominant genes at more than one locus. The F_2 population of two resistant sources S. virgatum x Sudan-grain did not segregate for resistance. It means that genes conditioning resistance in S. virgatum and Sudan-grain appear to be at the same locus.

Weibel et al. (1972) determined the inheritance of greenbug resistance and the feasibility of transferring the resistance to adapted lines in F_1 and F_2 populations. The greenbug-resistant parents were 'Shallu Grain' (SA 7536-1), IS 809, and PI 264453 which were crossed with greenbug-susceptible parents being used in the

Oklahoma Agricultrual Experiment Station sorghum breeding program. After individually rating plants injured, four of six populations involving Shallu Grain and three of six involving PI 264453 and IS 809 were found to fit a ratio of 1:2:1 for resistant, intermediate and susceptible plants. F_1 hybrid reactions to greenbugs seemed intermediate between the parents, but close to the resistant parents. They concluded that resistance to greenbugs, at least in some of the populations, is probably controlled by a single major gene with an incompletely dominant factor, and that breeders should have little difficulty transferring resistance to adapted lines. Average number of dead plants per entry and average reduction in height due to greenbugs were highly correlated with damage scores.

Buajarern (1972) conducted his study on sorghum hybrids, 21 F_1's, 12 F_2's, and 18 backcross populations. He indicated that greenbug resistance in sorghum appeared to be conferred by genes at one locus with an indication of an allelic series at that locus. Gene actions appeared to be additive, with partial or complete dominance depending on the parents and crosses involved.

Schuster and Starks (1973) determined three components (nonpreferernece, antibiosis, and tolerance) to measure resistance to the greenbug in 11 sorghum selections. Five of the selections, PI 229828, IS 809, Shallu Grain, PI 302178, and PI 226096, indicated comparatively high degrees of all three resistance components.

Greenbug Resistance and Inheritance in Oats

Chada et al. (1961) studied greenbug resistance in oats at Denton,

Texas in 1954. Most of the varieties were highly susceptible. 'Andrew' (CI 4170) and 'New Mexico' (CI 3422) showed more resistance than any other varieties but did not have sufficient resistance to offer protection to the crop under field conditions. The United States Department of Agriculture's world oat collection of 4,998 varieties and strains was screened in 1955-1956. Seventy-seven were rated at least 10% more resistant than Andrew which was used as the resistant check. Seventy-four of the seventy-seven oats were selected for plant longevity, plant injury, and antibiosis tests in 1957. Thirty-seven were from eighteen states of the United States and thirty-six were from foreign countries. Among the foreign varieties, 12 came from Yugoslavia, 5 from Turkey, 4 from Argentina, and 3 from Canada. However, these oats were resistant only to biotypes A and B. Many varieites and strains were no longer resistant to the present greenbug biotype C when they were tested in 1960 by Daniels (1978)

Wood et al (1969b) tested three greenbug biotypes on small grains including oats in the laboratory. The results showed that PI 186270 was nonpreferred by all three biotypes, especially biotypes A and C.

Gardenhire (1964) studied the mode of inheritance of greenbug resistance in oats by making two crosses. 'Russian 77', (Avena sativa L.), a variety with a high degree of tolerance, was used as the resistant parent for crosses with 'New Nortex' (Avena byzantina C. Koch) and 'Texas Selection 2' ('Red Rustproof'-'Victoria'/'Richland'// Romger'). Based on his data of F_2 plants and F_3 families, he hypothesized that the inheritance of greenbug resistance in the oat variety 'Russian 77' is conditioned by a single gene pair.

Dickson and Laird (1969) tested the crop host preferences of greenbug biotypes attacking sorghum in California. They planted various crops of small grains in pots and a large pre-alate nymph was caged on each plant. The results showed that 'Moregrain' oats had a very small number of offspring, which indicated some antibiosis in this variety.

Daniels (1978) tested 4,343 oat selections from the United States Department of Agriculture's world collection for biotype C greenbug resistance in 1970-1977. Most of these selections were found to be highly susceptible. Of all selections, 31 were found to be resistant. The resistance ratings ranged from 2.3 to 3.5 with the rating scale ranging from 1 for no damage to 6 for dead plants. In addition, he found that FHB 28821 (PI No. 1579) and 'Black Tartarian' (PI No. 1580) are resistant to both greenbug biotypes B and C.

Wilson et al. (1978) tested and determined the type of resistance of four oat resistant lines to biotypes B and C for greenbug. The resistant lines were CI 1579, CI 1580, CI 4888, and PI 186270. They found that PI 186270 showed antibiosis, nonpreference, and tolerance to biotype C, the biotype predominant in the Great Plains. CI 4888 indicated antibiosis, nonpreference, and tolerance to biotype B. CI 1579 and CI 1580, which have agronomic similarities, showed antibiosis to biotypes B and C and nonpreference to biotype C.

CHAPTER III

MATERIALS AND METHODS

The Oat Parents (*Avena sativa* L.)

The greenbug resistant oats used in this study were PI 186270, CI 1580, and CI 4888. The component of resistance to two biotypes of greenbug in the three resistant lines was determined by Wilson et al. (1978) at Oklahoma State University, Stillwater. The susceptible varieties were 'Chilocco' and 'Nora'.

PI 186270 was introduced from Argentina in 1950. It showed antibiosis, nonpreference, and tolerance to biotype C and showed only antibiosis to biotype B.

CI 1580 came from Scotland in 1920. It was originally screened for greenbug resistance at the Texas Agricultural Experiment Station, Denton, in 1966. In the test by Wilson et al. (1978) it showed antibiosis to both biotypes B and C and nonpreference to biotype C.

CI 4888 was introduced from Italy in 1947. It was initially screened for resistance by the USDA FR/SEA and Oklahoma Agricultural Experiment Station workers at Stillwater in 1975. This variety had high resistance to biotype B in all three components.

Chilocco (CI 8183) originated from the cross 'Wintok Early Selection'/'Le Conte', made in 1955 at the Oklahoma Agricultural Experiment Station. It was approved for release and named in 1970.

Chilocco is a high yielding winter oat variety with extremely good weight per hectoliter, winterhardiness, and lodging resistance. Plants tiller well and have very stiff culm. Chilocco is superior to all currently grown varieties in Okahoma for winterhardiness (Edwards et al., 1971).

Nora (CI 8163) resulted from a cross of ('Lee x Victoria' 2 x 'Fulwin' 3 x 'Bonda' 4 x 'Landhafer') x 'Moregrain', made in 1957 at the Arkansas Agricultural Experiment Station. It was released by this station in 1966. Nora is a winter oat which had improved winterhardiness and a wide range of adaptation and high yielding ability. It is resistant to crown rust, Puccinia coronata, races 203, 216, 290, 294, and 326, and resistant to Helminthosporium blight. It is short strawed and has high lodging resistance (Smith and Jones, 1968)

Crosses Made

All of the parents were planted in pots containing a soil-peat moss mixture in May, 1978 and nine crosses were made in June and July, 1978. In making crosses, equipment consisted of scissors and straight pronged forceps. The technique was much the same as generally used by oat breeders and explained by Coffman (1961) except the clipped method was used in emasculation. The plants after emasculation and pollination were kept in growth chambers at an optimum temperature of 21-23°C since high temperatures for three to four days intervals between emasculation and pollination can decrease seed set (Brown and Shands, 1956). After seed set, plants were transferred to a greenhouse at ambient temperature.

Only seven crosses had seedsets and could be used to study the inheritance of greenbug resistance. They were as follows:

1. Chilocco x PI 186270
2. Nora x PI 186270
3. Chilocco x CI 1580
4. CI 1580 x Nora
5. CI 1580 x PI 186270
6. Chilocco x CI 4888
7. CI 1580 x CI 4888

The F_1 Hybrids

All of the F_1 hybrids and male and female parents were grown in pots in the greenhouse in November, 1978. Observations of plant type, awns, type of head, shape of kernel, and some marked characteristics of F_1 hybrids were recorded so as to check self-pollination. All of the plants were harvested in April and May, 1979. All seeds from F_1 plants were kept in cold temperature at 7°C for at least three weeks.

F_1 hybrids were not tested for greenbug resistance because the number of seeds was limited. Also, F_1 plants in comparison to F_2 plants do not furnish as much information about inheritance.

Greenbug Resistance Testing

The plants that were used in greenbug test were F_2 hybrids and all susceptible and resistant parents (Table I). All oat entries had seed treated with a fungicide and were planted June 28, 1979. Techniques for screening and evaluation were similar to those of

TABLE I

DESCRIPTION OF OAT ENTRIES USED FOR TESTING
WITH GREENBUG BIOTYPES C AND B

Entry	Variety or Cross	Generation	Description
1	PI 186270	P	Resistant to biotype C
2	CI 1580	P	Resistant to biotype C, Susceptible to biotype B
3	CI 4888	P	Susceptible to biotype C, Resistant to biotype B
4	Chilocco	P	Susceptible to biotype C, Susceptible to biotype B
5	Nora	P	Susceptible to biotype C, Susceptible to biotype B
6	Chilocco x PI 186270	F_2	Susceptible x Resistant to biotype C (Segregating)
7	Nora x PI 186270	F_2	Susceptible x Resistant to biotype C (Segregating)
8	Chilocco x CI 1580	F_2	Susceptible x Resistant to biotype C (Segregating)
9	CI 1580 x Nora	F_2	Resistant to biotype C x Susceptible (Segregating)
10	Chilocco x CI 4888	F_2	Susceptible x Resistant to biotype B (Segregating)
11	CI 1580 x PI 186270	F_2	Resistant to biotype C x Resistant to biotype C (Segregating)
12	CI 1580 x CI 4888	F_2	Resistant to biotype C x Resistant to biotype B (Segregating)

Wood (1961a), and Starks and Burton (1977a). The entries were grown in galvanized metal flats, 14 x 20 x 3 3/4 inches, containing sterilized soil-peat mixture in the greenhouse. Each flat had 10 rows spaced 2 inches apart with 20 seeds per row. Seeds were covered with about 1 inch layer of sand. Each flat had two rows of resistant and susceptible parents randomly located as checks. Tests were conducted in three growth chambers at a temperature of 22°C and a 14 hour photoperiod. A small amount of complete fertilizer mixed with water was used at seeding time.

The plants were infested when they were 4-5 cm tall with greenbugs of varying age brushed from the culture pots on to the flats. Flats were lightly reinfested two or three times to obtain uniform and adequate greenbug levels. Most of the greenbugs which were used for infestation were apterous viviparities. The greenbugs were allowed to feed and reproduce until all susceptible parents were killed and then data were taken. This usually took 8-10 days after infestation.

The greenbug biotype B that was used for infesting was cultured on susceptible barley (Hordeum vulgare L.) in 15 cm plastic pots. Pots were covered with cylindrical nitrocellulose plastic cages 12 inches in height to prevent contamination from other insects and to confine the greenbugs. The ventilation holes and the tops of the cages were covered with glue-on cloth which had a weave sufficiently large enough to allow aeration but small enough to block the passage of insects. By this way greenbug populations rapidly built-up. The greenbug biotype C for infesting was cultured in the same manner as

biotype B except plant cultures were a mixture of susceptible barley and sorghum (Sorghum bicolor, L. Moech).

For measuring greenbug resistance, individual plants were rated visually by using a scale ranging from 1 for no damage to 6 for dead plants. The procedure and evaluation were the same for biotype B and C. The observed data did not fit any genetic ratios using this classification. Therefore, the classes 1 through 4 were classified as resistant and classes 5 and 6 classified as susceptible. The segregation of the F_2 generation in each cross was tested for goodness of fit to an expected ratio by chi-square.

CHAPTER IV

RESULTS AND DISCUSSION

Parents

PI 186270

A description of PI 186270 is presented in Table I. It exhibits resistance to biotype C. It was used as the resistant check in tests with biotype C. All plants of PI 186270 were classified into damage rating classes one, two, or three (Table II). The average greenbug damage rating for PI 186270 was 1.35 and was the lowest of any population (Table III). Also, no dead plants were observed in this population. Thus, PI 186270 exhibited the highest levels of resistance to biotype C of any variety tested.

CI 1580

This vareity was also used as a source for resistance to biotype C (Table I). There were 120, 39, and 9 plants placed in resistant classes one, two, and three, respectively (Table II). However, there was also one plant in each of the susceptible classes five and six. These two plants were probably seed mixtures in the CI 1580 population or were damaged by something other than the greenbugs. The average greenbug damage rating of CI 1580 as shown in Table III was 1.39. Again the dead plants presented in Table III

TABLE II

FREQUENCY SEGREGATIONS OF PLANTS IN GREENBUG
DAMAGE TO BIOTYPE C

Entry	Variety or Cross	Generation	Damage Rating[1]					
			1	2	3	4	5	6
1	PI 186270	P	105	31	10	---	---	---
2	CI 1580	P	120	39	9	---	1	1
3	CI 4888	P	---	---	---	7	6	11
4	Chilocco	P	---	---	---	---	6	96
5	Nora	P	---	---	---	---	2	87
6	Chilocco x PI 186270	F_2	5	52	53	34	31	30
7	Nora x PI 186270	F_2	34	82	100	69	36	68
8	Chilocco x CI 1580	F_2	58	128	92	35	23	90
9	CI 1580 x Nora	F_2	12	57	52	13	7	40
10	CI 1580 x PI 186270	F_2	38	52	54	41	23	52
11	CI 1580 x CI 4888	F_2	6	22	18	7	13	6

[1] Damage Rating Scale: 1 = Resistant to 6 = Dead Plant.

TABLE III

AVERAGE GREENBUG DAMAGE CLASS AND PERCENTAGE OF DEAD PLANT BY BIOTYPE C

Entry	Variety or Cross	Generation	Average Damage[1] Class	% Dead Plants
1	PI 186270	P	1.35	---
2	CI 1580	P	1.39	0.59
3	CI 4888	P	5.17	45.83
4	Chilocco	P	5.94	94.12
5	Nora	P	5.98	97.75
6	Chilocco x PI 186270	F_2	3.60	14.63
7	Nora x PI 186270	F_2	3.50	17.48
8	Chilocco x CI 1580	F_2	3.25	21.13
9	CI 1580 x Nora	F_2	3.36	22.10
10	CI 1580 x PI 186270	F_2	3.44	20.00
11	CI 1580 x CI 4888	F_2	3.24	8.33

[1] Damage Rating Scale: 1 = Resistant to 6 = Dead Plant.

probably resulted from causes not related to greenbug susceptibility. CI 1580 is highly resistant to greenbug biotype C.

CI 1580 was also infested with greenbug biotype B. The evaluation placed 6, 20, and 29 plants into classes four, five, and six, respectively (Table IV). The six plants classified into resistant damage rating four could have been misclassified and probably belong to susceptible class five. The average damage rating to biotype B of CI 1580 as shown in Table V was 5.42. Thus, CI 1580 was susceptible to greenbug biotype B.

CI 4888

Twenty-four plants of CI 4888 were infested with greenbug biotype C (Table II). There were seven plants rated four, six plants rated five, and eleven rated six. Again, the plants classified as four probably could have been classified as five resulting in all plants being classified as susceptible. The average damage rating of CI 4888 to biotype C was 5.17. Therefore, CI 4888 was judged susceptible to greenbug biotype C.

CI 4888 was also infested with greenbug biotype B. All plants were in the resistant classes one, two, and three (Table IV), and the average greenbug damage was 1.44 (Table V). This indicated that CI 4888 is resistant to greenbug biotype B.

Chilocco

Chilocco was infested with both biotypes B and C. All 102 plants tested for reaction to biotype C were classified into damage rating classes five or six (Table II); therefore, were classified

TABLE IV

FREQUENCY SEGREGATIONS OF PLANTS IN GREENBUG
DAMAGE RATING TO BIOTYPE B

Entry	Variety or Cross	Generation	Damage Rating[1]					
			1	2	3	4	5	6
1	CI 4888	P	23	15	1	--	--	--
2	CI 1580	P	--	--	--	6	20	29
3	Chilocco	P	--	--	--	--	3	45
4	Chilocco x CI 4888	F_2	20	59	62	84	57	29
5	CI 1580 x CI 4888	F_2	10	28	33	72	35	16

[1] Damage Rating Scale: 1 = Resistant to 6 = Dead Plant.

TABLE V

AVERAGE GREENBUG DAMAGE CLASS AND PERCENTAGE OF DEAD PLANT BY BIOTYPE B

Entry	Variety or Cross	Generation	Average Damage Class[1]	% Dead Plants
1	CI 4888	P	1.44	---
2	CI 1580	P	5.42	52.73
3	Chilocco	P	5.94	93.75
4	Chilocco x CI 4888	F_2	3.60	9.32
5	CI 1580 x CI 4888	F_2	3.73	8.25

[1] Damage Rating Scale: 1 = Resistant to 6 = Dead Plant.

as susceptible (Table VI). The average damage rating of Chilocco to biotype B was 5.94 (Table V) and 94% of the plants tested were killed. Therefore, Chilocco is classified as susceptible to biotype B, also.

Nora

Nora was infested with biotype C. All 89 plants tested for reaction to biotype C were classified into damage rating classes five and six (Table II). They were recorded as being susceptible (Table VI). The average damage rating of Nora was 5.98 with 98% of the plants killed (Table III). Nora appears to be the most susceptible variety tested to biotype C.

F_2 Populations

Reaction to Biotype C

The F_2 population resulting from the cross Chilocco x PI 186270 were classified into six damage rating classes (Table II). However, this six-class segregation did not fit any well-defined genetic ratio. Therefore, plants with a damage rating of one through four were classified as resistant and those with a rating of five or six were classified as susceptible. These data are summarized in Table VI. The segregation of 144 resistant and 61 susceptible was tested for goodness of fit to a 3:1 genetic ratio by the chi-square test. The data satisfactorily fit this 3:1 ratio with an acceptable probability of .10 to .25. Thus, the resistance of PI 186270 to greenbug biotype C appears to be conditioned by a single dominant gene pair.

TABLE VI

GREENBUG REACTION OF PARENTS AND F_2 OF BIOTYPE C

Entry	Variety or Cross	Generation	Number of Plants			Ratio	P Value
			Resistant[1]	Susceptible[2]	Total		
1	PI 186270	P	146	---	146	---	----
2	CI 1580	P	168	2	170	---	----
3	CI 4888	P	7	17	24	---	----
4	Chilocco	P	---	102	102	---	----
5	Nora	P	---	89	89	---	----
6	Chilocco x PI 186270	F_2	144	61	205	3:1	.25-.10
7	Nora x PI 186270	F_2	285	104	389	3:1	.50-.25
8	Chilocco x CI 1580	F_2	313	113	426	3:1	.50-.25
9	CI 1580 x Nora	F_2	134	47	181	3:1	.90-.75
10	CI 1580 x PI 186270	F_2	185	75	260	11:5	.50-.25
11	CI 1580 x CI 4888	F_2	53	19	72	3:1	.90-.75

[1]Resistant plants from damage rating classes one through four.

[2]Susceptible plants from damage rating classes five and six.

Nora x PI 186270 was another cross between parents susceptible x resistant to biotype C. The F_2 population was classified 285 resistant and 104 susceptible (Table VI). These data showed a good fit to a 3:1 genetic ratio with a probability of .25 to .50. These data substantiate the previous conclusion that resistance to greenbug biotype C of PI 186270 is conditioned by a single major gene showing complete dominance. The genotype of PI 186270 may be tentatively designated as Grb_1Grb_1 and the genotypes of Chilocco and Nora may be designated as grb_1grb_1.

Chilocco x CI 1580 was also a cross between a susceptible x a resistant line to biotype C. The greenbug reactions of the F_2 generation are shown in Tables II and VI. The population segregated 313 resistant to 113 susceptible to biotype C. There was a good fit to the 3:1 ratio of resistant to susceptible with a probability of .25 to .50. A single dominant gene appears to condition resistance to biotype C in CI 1580.

The F_2 generation of CI 1580 x Nora segregated into 134 resistant to biotype C to 47 susceptible (Table VI). This segregation also showed a good fit to the 3:1 resistant to susceptible ratio with a probability of .75 to .90. Therefore, the resistance to greenbug biotype C of CI 1580 appears to be controlled by a single dominant gene pair. The genotype of CI 1580 could be designated Grb_1Grb_1 if the gene which controls resistance to biotype C is the same as the resistance gene of PI 186270. However, the genotype of CI 1580 could be designated as Grb_2Grb_2 if the resistance gene of CI 1580 is different from the gene of PI 186270.

In order to determine if CI 1580 and PI 186270 contained the same or different genes for resistantce to biotype C, a cross was made between these two resistant lines. If CI 1580 and PI 186270 contain the same gene or closely linked genes for resistance, plants in the F_2 population should all be classified as resistant. However, segregation did occur in the F_2 population from this cross (Tables II and VI). The population segregated into 185 resistant to 75 susceptible. When evaluated by the chi-square goodness of fit test, this data fit a 11:5 ratio of resistant to susceptible with the probability .25 to .50. The 11:5 ratio indicates that two genes are segregating and each gene affects the same character. This digenic ratio indicates complete dominance at both gene pair with each gene pair affecting the same character in the same manner, i.e., resistance is dominant to susceptibility for both genes. However, an interaction occurs so that dominants at both genes when present together produce a resistant reaction. The absence of a dominant allele at one gene pair produces resistant plants only when the dominant allele at the other gene pair is homozygous, e.g., grb_1grb_1 Grb_2Grb_2 would be resistant, whereas, grb_1grb_1 Grb_2grb_2 would be susceptible. With this explanation, the susceptible plants would make up 5/16 of the F_2 population and would have one of the following genotypes: Grb_1grb_1 grb_2grb_2, grb_1grb_1 Grb_2grb_2, grb_1grb_1 grb_2grb_2.

However, Grb_1grb_1 grb_2grb_2 was observed to be resistant in the F_2 populations between PI 186270 and Chilocco and Nora. Likewise, grb_1grb_1 Grb_2grb_2 was resistant in the F_2 populations between CI 1580 and Chilocco and Nora. Therefore, the genetic explanation resulting from the 11:5 ratio is not satisfactory. No other satisfactory

ratio and genetic explanation would fit this data. However, since the F_2 population between PI 186270 and CI 1580 did segregate for resistance, these resistant varieties appear to have different genes which condition resistance to biotype C with complete dominance at each locus. Thus, the genotype of PI 186270 may be designated as Grb_1Grb_1 grb_2grb_2 and the genotype of CI 1580 may be designated as grb_1grb_1 Grb_2Grb_2. Both Chilocco and Nora would be homozygous recessive for both genes.

Wilson et al. (1978) indicated that PI 186270 showed three components of resistance to greenbug biotype C but CI 1580 showed only antibiosis and nonpreference. This would tend to further support the conclusion that PI 186270 and CI 1580 contain different genes for resistance to biotype C.

CI 1580 was crossed with CI 4888. The F_2 progenies of this cross were infested with greenbug biotype C. The population segregated 53 resistant to 19 susceptible which is a good fit to the 3:1 ratio with a probability of .75 to .90 (Table VI). Since CI 1580 contains the recessive grb_1 gene and the dominant Grb_2 gene, CI 4888 must be homozygous recessive for both of these genes.

Reaction to Biotype B

Chilocco x CI 4888 is a cross between a variety susceptible x a variety resistant to biotype B. The F_2 progenies from this cross were infested with greenbug biotype B. The damage rating segregations (Table IV) did not fit any well-defined genetic ratio. Therefore, ratings one through four were classified as resistant with ratings five and six classified as susceptible. This procedure resulted in

the segregation data presented in Table VII. The F_2 population contained 225 resistant and 86 susceptible plants which showed a good fit to the 3:1 ratio with a probability of .25 to .50. This indicates that a single dominant gene conditions greenbug resistance to biotype B in the variety CI 4888. Since CI 4888 appears to be homozygous recessive for grb_1 and grb_2, it must be dominant for genes at a third locus and could have the genotype grb_1grb_1 grb_2grb_2 Grb_3Grb_3.

F_2 plants from the cross CI 1580 x CI 4888 were infested with greenbug biotype B. The F_2 population contained 143 resistant and 51 susceptible plants (Table VII). This is a good fit to the 3:1 ratio with a probability of .50 to .75. This data would confirm the above genotype for CI 4888 and indicates that the genotype for CI 1580 may be modified to include the grb_3 gene. CI 1580 may be designated as grb_1grb_1 Grb_2Grb_2 grb_3grb_3.

The results of this study indicate that there are at least three major genes conditioning greenbug reistance in the genotypes studied. PI 186270 and CI 1580 contain different dominant genes for resistance to greenbug biotype C. CI 4888 contains a dominant gene for resistance to greenbug biotype B. All three of the above mentioned genes appear to be independently inherited. There should be little difficulty in developing oat varieties resistant to either biotype B or C or to both B and C using the resistant varieties of this study.

TABLE VII

GREENBUG REACTION OF PARENTS AND F_2 OF BIOTYPE B

Entry	Variety or Cross	Generation	Number of Plants			Ratio	P Value
			Resistant[1]	Susceptible[2]	Total		
1	CI 4888	P	39	---	39	---	---
2	CI 1580	P	6	49	55	---	---
3	Chilocco	P	---	48	48	---	---
4	Chilocco x CI 4888	F_2	225	86	311	3:1	.50-.25
5	CI 1580 x CI 4888	F_2	143	51	194	3:1	.75-.50

[1]Resistant plants from damage rating classes one through four.

[2]Susceptible plants from damage rating classes five and six.

CHAPTER V

SUMMARY AND CONCLUSIONS

The research was conducted to study the inheritance of resistance in oats to greenbug biotypes B and C and the number of genes involved, to investigate whether resistance is controlled by the same or different genes, to determine the feasibility of transferring the resistance to adapted lines.

Seven crosses were made in 1978 by crossing biotype C resistant entries PI 186270 and CI 1580 with released susceptible varieties Chilocco and Nora. CI 4888 which is resistant to biotype B was crossed with the susceptible variety Chilocco. Another two crosses were CI 1580 x PI 186270 (resistant x resistant to biotype C) and CI 1580 x CI 4888 (resistant to biotype C x resistant to biotype B).

Progenies of the F_2 generation of all crosses which used varieties resistant to biotype C as parents were infested with greenbug biotype C and all crosses which involved the variety resistant to biotype B were infested with biotype B. Experiments were tested at a temperature of 22°C in the growth chambers. Damage ratings of individual plants were used to obtain segregation ratios in the F_2's

Both entries with resistance to biotype C, PI 186270 and CI 1580, have resistance probably controlled by a single complete dominant gene pair. CI 4888 which is resistant to greenbug biotype B, is also probably conditioned by a single major gene with complete dominance.

F_2's from the resistant x resistant cross (CI 1580 x PI 186270) tested against biotype C segregated into a resistant and susceptible ratio of 11:5. This means that two different major genes are involved in this cross. Thus, resistant entries PI 186270 and CI 1580 have different genes or different loci which control resistance to biotype C, and two distinct loci were involved with complete dominance at each locus.

The F_2's from the cross of resistance to biotype C (CI 1580) x resistant to biotype B (CI 4888) were tested separately to the biotypes and the results indicated that the genes that controlled the resistance to biotype B was not effective against biotype C. Conversely, the gene that controlled biotype C was not effective against biotype B. Therefore, this cross had a combination of two genes which controlled resistance to the different biotypes of greenbugs.

This study indicated that there are at least three major genes conditioning greenbug resistance of two biotypes. All three genes appear to be independently inherited. There should be little difficulty in transferring the gene of greenbug resistance to either biotype B or C or to both B and C to otherwise adapted oat varieties by common hybridization.

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