GENETICS OF GREENBUG (*TOXOPTERA GRAMINUM* ROND.) RESISTANCE IN COMMON WHEAT (*TRITICUM AESTIVUM* L., EM. THELL.)

by

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GENETICS OF GREENBUG (TOXOPTERA GRAMINUM ROND.) RESISTANCE IN COMMON WHEAT (TRITICUM AESTIVUM L., EM. THELL.)

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INTRODUCTION

The discovery of greenbug resistant germ plasm in common wheat (Triticum aestivum L., em. Thell.) (25)[1/], after many years of search, has created excitement among wheat breeders in areas where this destructive pest is of great economic importance. Heretofore, a bleak outlook confronted the breeder who was interested in incorporating greenbug resistance into adapted commercial varieties. After this important discovery the breeder is offered a ray of hope in combatting the greenbug by methods other than expensive chemical control.

In order to make the most efficient progress in adding resistance to otherwise adapted varieties, it is imperative that knowledge of the genetic mechanism of greenbug resistance be made available as rapidly as possible. The objective of this investigation was to gain this knowledge through hybridization experiments of the resistant strains with susceptible adapted strains.

Since, at the onset of the investigation, nothing was known regarding the inheritance of resistance, it was decided to attempt to solve the problem through conventional genetic methods, i. e., a study of F_1, F_2, F_3 and testcross progeny. Later in the study, after more was known about the genetics of resistance, it seemed appropriate to study gene action more closely by the use of monosomics (45, 46, 49). The results of both types of genetic analyses are presented herein.

1/ Figures in parentheses refer to "Literature Cited", page 60.

REVIEW OF LITERATURE

History and Biology of the Greenbug

The greenbug (Toxoptera graminum Rond.) was first described in Italy in 1852 by C. Rondani, and was first recorded in the United States in 1882 (16). It belongs to the family Aphidae and the order Homoptera. According to Wadley (56) the greenbug may be distinguished from other aphids by the pea-green color with the darker dorsal line, black eyes, and green cornicles with dark tips. The winged form, he states, has a once-branched media in the wing. He mentioned further that the aphids are approximately 1.8 mm. in length and 0.8 to 0.9 mm. in width.

Both sexual and asexual forms occur in the United States. Dahms (8) reports that in the southern States, except at high altitudes, all wingless forms are female and are vivparous. Apparently, sexual reproduction occurs only in the northern States; however, Daniels (11) and Wood[2/] have reported eggs found on plants of small grains growing in greenhouses in Texas and Oklahoma, respectively. Attempts to hatch these eggs were unsuccessful. Daniels (11) mentions the possibility of the egg being one of the oversummering stages in the southern States.

Greenbugs start reproducing 6 to 30 days after birth (8, 12, 16, 56). These authors report varying rates of reproduction, but generally

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2/ Personal communication with E. A. Wood, Jr., USDA Entomologist.

it can be concluded that each female will produce from 40 to 60 young at the rate of 2 to 4 per day. All agree that temperature is highly important in the rate of reproduction. Reproduction is most rapid at temperatures of 55° to 80°F. with some reproduction at 40°.

Wadley (56) revealed that no further molting occurs after the fourth molt and that reproduction begins within a few hours after the last molt.

The host plants of the greenbug appear to be confined to the Gramineae. Patch (35) observed the greenbug on 62 species of grasses, and Dahms et al. (9) subjected 23 grass species to a greenbug infestation and found only 2 that failed to maintain a greenbug population. Eleven of these species were not mentioned in the work of the former author.

Chatters and Schlehuber (6) made an intensive study of the method of feeding and subsequent damage caused by the greenbug when feeding on small grains. They observed the stylet penetrating the leaf intercellularly. The stylets were selective, ultimately seeking out the phloem where active feeding took place. They stated that the major damage was caused by the highly enzymatic saliva which resulted in lysis of Hordeum cells, cell-wall modification in Avena, and a combination of lysis and cell-wall modification in Triticum. Wadley (56) also suspected that an enzyme secreted by the greenbug was the major cause of injury.

The greenbug is attacked by a number of insect species belonging to the genera, Hippodamia, Nabis, Syrphidae, Chrysopa, Aphidius and Aphelinus (12).

Inheritance of Insect Resistance in Cereals

Inheritance studies of insect resistance in cereal crops are relatively few in number. Resistance to several insects is known in some of the cereal crops, but detailed genetic studies of resistance have been reported for only a few insects. In this review only those papers dealing primarily with the inheritance of insect resistance are reported. For a complete review of insect resistance in crop plants the reader is referred to Painter (33).

In wheat, studies have been reported on the inheritance of resistance to the Hessian fly (Phytophaga destructor Say), the wheat stem sawfly (Cephus cinctus Nort.) and the greenbug (Toxoptera graminum Rond.). The genetics of greenbug resistance in barley has been investigated. Inheritance studies of insect resistance in corn have been limited mainly to those on the European corn borer (Pyrausta nubilalis Hbn.). Some literature references were found on the inheritance of locust resistance in corn, but these were published in South America and were not available for review. The inheritance of chinch bug (Blissus leucopterus Say) resistance in sorghum has been studied on a limited scale. The above studies are reviewed in some detail below.

The Hessian fly is a pest in most parts of the holarctic region where winter wheat is grown and in some areas where spring wheat occurs (33). Resistant varieties have been known for over 150 years, but the first detailed inheritance study on resistance in wheat was not reported until 1936 when Cartwright and Wiebe (5) studied the progenies of resistant wheat crossed with susceptible wheat. Dawson, a white soft winter wheat resistant to the race of fly present in the Montezuma Hills region of Solano County, California, was crossed with Big Club and Poso,

2 club spring wheats. The F_2 plants, classified on the basis of behavior in F_3 rows, segregated in the ratio of 15 resistant to 1 susceptible. These investigators concluded that Dawson contained 2 dominant factors for resistance which are complementary and perhaps cumulative.

Noble and Suneson (30) presented data confirming the presence of 2 genetic factors in Dawson. From the Dawson x Poso cross and subsequent backcrosses to Poso they were able to produce 2 tester lines: Selection No. 6179 having the genotype $H_1H_1h_2h_2$ and Selection 6232 having the genotype $h_1h_1H_2H_2$. The H_1 and H_2 genes appeared to impart equal resistance but were definitely inferior to the double combination. The tester lines each showed an infestation percentage ranging from 0 to 10% while Dawson was infested from 0 to 2% and Poso about 83%.

Caldwell et al. (2) in Indiana studied the inheritance of Hessian fly resistance derived from the spring wheat, W38, and the durum, P.I. 94587[3/]. F_1, F_2 and F_3 data from crosses of W38 with Wabash, 4 Fultz sel. x Hungarian selections, and Dawson (susceptible to the Indiana fly) indicated that W38 differed from the susceptible wheats by a single gene pair governing resistance. Since this gene differed from the Dawson genes, H_1 and H_2, it was assigned the symbol H_3. The H_3 gene appears incompletely dominant under field conditions at normal temperatures, but in greenhouse-grown seedling plants it acted as a recessive. The occurrence of high temperatures under greenhouse conditions was offered to explain the reversal in expression of the gene. Further evidence indicated that the H_3 gene also governs resistance to the California

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3/ P.I. and C.I. refer to accession numbers assigned by the Division of Cereal Crops and Diseases, U. S. Department of Agriculture.

strain of fly. Limited data suggested that resistance in P.I. 94587 was controlled by at least 2 dominant genes. The crosses of the durum P.I. 94587 (28 chromosomes) with the common bread wheats (42 chromosomes) did not permit definite conclusions regarding the exact factorial basis of resistance because of meiotic disturbances which are usually encountered in interspecific crosses.

Suneson et al. (54) presented genetic information on additional sources of resistance to the California fly. Java was found to have a recessive resistance factor, h_4, that is independent of the factors H_1, H_2 or H_3. Marquillo resistance behaved as a recessive and apparently was independent of the H_1, H_2, H_3 or h_4 factors. Dixon showed a partly dominant type resistance in crosses with Poso. F_2 data indicated that the gene in Dixon may be common with the h_4 gene of Java. Kawvale was shown to have resistance different than that of H_1 and H_2, but further genetic differentiation was not possible.

A fifth gene conditioning Hessian fly resistance in common wheat was reported by Shands and Cartwright (51) in 1953. Three fly resistant spring wheats, Ribeiro and 2 unnamed strains, P.I. 94549-6 and P.I. 94571-14, were crossed with each other, with Thatcher as a susceptible variety, and with the tester varieties Selection No. 6179 and Selection No. 6232. F_1, F_2, F_3 and backcross data from crosses with Thatcher indicated a single incompletely dominant gene pair difference for fly resistance. Crosses among the 3 resistant parents resulted in no susceptible F_3 families suggesting a resistance gene common to all. Crosses of the same resistant parents with Selection No. 6179, Selection No. 6232, Java and W38 resulted in segregating populations, indicating still another resistance gene, designated as H_5. In this study

it was also determined that Hessian fly resistance was independent from the stem rust reaction and the awnedness condition of Thatcher.

The wheat stem sawfly has been a major limiting factor in wheat production in the Canadian provinces of Alberta and Saskatchewan and into the states of North Dakota and Montana and neighboring states (33). Wheat is damaged as a result of larvae tunneling inside the stem and also by the larvae cutting the stem which may fall and not be recovered by harvesting equipment (21).

Solid stemmed wheats have afforded good protection to this insect since the larvae are unable to survive in solid stems (21). Inheritance studies of wheat stem sawfly resistance have been confined to studies of the inheritance of stem solidness. Only a few such studies have been made.

Platt et al. (39) studied the genetics of solid stem in common wheats. The solid-stemmed S-615 and S-633 crossed with Renown and Thatcher showed that the difference between hollow and solid stem depended on 3 gene pairs with the triple recessive resulting in solid stem. It was suggested that the factors are cumulative and that 4 or more dominant genes will produce phenotypically hollow plants.

Putnam (42) presented results indicating that the inheritance of solid straw as found in the durum, Golden Ball, is unifactorial when Golden Ball is crossed with other durum varieties. The solid character was partially dominant. Platt and Larson (40) attempted to transfer solid stem from Golden Ball to T. aestivum but without success. A total of 25,000 F_2 plants were examined. Although they could not explain the genetic mechanism on a factorial basis, the failure to transfer stem solidness was attributed to a gene for hollowness in the C genome that

was epistatic to all other genes for solidness.

For his doctoral dissertation McNeal (28) studied the genetics of solid stem in a cross of the solid-stemmed Rescue with Thatcher. An analysis of the F_1, F_2 and testcross data by the partitioning method suggested that 1 major gene pair and possible 2 to 4 minor modifying factors for stem solidness separate Rescue and Thatcher.

In a later investigation McNeal et al. (29) found the Portuguese wheats, P.I. 56219-12, P.I. 56219-9, P.I. 56229-2 and P.I. 56225-8 to possess the same major gene or genes for stem solidity as Rescue. "The last three named apparently differ from Rescue by an undetermined number of minor genes that affect the expression of solidness."

Larson (22) attempted to identify the chromosomes bearing genes for solid stem in S-615 by crossing it with Chinese Spring monosomics. F_2 monosomic populations of lines XIII, XIX, XX and XXI were more solid than the normal F_2 population of Chinese Spring x S-615. This showed that these chromosomes, at least in Chinese Spring, carry genes for hollow stem. No genes for solid stem in S-615 were located, probably because of their recessive nature. This study further supports the theory of Platt and Larson (40) that the C genome tends to make culms of wheat hollow, since the loss of 3 C-genome chromosomes XIX, XX and XXI resulted in a more nearly solid stem.

Published reports on the inheritance of greenbug resistance in wheat are limited to 2 papers, one by Painter and Peters (34) and another by Daniels and Porter (13). In both investigations the greenbug resistant wheat used was Dickinson Selection, which was discovered by Dahms et al. (10) at the Oklahoma Experiment Station in the 1952-53 season. In the investigation by Painter and Peters (34) Dickinson Selection was

crossed with Pawnee, Concho and C.I. 12518. F_2 data indicated a single gene pair difference between resistant and susceptible plants. Susceptibility was dominant to resistance. Similar results were obtained by Daniels and Porter (13) from crosses of Dickinson Selection with Westar, Blue Jacket, Kanred and Crockett. They suggested, however, that minor modifying genes may also be involved. In another cross, Dickinson Selection x Vaughn Turkey, they found too many resistant plants in the F_2 population for a good fit to a 3:1 ratio.

McDonald (27) studied the genetics of greenbug resistance in barley by crossing 2 resistant varieties, Omugi and Dobaku, and a semi-resistant variety, C.I. 5087, with the susceptible varieties, Tenkow and Ward. Dobaku was also crossed with C.I. 5087. F_2 and limited F_1 data, based on amount of leaf damage and retardation of growth caused by the greenbug, suggested that resistance was dominant to susceptibility. Genotypes were assigned as follows: Dobaku, Grb_1Grb_1 grb_2grb_2; Omugi, Grb_1Grb_1 Grb_3Grb_3; C.I. 5087, grb_1grb_1 grb_2grb_2; Tenkow, grb_1grb_1 grb_3grb_3; and Ward, grb_1grb_1 Grb_2Grb_2.

The genetics of European corn corer resistance has been studied, particularly in recent years. One of the earliest reports of resistance was made by Marston (26) in 1930. A South American corn known as Maize Amargo received fewer corn borer eggs from natural oviposition and sustained a lower rate of larval survival. F_1 and F_3 data of crosses of Maize Amargo and standard varieties suggested that resistance was controlled by a single recessive gene. Singh, as reported by Penny and Dicke (36), obtained data to support a two-factor-pair hypothesis in a cross between a resistant and a susceptible inbred line. Mean values for the F_2 population and for the backcross to the susceptible parent

indicated a slight phenotypic dominance of susceptibility.

Schlosberg and Baker (44) stated that in sweet corn high borer resistance was probably due to the cumulative effects of several factors. Their tests indicated incomplete dominance of either resistance or susceptibility.

Ibrahim (20) used 23 chromosomal interchange lines in an attempt to determine which chromosome or chromosomes carry the genetic factors which normally differentiate the borer resistance of inbred line A411 from the susceptible line A344. Resistance was dominant in all the F_1's and backcrosses studied. His results indicated that the resistance of A411 was due to at least 1 gene in each of the long arms of chromosome 3, 4 and 5.

According to Penny and Dicke (36), Rubis concluded that the greater part of the genetic variability for leaf feeding resistance could be attributed to additive genetic effects and a small part to either dominance deviations or epistatic interactions.

Penny and Dicke (36) studied the inheritance of corn borer resistance in crosses of the inbred M14 with resistant inbreds MS1 and N32. Leaf feeding ratings of F_3 and backcross progenies indicated segregation of genes for borer resistance at 3 or more loci in the M14 x MS1 hybrids with at least partial dominance of susceptibility. N32 appeared to have 1 or 2 gene pairs for resistance. In a later study Penny and Dicke (37) crossed susceptible inbreds M14 and WF9 with gl_7v_{17}, a corn borer resistant inbred that produces glossy and virescent seedlings. Resistance appeared due to a single dominant gene which was linked with gl_7 and v_{17} genes with crossover frequencies estimated at 31% and 37%.

The chinch bug causes much loss to producers of sorghum. Results of studies conducted by Snelling et al. (53) suggest that chinch bug resistance in sorghum may be dominant or partially dominant. There was evidence that led these investigators to regard the genetics of resistance as being somewhat complex since genetic factors controlling such plant characters as earliness, vigor of early growth and others had an effect on the reaction of the plant to the chinch bug.

Monosomic Analysis

Genetic analysis by conventional methods has proved to be relatively unsatisfactory in common wheat because of its hexaploid nature. Although wheat is an allohexaploid, much of its genic material is duplicated or triplicated (48, 49). This has precluded the discovery of a large number of genes and linkage groups which are desirable in a wheat breeding program. The use of monosomic plants offers a special method for inheritance studies in such polyploid species. Monosomic (2n-1) wheat plants have frequently been reported in the literature (18, 19, 24, 41, 45, 50). However, extensive use of them in genetic studies was not employed until Sears (45, 46, 48, 49) isolated monosomics representing each chromosome in the wheat variety Chinese Spring.

A number of genes have been located in T. aestivum by use of monosomics. Sears (46) located the following genes of Chinese Spring: (1) b_1 on chromosome IX slightly suppresses awn development, but less actively than its allele B_1; (2) other genes on chromosome IX are responsible for suppression of speltoidy, for squareheadedness and for pubescent nodes; (3) a hooded factor, Hd, on chromosome VIII shortens and recurves awns; (4) chromosome X carries an active awn-suppressing

gene, B_2; (5) chromosome XVI has a gene for red seeds and dominant allele to the sphaerococcum gene which causes short culms, dense spikes, and small, spherical grains; (6) chromosomes II and XX probably carry weak factors promoting awn growth; and (7) chromosome III carries genes essential to normal synapsis. Later Sears (47) reported the recessive sphaerococcum gene to be ineffective in hemizygous (single dose) condition, both genes being required for effect. O'Mara (32) found that Marquis wheat carries a strong awn inhibitor, B_1, on chromosome IX. Unrau (55) stated that a dominant gene for red glumes is located on chromosome I in Federation 41. Heyne and Livers (15) reported that Pawnee wheat has a major factor for resistance to leaf rust race 9 located on chromosome X. They also stated that Pawnee, an awned variety, has the recessive alleles hd, b_1 and b_2 for awns located on chromosomes VIII, IX and X, respectively. In addition, Pawnee was found to have the same recessive factors as Chinese Spring on chromosomes II and XX for promoting awn growth.

Wiggin (57) found that Kentana 52 wheat has a dominant gene for resistance to race 56 and another for resistance to race 15B of stem rust, located on chromosome XX, which are loosely linked with a recombination value of 37.6%. Nyquist (31) reported that the duplicate dominant genes for stem rust resistance of C.I. 12633 are located on chromosome XIII. Campbell and McGinnis (3), using the recently developed monosomic series of Redman spring wheat in crosses with Prelude, found that chromosomes III, VIII and XIII of Redman carry factors for adult plant resistance to race 56 of stem rust. These factors are complementary and dominant in action. Hurd (17), also working with Redman monosomics, reported that Redman possesses 2 genes for dwarfing on chrom-

osomes VIII and XIII that are effective only in the presence of a third dwarfing gene in Kenya Farmer. They stated that the absence of any one of these genes results in a normal plant.

The breeding behavior of monosomic plants has been demonstrated by Sears (46, 48). In a self-fertilized monosomic plant about 73, 24 and 3% of the progeny will be monosomic (2n-1), disomic (2n) and nullisomic (2n-2), respectively. Female transmission of whole-chromosome deficiencies is about 75% and male transmission varies from 1 to 15% depending on the chromosome. To account for the difference in gamete transmission Sears (46) stated, "The preponderance of deficient female gametes is attributable to the frequent elimination of the univalent monosome through its failure to be included in a daughter nucleus at the reduction division. The low number of functioning deficient male gametes is presumably due to the considerable elimination of deficient pollen through competition with normal pollen." The actual mechanical process which causes an excess of deficient female gametes to be produced is apparently not well understood.

Person (38) warns that caution should be exercised in monosomic studies because of "univalent shift" (progeny of a monosomic plant being monosomic for a different chromosome than the parent plant). He stated that in F_1 and early backcross generations normal plants crossed with monosomic plants partial-asynapsis may occur for one or more chromosome pairs and result in plants with irregular karyotypes. He further stated that the probability of univalent shift is minimal in the original lines established by Sears and is also less in hybrids after about 5 generations of

backcrossing to the recurrent parent. Another feature observed by Person was the rather common occurrence of reciprocal translocations in F_1 hybrids. This suggests that the use of monosomics in genetic studies may not be as simple as first proposed.

MATERIALS AND METHODS

Wheat Parents and Greenbug Cultures

The greenbug resistant wheats used in this study were Dickinson Selection 28A (DS28A)[4] and C.I. 9058. The susceptible wheats used were Ponca (Pc), Concho (Cc), Crockett (Ctt) and the 21 Chinese Spring (CS) monosomics.

DS28A was originally found as a mixture in a variety of Triticum durum, Dickinson No. 485 C.I. 3707 (10). The seed of C.I. 3707 was obtained from the World Wheat Collection and originally came from the North Dakota Agricultural Experiment Station at Fargo. Additional seed lots of C.I. 3707 obtained directly from North Dakota were found to contain admixtures that resembled the seed of DS28A and which subsequently produced greenbug resistant plants. DS28A is a hexaploid and has all the characteristics of T. aestivum. Where this hexaploid originated and how it became a mixture in C.I. 3707 is not known. Dr. R. M. Heermann[5] reports that no special effort has been made to purify C.I. 3707 and that mixtures of "vulgare" types have been observed in the durum nurseries at Fargo.

4/ The abbreviations following the varietal names are based on the syllable system now being recommended by wheat workers and the abbreviations will be used henceforth in this dissertation.

5/ Personal letter from Dr. R. M. Heermann, May 16, 1955.

DS28A has a spring growth habit but appears to have some degree of cold hardiness. The spike is lax, awned, fusiform to oblong and contains red seed. The beaks (apical projection of the glume) are medium long. The chaff color varies from light black underlain by brown to a dark chocolate color. Dr. E. S. McFadden[6/] states that the spike and glume characteristics are very similar to those of the variety Webster. However, a field comparison of DS28A with Webster, Brevit and Loros showed it differed in several characters from these varieties. DS28A is highly susceptible to the prevalent leaf rust races in Oklahoma.

C.I. 9058 is an unnamed strain originating from Russia. It was first discovered as a greenbug resistant strain in the 1955-56 season by Mr. E. A. Wood, Jr. while screening a portion of the World Wheat Collection for sources of greenbug resistance. C.I. 9058 is a true spring type with red seed. The spike is lax, awned and fusiform to oblong. The beaks are short to mid-long. The chaff color is similar to that of DS28A. Juvenile plant color is light green compared to the dark green color of DS28A. C.I. 9058 is highly susceptible to prevalent races of leaf rust in Oklahoma.

Pc, C.I. 12128, is a winter wheat variety selected from the cross Kawvale-Marquillo x Kawvale-Tenmarq (1, 23). It is an awned, white-chaffed and red-seeded variety. The spikes are fusiform and mid-dense. It is medium in maturity and height and possesses excellent Hessian fly resistance and good mature-plant resistance to leaf rust. It is susceptible to bunt.

Cc, C.I. 12517, is a selection from the cross Comanche x Blackhull-

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6/ Personal letter from Dr. E. S. McFadden, January 31, 1955.

Hard Federation (1, 43). It is a bronzed-chaff, awned and red-seeded variety of winter habit. The spikes are bearded, lax, fusiform and mid-dense. Cc is medium in height and maturity. It is resistant to the important races of bunt and has some leaf rust resistance. It is susceptible to the Hessian fly.

Ctt, C.I. 12702, was selected from the cross (Sinvalocho-Wichita x Hope-Cheyenne) x Wichita (14). It is a red-seeded winter wheat variety resembling Wichita in many characteristics. The spikes are awned and the chaff is white with black stripes. Ctt is medium early in maturity and possesses good mature-plant resistance to prevalent races of leaf rust in Oklahoma. It is susceptible to the Hessian fly and bunt.

The CS monosomics, numbered I through XXI, were kindly furnished by Dr. E. R. Sears of the University of Missouri. A complete description of the monosomics is given by Sears (49).

The initial greenbug cultures used for testing in the 1956-57 and 1957-58 seasons were obtained from Dr. H. L. Chada, Entomologist at Denton, Texas. The greenbugs used in the fall of 1958 were a mixed culture. A few hundred greenbugs that were oversummered in a partially air-conditioned greenhouse at Stillwater were mixed with several hundred obtained from Denton, Texas. The cultures used in 1959 were obtained from Dr. R. H. Painter, Entomologist, Kansas Agricultural Experiment Station, Manhattan, Kansas.

Testing Procedures

All greenbug reaction tests were seeded in the greenhouse in wooden flats having inside measurements of 15 x 20 x 3 inches. The

flats were filled within 1/2 to 3/4 inches of the top with a soil mixture consisting of 5 parts of a silt loam, 1 part washed river sand, 1 part peat moss and 1 part sterilized manure. The soil mixture was changed to a 4:1:1:1 ratio in the 1957-58 and 1958-59 seasons. Each flat was divided into 10 rows, 15 inches long, 2 inches apart and 1/2 inch deep with a corrugated row marker that fitted the inside dimensions of the flat. The seeds were spaced equidistant. The spacings depended on the number of seed planted per row. The flats were then filled to the top with sand and watered. After watering, the flat contents usually settled about 1/4 inch leaving ample space for subsequent watering. The temperature was maintained as close to 70°F. as possible.

The greenbugs were cultured on a susceptible variety of winter barley (Ward). Approximately 50 seeds were planted in 6-inch pots. Two weeks later when the plants were 4 to 6 inches high, approximately 100 greenbugs were distributed among the plants. The plants were then covered with a plastic cylinder 10 inches high and 5 1/4 inches in diameter. The cultures were maintained at approximately 70°F. At this temperature each pot yielded from 1000 to 3000 greenbugs after about 14 days.

To infest the wheat hybrids the barley culture plants were clipped off at soil level and the greenbugs were brushed onto an 8 1/2 x 11 inch sheet of paper. About 1000 to 1200 greenbugs were brushed on the paper for each flat. Actual counts of the number of greenbugs on the paper were made only at the beginning of the study to determine the population density that would represent 1200 greenbugs. The greenbugs were scattered among the plants by holding the paper above the flat and tapping with

the handle of the brush. The paper was moved over the flat so that the greenbugs were scattered as uniformly as possible. For the first few days of each test the greenbug populations were checked closely and additional greenbugs were added to flats having low infestations.

Conventional Genetic Methods

A single F_1 plant of the cross DS28A x Pc, 54 x 26d[7/], was grown in an irrigated plot along with the parents in 1955. In 1956 a total of 528 F_2 plants were grown under irrigated field conditions to furnish seed for testing as F_3 lines. Twenty-two seeds from each of 524 F_2 plants were seeded in the greenhouse insectary in 2 replications of 11 seeds each. Replication I was seeded on December 12, 1956 and replication II on February 1, 1957. In each replication each F_3 line was seeded in a single row with 8 lines per flat. The parent varieties, DS28A and Pc, were seeded in rows 4 and 7, respectively, of each flat.

The plants in both replications were infested when most of the plants were in the 2-leaf stage and 5 to 8 inches tall. Replication I was infested January 2, 1957 and replication II received 400 greenbugs on February 12 and an additional 800 on February 18.

The F_3 lines in replication I were rated on January 31 as to whether they were resistant, susceptible or segregating. Replication II was rated March 23. In replication I the ratings were easy to make. The Pc plants were completely dead and plants of DS28A were from 10 to 12 inches tall and sustaining injury only on the basal leaf and at the tips of other leaves. The F_3 lines were all alive, all dead or segre-

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7/ Stillwater cross number.

gating for live and dead plants. Replication II gave essentially the same results, but some difficulty was encountered in rating because of reduced greenbug populations due to a small parasitic wasp (Aphelinus).

A more comprehensive study of the genetics of greenbug resistance was begun in the 1955-56 season. DS28A and C.I. 9058 were crossed with Pc, Cc and Ctt and with each other. The crosses were made in the greenhouse in February and March. Three F_1 and reciprocal F_1 plants from each cross were grown along with parent plants in the 1956-57 season. The F_1 plants were used to make testcrosses with each parent and to produce F_2 seed. Plans were to obtain 25 seeds of each testcross. However, because of the difficulty in matching the maturity dates of the F_1's and the parents, only 25 of the 28 planned testcrosses were effected. Also, in only 8 testcrosses were 25 or more seed obtained.

In the 1957-58 season the parents, F_1's, F_2's and testcrosses were tested for greenbug reaction as shown in Table 1. From 1 to 13 seeds of the F_1's and testcrosses and no more than 10 seeds of the parents and F_2's were planted in each row. In flats containing resistant x susceptible hybrids the resistant parent was seeded in row 4 and the susceptible parent in row 7. In crosses of resistant x resistant parents C.I. 9058 was seeded in row 4 and DS28A in row 7.

The plantings were made on November 19, 1957 and emergence was complete on November 24. Five days later, when the plants were about 5 inches tall and in the 2-leaf stage, they were infested. A few of the flats maintaining low populations were re-infested with an additional 500 to 600 greenbugs on December 4.

The plants were rated as resistant or susceptible based on whether they were alive or dead by January 5. The date of death for each sus-

Table 1.--Number of parent and hybrid seed planted and emerged in studies on the genetics of greenbug resistance conducted in the greenhouse insectary on the Agronomy Farm, Stillwater, Oklahoma in 1957-58.

Variety or Cross	Parents		F_1		F_2		Testcross to Susc.parent		Testcross to Res.parent	
	sown	emer.	sown	emer.	sown	emer.	sown	emer.	sown	emer.
			(10)1/		(140)		(25)		(25)	
DS28A	200	192	-	-	-	-	-	-	-	-
C.I. 9058	200	175	-	-	-	-	-	-	-	-
Pc	100	97	-	-	-	-	-	-	-	-
Cc	100	95	-	-	-	-	-	-	-	-
Ctt	100	89	-	-	-	-	-	-	-	-
DS28A x Pc	-	-	12	11	120	117	24	23	19	17
Pc x DS28A	-	-	8	7	160	155	6	5	26	25
DS28A x Cc	-	-	20	20	140	134	35	35	26	24
Cc x DS28A	-	-	13	13	130	129	30	30	2	2
DS28A x Ctt	-	-	20	20	140	137	0	0	11	8
Ctt x DS28A	-	-	6	6	160	159	12	12	7	6
C.I. 9058 x Pc	-	-	13	13	130	125	31	29	31	28
Pc x C.I. 9058	-	-	12	12	160	153	9	8	0	0
C.I. 9058 x Cc	-	-	14	14	190	187	23	23	43	39
Cc x C.I. 9058	-	-	1	1	97	97	10	10	0	0
C.I. 9058 x Ctt	-	-	11	9	150	144	19	18	31	28
Ctt x C.I. 9058	-	-	12	10	130	123	9	9	5	3
DS28A x C.I. 9058	-	-	11	11	150	139	21	17[2/]	13	10[3/]
C.I. 9058 x DS28A	-	-	7	7	130	123	7	5[2/]	25	24[3/]

1/ Numbers in parentheses refer to the number of seed for each cross initially planned.

2/ Testcross to C.I. 9058.

3/ Testcross to DS28A.

ceptible plant was recorded. The resistant F_2 plants from the resistant x susceptible crosses were transplanted to waxed paper cups and placed in a cold frame until they were transplanted to the field on February 4. The greenbugs were killed with a 1% parathion dust after the plants were transferred to cups.

Because of the variation observed among the plants labeled as resistant in F_2 hybrids of C.I. 9058 with Pc, Cc and Ctt, additional F_2 populations of these crosses were grown for further study. Hybrid and parent seed were planted January 18, 1958 as follows:

Variety or Cross	No. seeds	
	planted	emerged
C.I. 9058 x Pc	110	107
Pc x C.I. 9058	28	27
C.I. 9058 x Cc	141	137
C.I. 9058 x Ctt	157	151
C.I. 9058	60	57
Pc	40	40
Cc	20	20
Ctt	20	18

This test was conducted as before. Emergence was complete on January 25 and the plants were infested the same day. The living plants were labeled as highly resistant (HR) and moderately resistant (MR) at the final reading on March 3. The plants were transplanted to waxed paper cups and placed in a cold frame until March 27, when they were transplanted to the field.

Transplants were spaced at 1 foot intervals in 10-foot rows 1 foot apart. The nursery received an overhead sprinkler irrigation immediately after transplanting and 2 additional irrigations in early June. All plants were harvested and threshed separately.

F_3 lines produced from resistant F_2 plants of crosses of resistant x susceptible wheats were tested for greenbug reaction in February

and March, 1959. Table 2 shows the number of lines tested. Table 3 shows the number of lines tested from the highly resistant and moderately resistant F_2 plants of C.I. 9058 crossed with Pc, Cc and Ctt. Both F_3 tests were conducted similar to the F_2 tests. Eight lines were seeded in each flat. Fifteen seeds per row were planted for each line and parent. The material shown in Table 2 was seeded on February 11 and emerged on February 16. The plants were infested on February 16. The F_3 lines shown in Table 3 were planted February 26, emerged on March 3 and were infested the same day. The test was later discarded because of erratic response due to high March temperatures.

In January, 1958 an additional F_2 population of each of the resistant x resistant crosses was planted because of the questionable results obtained in the initial F_2 test. The tested F_2 populations originated from 5 different F_1 plants. Inasmuch as F_2 populations from 4 of the plants failed to show any susceptible plants while the F_2 from the other plant produced several susceptible plants, additional plantings of F_1 seed were made from each of the 5 plants for further study as follows:

Variety or Cross	Source of Seed	No. seed	
		sown	emerged
DS28A x C.I. 9058	57 G 1207-1	40	40
DS28A x C.I. 9058	57 G 1207-2	30	30
DS28A x C.I. 9058	57 G 1207-3	60	58
C.I. 9058 x DS28A	57 G 1208-1	10	9
C.I. 9058 x DS28A	57 G 1208-2	40	38
C.I. 9058	57 G 1236-3	50	50
DS28A	57 G 1237-1,-3	50	46
Pc	57 G 1231-1,-2,-3	80	74

The planting was tested as before except a susceptible check variety, Pc, was included in each flat. The planting was made on January 6, emerged January 11 and were infested on January 12.

Table 2.--Number of F_3 lines from crosses of resistant x susceptible wheats tested for greenbug reaction in the greenhouse insectary in February and March, 1959.

Cross	No. F_3 lines	Cross	No. F_3 lines
DS28A x Pc	37	C.I. 9058 x Pc	28
Pc X DS28A	37	Pc x C.I. 9058	47
DS28A x Cc	28	C.I. 9058 x Cc	62
Cc x DS28A	28	Cc x C.I. 9058	33
DS28A x Ctt	36	C.I. 9058 x Ctt	43
Ctt x DS28A	41	Ctt x C.I. 9058	36

Table 3.--Number of F_3 lines tested for greenbug reaction in 1959 from highly resistant and moderately resistant F_2 plants of C.I. 9058 x susceptible wheats.

Cross	No. F_3 lines from	
	Highly resistant F_2 plants	Moderately resistant F_2 plants
C.I. 9058 x Pc	23	9
Pc x C.I. 9058	3	0
C.I. 9058 x Cc	27	8
C.I. 9058 X Ctt	26	3

Plans were to grow to maturity the surviving plants from the segregating population; but because of failure to water the plants properly, only small shriveled seeds were produced. The F_3 lines were planted in a greenbug reaction test in 1959 but the test was discarded because of poor emergence.

Monosomic Tests

In the Spring of 1956 DS28A was crossed with 2 to 3 plants each of the 21 CS monosomics. The monosomic plants were used as females. Cytological examination was not made on the monosomic plants, thus it was not known for certain whether the crosses were made with a monosomic or disomic plant.

In the 1956-57 season an additional "crossing block" was planted of DS28A and the CS monosomics. The plants were seeded in flats on September 1 and left outside until October 12 when they were transplanted to 6-inch pots in the greenhouse. In December and January DS28A was crossed with from 1 to 4 of the monosomic plants. The monosomics were not analyzed cytologically. Instead, seed of each plant used was planted in the field in February and the resulting progenies were examined cytologically to determine the chromosome constitution of the parent plants. From this it was determined that DS28A had been crossed with 2n-1 plants representing each chromosome.

The spikes for cytological examination were killed by immersing them in a solution containing 6 parts ethyl alcohol, 3 parts chloroform and 1 part acetic acid. A part of the "fixed" material was stored in a 1:1 mixture of 70% alcohol and glycerol to improve spreading of the chromosomes for study. The acetocarmine smear technique, as described

by Smith (52), was used for cytological observations. In all studies except the F_2 the monosomic plants were determined by actual count of 41 chromosomes. In F_2, plants were considered monosomic if a number of microsporocytes showed a univalent at metaphase I.

F_1 plants from each of the above series of crosses were tested for greenbug reaction in November and December, 1957 on the assumption that the critical chromosome carrying the gene for greenbug resistance might be determined in the F_1 generation. The F_1's were grown in 2 separate nurseries. One nursery contained F_1 plants of which the chromosome constitution of the parents was determined. The other contained F_1 plants of which the chromosome constitution of the parents was not determined. The sequence of planting was CS (check), F_1 and DS28A (parent). Ten to twenty seeds of all entries were planted except where less than 10 seeds were available. The nurseries were seeded November 19 and infested November 29.

In the 1957-58 season F_1 plants of the entire CS monosomic series crossed with DS28A were grown in 6-inch pots for the purpose of producing F_2 seed. This nursery was seeded as a precautionary measure in case the F_1 plants tested for greenbug reaction did not reveal the critical chromosome. The F_1 plants were examined cytologically. Each spike was covered with a glassine bag prior to anthesis to prevent cross pollination.

Eighty seeds from monosomic F_1 plants involving each chromosome were planted 10 seeds per row in a greenbug reaction test on December 1, 1958. CS (check) and DS28A were seeded, respectively, in row 5 and 6 of each flat. The plants were infested shortly after emergence on December 5.

An unforeseen event occurred in the above nursery. All plants, including DS28A, were killed by the greenbug. Because of this, it was decided to accept an invitation to conduct a similar F_2 greenbug reaction test at the Kansas Agricultural Experiment Station, Manhattan, Kansas, where the greenbug resistance of DS28A was still being maintained. In this test from 2 to 48 seeds from each monosomic F_1 plant were planted along with seeds of CS and DS28A. The testing procedure was similar to that used by Painter and Peters (34) except the plants were infested immediately after emergence. The material was planted January 15 and infested January 24, 1959. On February 11 when the CS plants were near death the entire test (including greenbugs) of 6 flats was transported by automobile to the greenhouse insectary at Stillwater, Oklahoma. Shortly after this the plants became infected by a disease and practically all plants including DS28A were killed.

Another F_2 test was seeded in the greenhouse at Stillwater on February 16. Twenty-four to 27 seeds of monosomic F_1 plants representing each chromosome were planted along with seeds of CS (check) and DS28A, which were planted in row 5 and 6 of each flat, respectively. The plants were infested at emergence, February 20, with a culture of greenbugs from Kansas. The resistant F_2 plants and several plants of DS28A were transplanted to plant bands on March 4 and to 6-inch pots on March 20. The pots were placed in a cold frame. Most of the spikes on all plants were killed and fixed for cytological study.

Rate of Reproduction Tests

The rate of greenbug reproduction was studied on the varieties DS28A, C.I. 9058, Pc, Cc and Ctt and the F_1 hybrids DS28A x Pc, DS28A

x Cc, DS28A x Ctt, DS28A x C.I. 9058, Pc x C.I 9058, C.I. 9058 x Cc, and C.I. 9058 x Ctt. The Parents and F_1 of each cross were seeded in a 6-inch pot, 3 seeds per pot. Three days after emergence a single newly winged adult greenbug was placed on each plant and the plants were caged separately. Eight days later the rate of reproduction was determined on each plant by counting the number of greenbugs per plant. The test was seeded in a completely randomized design consisting of 25 pots (75 plants). The data were analyzed statistically to determine if differences existed in the reproduction rate of the greenbug among the parents and F_1 hybrids.

EXPERIMENTAL RESULTS

Genetics of Resistance in DS28A

F_1 hybrids

The greenbug reaction of parents and F_1 hybrids of DS28A crossed with Pc, Cc and Ctt are presented in Table 4. All F_1 plants were susceptible regardless of cross or direction of cross. However, the F_1's lived an average of 7.6 days longer than the average of the susceptible parents. In no case was the average life of the F_1 populations less than the susceptible parents. The variation in average days survived among parent and among F_1 populations can probably be accounted for by variable greenbug population densities among plants. The important feature shown by the F_1 data is the lack of complete dominance of susceptibility, as indicated by the F_1 plants being slightly more tolerant than the susceptible parents.

F_2 and selected F_3 hybrids

The greenbug reaction of F_2 hybrids of DS28A crossed with Pc, Cc and Ctt are shown in Table 5. The F_2 ratios (susceptible: resistant) were adjusted based on the reaction of F_3 lines produced from resistant F_2 plants. In making the adjustment the plants classed as resistant in F_2 which produced segregating or susceptible F_3 lines were reclassified as susceptible F_2 plants. The number of segragating and susceptible F_3

Table 4.--Greenbug reaction of parents and F_1 hybrids of DS28A crossed with Pc, Cc and Ctt.[1/]

Variety or cross	No. plants		Days lived	
	Susc.	Res.	Av.	Range
DS28A	0	142	--	--
Pc	48	0	12.8	11-17
Cc	47	0	14.8	11-19
Ctt	43	0	12.7	11-19
DS28A x Pc	11	0	19.9	17-29
Pc x DS28A	7	0	25.6	23-31
DS28A x Cc	20	0	19.2	11-27
Cc x DS28A	13	0	18.4	13-23
DS28A x Ctt	20	0	20.2	17-23
Ctt x DS28A	6	0	22.3	21-25

1/ See App. Tables 1, 2 and 3 for detailed data.

Table 5.--Number of greenbug susceptible and resistant plants in 6 F_2 populations of DS28A crossed with Pc, Cc and Ctt, with numbers expected under the 3:1 hypothesis, and values of chi-square.

Cross	Number of plants	Observed[1]		Expected		Value of	
		Susc.	Res.	Susc.	Res.	Chi-square	P
DS28A x Pc	117	88 (80)[2]	29 (37)	87.75	29.25	0.003	.95-.98
Pc x DS28A	155	119 (118)	36 (37)	116.25	38.75	0.270	.50-.70
DS28A x Cc	134	108 (102)	26 (32)	100.50	33.50	2.239	.10-.20
Cc x DS28A	129	102 (100)	27 (29)	96.75	32.25	1.140	.20-.30
DS28A x Ctt	137	103 (101)	34 (36)	102.75	34.25	0.002	.95-.98
Ctt x DS28A	159	123 (116)	36 (43)	119.25	39.75	0.472	.30-.50
Sum of 6 chi-squares						4.126	.50-.70

1/ Adjusted - based on the reaction of F_3 lines from resistant F_2 plants.

2/ Numbers in parentheses refer to actual F_2 data.

lines of 6 populations are as follows:

Cross	Number of lines tested		
	Total	Seg.	Susc.
DS28A x Pc	37	8	0
Pc x DS28A	37	1	0
DS28A x Cc	28	5	1
Cc x DS28A	28	2	0
DS28A x Ctt	36	2	0
Ctt x DS28A	41	6	1

In 4 populations the number of F_3 lines tested varies slightly from the number of resistant F_2 plants because of losses incurred while propagating the plants. The adjustments were made only with actual lines tested.

The chi-square probability levels obtained on adjusted F_2 data show a good fit to a 3:1 ratio. A probability of .50-.70 was obtained using the sum of chi-squares for all populations. These data indicate that the greenbug resistance of DS28A is controlled by a single recessive gene pair. The gene symbol gbgb is assigned.

Testcrosses

Table 6 shows the greenbug reaction of testcrosses to DS28A and to the respective parents Pc, Cc and Ctt. Testcrosses to DS28A segregated in a 1:1 ratio of resistant to susceptible as expected based on the F_2 data. The chi-square probability values ranged from .05-.10 to .99 for the 6 populations indicating a good fit. Further, the total population of 82 plants segregated 41 resistant and 41 susceptible. The susceptible plants were assumed to have the genotype Gbgb and the resistant plants gbgb.

In Table 7 are shown the average days survived for the susceptible parents, F_1 and susceptible testcross hybrids. F_1 and suscep-

Table 6.--Greenbug reaction of testcrosses of F_1 hybrids to the resistant and susceptible parents and chi-square values (1:1 ratio) where applicable.

Testcross	No. plants			Values of	
	Susc.	Res.	Total	Chi-square	P
To resistant parent:					
DS28A x (DS28A x Pc F_1)	12	5	17	2.882	.05-.10
DS28A x (Pc x DS28A F_1)	13	12	25	0.040	.80-.90
DS28A x (DS28A x Cc F_1)	10	14	24	0.666	.30-.50
DS28A x (Cc x DS28A F_1)	0	2	2	0.500	.30-.50
DS28A x (DS28A x Ctt F_1)	4	4	8	0.000	.99
DS28A x (Ctt x DS28A F_1)	2	4	6	0.166	.50-.70
Sum of 6 chi-squares				4.254	.50-.70
Total	41	41	82	0.000	.99
To susceptible parent:					
Pc x (DS28A x Pc F_1)	23	0	23	--	--
Pc x (Pc x DS28A F_1)	5	0	5	--	--
Cc x (DS28A x Cc F_1)	35	0	35	--	--
Cc x (Cc x DS28A F_1)	30	0	30	--	--
Ctt x (Ctt x DS28A F_1)	12	0	12	--	--
Total	105	0	105	--	--

tible testcross hybrids to DS28A lived approximately the same length of time while testcrosses to the susceptible parents were intermediate between the susceptible parent and F_1's.

Table 7.--Average number of days survived for the susceptible parents, F_1 and susceptible testcross hybrids with DS28A.

Susceptible parent	Average number of days survived for			
	Parent	F_1	Testcross to susc. parent	Testcross to DS28A
Pc	12.8	22.8	17.4	22.8
Cc	14.8	18.8	15.2	16.6
Ctt	12.7	21.3	15.5	21.7
Av.	13.4	21.0	16.0	20.3

Unselected F_3 hybrids

The greenbug reaction of 524 F_3 lines grown from unselected F_2 plants are shown in Table 8. The lines segregated 125 resistant: 263 segregating: 136 susceptible which closely fit a 1:2:1 ratio with a probability of .70-.80. This is further evidence that the resistance of DS28A is controlled by a single gene pair. The recessive nature of the gene pair was confirmed by a preponderance of susceptible plants in the segregating F_3 lines.

Table 8.--Greenbug reaction of F_3 lines of the cross DS28A x Pc (54 x 26d) and the chi-square probability level for a 1:2:1 ratio.

	Number of lines				Value of	
	Res.	Seg.	Susc.	Total	chi-square	P
Observed	125	263	136	524	0.470	.70-.80
Expected	131	262	131	524	--	--

Genetics of Resistance in C.I. 9058

F_1 hybrids

In Table 9 are presented the greenbug reaction of parents and F_1 hybrids of C.I. 9058 crossed with Pc, Cc and Ctt. F_1 plants, although killed by the greenbug, outlived the susceptible parents by an average of 13.9 days. The F_1 data thus indicate a lack of complete dominance of susceptibility.

F_2 and selected F_3 hybrids

The number of greenbug susceptible and resistant plants in 6 F_2 populations of C.I. 9058 crossed with Pc, Cc and Ctt are given in Table 10. The F_2 data were adjusted based on F_3 data as explained for the DS28A F_2 hybrids. All populations segregated within acceptable probability limits of 3 susceptible: 1 resistant except C.I. 9058 x Pc ($P < .01$). The probability levels for the other 5 populations ranged from .10-.20 to .70 and the probability for the sum of the 5 chi-square values was .30-.50. No logical explanation is offered for the behavior of the population C.I. 9058 x Pc unless it can be attributed to chance.

The unadjusted F_2 data show an excess of resistant plants but many of these segregated as F_3 lines, as shown below:

Cross	Number of lines tested		
	Total	Seg.	Susc.
C.I. 9058 x Pc	33	15	0
Pc x C.I. 9058	47	17	0
C.I. 9058 x Cc	62	24	0
Cc x C.I. 9058	33	7	0
C.I. 9058 x Ctt	45	11	0
Ctt x C.I. 9058	37	10	0

It was observed that a number of the F_2 plants classed as resistant sustained more injury than others. However, these were not classed

Table 9.--Greenbug reaction of parents and F_1 hybrids of C.I. 9058 crossed with Pc, Cc and Ctt[1/]

Variety or cross	No. plants		Days lived	
	Susc.	Res.	Av.	Range
C.I. 9058	0	132	--	--
Pc	49	0	13.9	11-17
Cc	48	0	15.3	11-23
Ctt	46	0	13.4	11-17
C.I. 9058 x Pc	13	0	25.6	17-37
Pc x C.I. 9058	12	0	21.5	15-31
C.I. 9058 x Cc	14	0	30.6	19-39
Cc x C.I. 9058	1	0	23.0	--
C.I. 9058 x Ctt	9	0	29.2	23-37
Ctt x C.I. 9058	10	0	23.0	19-29

1/ See App. Tables 4, 5 and 6 for detailed data.

Table 10.--Number of greenbug susceptible and resistant plants in 6 F_2 populations of C.I. 9058 crossed with Pc, Cc and Ctt, with numbers expected under the 3:1 hypothesis, and values of chi-square.

Cross	Number of plants	Observed[1]		Expected		Value of	
		Susc.	Res.	Susc.	Res.	Chi-square	P
C.I. 9058 x Pc	125	107 (92)[2]	18 (33)	93.75	31.25	7.491	< .01
Pc x C.I. 9058	153	123 (106)	30 (47)	114.75	38.25	2.373	.10-.20
C.I. 9058 x Cc	187	149 (125)	38 (62)	140.25	46.75	2.184	.10-.20
Cc x C.I. 9058	97	71 (64)	26 (33)	72.75	24.25	0.168	.50-.70
C.I. 9058 x Ctt	144	110 (99)	34 (45)	108.00	36.00	0.148	.70
Ctt x C.I. 9058	123	96 (86)	27 (37)	92.25	30.75	0.610	.30-.50
Sum of 6 chi-squares						12.974	.02-.05
Sum of 5 chi-squares (excluding C.I. 9058 x Pc)						5.483	.30-.50

1/ Adjusted - based on the reaction of F_3 lines from resistant F_2 plants.

2/ Numbers in parentheses refer to actual F_2 data.

as susceptible because in later stages of the test they began to recover, particularly when greenbug populations declined. It was hypothesized that these plants were heterozygous for the resistant factor, assuming of course that resistance is due to a single recessive gene pair.

To test the above hypothesis 4 additional F_2 populations were grown. The results are shown in Table 11. The F_2 plants reacted similarly to the above. The resistant plants were further classified as moderately resistant (MR) and highly resistant (HR). Under the assumption that MR plants were heterozygous they were added to the susceptible class. Under these conditions the probabilities for goodness of fit to a 3:1 ratio of susceptible:resistant were very high. The sum of the 4 chi-square values was within the .95-.98 level of probability. F_3 lines from MR and HR plants were planted in the fall of 1958 but all were killed presumably by a "new race"[8/] of the greenbug. A subsequent planting made in late February and infested with Kansas greenbugs produced erratic results because of high March temperatures and it was, therefore, discarded.

Testcrosses

The greenbug reaction of testcrosses to C.I. 9058 and to the respective parents Pc, Cc and Ctt are presented in Table 12. Three of the 4 testcrosses to C.I. 9058 segregated very closely to 1 resistant: 1 susceptible with chi-square probabilities above .70. The cross C.I. 9058 x (C.I. 9058 x Cc F_1) produced 11 susceptible to 28 resistant plants which was beyond the .01 level of probability. Why this population deviated

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8/ Whether this is a new race or a population carrying an infectuous disease has not been established. In any event, it destroyed all plants of greenbug resistant wheats.

Table 11.--Number of greenbug susceptible, moderately resistant and highly resistant F_2 plants of 4 populations of C.I. 9058 crossed with Pc, Cc and Ctt.

Cross	No. plants			Totals		Value of Chi-square (3:1 ratio)	P
	Susc.	MR[1/]	HR[2/]	Susc.+ MR	HR		
C.I. 9058 x Pc	52	28	27	80	27	0.003	.95-.98
Pc x C.I. 9058	18	3	6	21	6	0.111	.70-.80
C.I. 9058 x Cc	67	37	33	104	33	0.061	.80-.90
C.I. 9058 x Ctt	88	22	41	110	41	0.373	.50-.70
Sum of 4 chi-squares						0.548	.95-.98

1/ Moderately resistant.

2/ Highly resistant.

Table 12.--Greenbug reaction of testcrosses of F_1 hybrids to the resistant and susceptible parents and chi-square values (1:1 ratio) where applicable.

Testcross	No. Plants			Values of	
	Susc.	Res.	Total	Chi-square	P
To resistant parent:					
C.I. 9058 x (C.I. 9058 x Pc F_1)	13	15	28	0.143	.70-.80
C.I. 9058 x (C.I. 9058 x Cc F_1)	11	28	39	6.741	.01
C.I. 9058 x (C.I. 9058 x Ctt F_1)	14	14	28	0.000	.99
C.I. 9058 x (Ctt x C.I. 9058 F_1)	2	1	3	0.000	.99
Sum of 4 chi-squares				6.884	.10-.20
Total	40	58	98	3.306	.05-.10
To susceptible parent:					
Pc x (C.I. 9058 x Pc F_1)	29	0	29	--	--
Pc x (Pc x C.I. 9058 F_1)	8	0	8	--	--
Cc x (C.I. 9058 x Cc F_1)	23	0	23	--	--
Cc x (Cc x C.I. 9058 F_1)	10	0	10	--	--
Ctt x (C.I. 9058 x Ctt F_1)	18	0	18	--	--
Ctt x (Ctt x C.I. 9058 F_1)	9	0	9	--	--
Total	79	0	79	--	--

so widely from the others is not explained. However, based on the number of heterozygous "escapes" in the F_2 populations this response is not too surprising. It is noteworthy that the testcross data involving Pc closely fitted a 1:1 ratio since the adjusted F_2 data deviated considerably from a 3:1.

In Table 13 are shown the average number of days survived for the susceptible parents, F_1 and testcross hybrids. F_1 hybrids and susceptible testcrosses to C.I. 9058 lived the greatest number of days (28.1 and 25.5), while testcrosses to the susceptible parents averaged 17.0 days and Pc, Cc and Ctt averaged 14.2 days.

Table 13.--Average number of days survived for the susceptible parents, F_1 and testcross hybrids with C.I. 9058.

Susceptible Parent	Average number of days survived for			
	Parent	F_1	Testcross to susc. parent	Testcross to C.I. 9058
Pc	13.9	23.8	14.5	23.6
Cc	15.3	30.1	19.4	26.8
Ctt	13.4	30.6	17.1	26.1
Av.	14.2	28.1	17.0	25.5

Hybrids of DS28A and C.I. 9058

The greenbug reaction of DS28A and C.I. 9058 and their F_1, F_2 and testcross hybrids are presented in Table 14. The reaction of a susceptible variety, Pc, is also given. The F_1 and testcross hybrids were resistant regardless of direction of cross. Four F_2 progenies from 5 F_1 plants were completely resistant while progeny from the other F_1 plant segregated approximately 11 resistant: 5 susceptible. This is given further consideration in the discussion.

Table 14.--Greenbug reaction of Pc, DS28A, C.I. 9058 and F_1, F_2 and test-cross hybrids of DS28A x C.I. 9058 1/

Variety or cross	No. plants		
	Res.	Susc.	Total
Pc	0	74	74
DS28A	96	0	96
C.I. 9058	93	0	93
DS28A x C.I. 9058 F_1	24	0	24
C.I. 9058 x DS28A F_1	8	0	8
DS28A x (DS28A x C.I. 9058 F_1)	10	0	10
DS28A x (C.I. 9058 x DS28A F_1)	24	0	24
C.I. 9058 x (DS28A x C.I. 9058 F_1)	17	0	17
C.I. 9058 x (C.I. 9058 x DS28A F_1)	5	0	5
DS28A x C.I. 9058 F_2:			
57 G 1207-1 2/	71	33	104
57 G 1207-2	77	0	77
57 G 1207-3	86	0	86
C.I. 9058 x DS28A F_2:			
57 G 1208-1	64	0	64
57 G 1208-2	106	0	106

1/ Data combined from tests seeded on November 19, 1957 and January 6, 1958.

2/ Source of individual F_1 plant.

Monosomic Analysis

F_1 hybrids

The average number of days lived for CS and F_1 hybrids of the 21 CS monosomics and DS28A are shown in Table 15. All F_1 families lived longer than the CS check but no one family was sufficiently more resistant than another to aid in determining the critical chromosome carrying the gene for greenbug resistance. Additional F_1 data from crosses in which the chromosome number of the CS parent was not known are shown in Table 16. The CS plants used were descendants from 2n-1 plants and thus some crosses were probably made with disomic CS plants. The data in Tables 15 and 16 show similar results.

F_2 hybrids

The number of greenbug susceptible and resistant plants and chromosome constitution of resistant plants of progeny of monosomic F_1 plants in the F_2 generation are shown in Table 17. A good fit to a ratio of 3 susceptible plants to 1 resistant plant was obtained for all chromosome families. A probability of .99 was obtained for the sum of chi-squares for the 21 F_2 families. A cytological analysis showed no family to have all disomic resistant plants. Four families, X, XI, XIII and XXI, produced 50% disomic resistant plants but none exceeded this. Elucidation of this phase of the study is given in the discussion.

Rate of Greenbug Reproduction on Resistant and Susceptible Parents and F_1 Hybrids

The number of young produced during an 8-day period from 1 newly winged adult greenbug on individual plants of parents and F_1 hybrids of resistant and susceptible wheats are shown in Table 18. An analysis of

Table 15.--Average number of days lived following a greenbug infestation for CS and F_1 hybrids of DS28A crossed with the 21 CS monosomic plants.[1]

Parent, check or F_1 hybrid	No. plants tested	Av. No. days lived
DS28A (Parent)	279	--
CS (check)	288	13.7
I x DS28A	10	20.9
II x DS28A	20	21.5
III x DS28A	9	20.8
IV x DS28A	18	19.2
V x DS28A	9	17.8
VI x DS28A	10	16.1
VII x DS28A	10	14.5
VIII x DS28A	7	14.9
IX x DS28A	15	20.1
X x DS28A	10	19.1
XI x DS28A	8	18.8
XII x DS28A	10	18.6
XIII x DS28A	20	19.8
XIV x DS28A	20	15.6
XV x DS28A	16	15.3
XVI x DS28A	9	16.8
XVII x DS28A	10	14.3
XVIII x DS28A	8	20.0
XIX x DS28A	20	15.0
XX x DS28A	17	20.7
XXI x DS28A	9	19.0
Av. F_1 plants	--	18.0

Table 16.--Average number of days lived following a greenbug infestation for CS and F_1 hybrids of DS28A and the 21 CS "monosomics".[1/]

Parent, check or F_1 hybrid	No. plants tested	Av. No. days lived	Parent, check or F_1 hybrid	No. plants tested	Av. No. days lived
DS28A (Parent)	196	--	X x DS28A	10	17.7
CS (check)	214	14.5	X x DS28A	10	16.3
I x DS28A[2/]	9	22.1	XI x DS28A	9	15.6
I x DS28A	10	18.4	XI x DS28A	10	15.8
II x DS28A	10	22.2	XII x DS28A	10	16.3
II x DS28A	2	23.5	XII x DS28A	10	18.7
III x DS28A	10	22.6	XIII x DS28A	10	18.0
III x DS28A	9	18.8	XIII x DS28A	10	18.6
IV x DS28A	10	20.5	XIV x DS28A	9	18.7
IV x DS28A	10	21.3	XIV x DS28A	10	19.6
IV x DS28A	10	21.5	XV x DS28A	9	18.6
V x DS28A	10	16.3	XV x DS28A	9	17.8
V x DS28A	10	17.0	XVI x DS28A	9	17.3
VI x DS28A	10	20.2	XVI x DS28A	10	19.8
VI x DS28A	10	15.3	XVII x DS28A	4	20.5
VI x DS28A	10	16.4	XVII x DS28A	6	21.8
VII x DS28A	8	13.4	XVIII x DS28A	10	16.8
VII x DS28A	10	13.7	XIX x DS28A	9	14.9
VII x DS28A	10	17.4	XIX x DS28A	10	17.5
VIII x DS28A	10	18.0	XX x DS28A	7	22.4
VIII x DS28A	2	17.0	XX x DS28A	10	19.9
IX x DS28A	10	19.5	XXI x DS28A	10	19.6
IX x DS28A	10	18.1	XXI x DS28A	9	17.2
Av. F_1 plants				--	18.5

1/ CS plants crossed with DS28A are descendants from 2n-1 plants but were not analyzed cytologically to determine chromosome number.

2/ Each entry represents a cross with a different "monosomic" plant.

Table 17.--Number of greenbug susceptible and resistant plants and chromosome constitution of resistant plants from 21 F_2 populations of monosomic F_1 plants of CS x DS28A.

Chromosome involved	No. plants			Value of		No. res. plants		
	Total	Susc.	Res.	Chi-square	P	Analyzed	Monosome	Disome
				(3:1 ratio)				
I	24	19	5	0.222	.50-.70	4	4	0
II	23	17	6	0.015	.90-.95	5	3	2
III	24	15	9	2.000	.10-.20	8	4 1/	2
IV	23	18	5	0.130	.70-.80	4	4	0
V	24	18	6	0.000	.99	6	4	2
VI	24	20	4	0.889	.30-.50	4	4	0
VII	26	18	8	0.462	.30-.50	7	4	3
VIII	19	14	5	0.018	.80-.90	4	3	1 2/
IX	22	18	4	0.546	.30-.50	3	3	0
X	22	18	4	0.546	.30-.50	4	2	2
XI	24	18	6	0.000	.99	6	3	3
XII	23	17	6	0.015	.90-.95	6	6	0
XIII	23	17	6	0.015	.90-.95	6	3	3
XIV	24	18	6	0.000	.99	4	3	1
XV	24	17	7	0.222	.50-.70	7	6 3/	0
XVI	24	18	6	0.000	.99	5	3	2
XVII	23	17	6	0.015	.90-.95	6	5	1
XVIII	24	18	6	0.000	.99	6	5	1
XIX	24	18	6	0.000	.99	5	4	1
XX	24	18	6	0.000	.99	4	4	0
XXI	23	19	4	0.710	.70-.80	4	2	2
Sum of 21 chi-squares				5.850	.99			
Total	491	370	121	0.033	.80-.90	108	79	26

1/ In addition 1 nullisomic and 1 monotelocentric plant.

2/ Plant had $20_{II} + 1_I$ + 1 isochromosome.

3/ In addition 1 nullisomic plant.

Table 18.--Number of young produced during an 8-day period from 1 newly winged adult greenbug on individual plants of parents and F_1 hybrids of resistant and susceptible wheats.[1/]

Variety or cross	Plant No.												
	1	2	3	4	5	6	7	8	9	10	11	12	Av.
DS28A	10	13	10	11	12	8	6	13	5	12	2	8	9.2
C.I. 9058	12	8	5	11	13	9	9	12	8	13	10	12	10.2
Pc	7	14	15	18	13	20	15	-	-	-	-	-	14.6
Cc	15	11	13	-	-	-	-	-	-	-	-	-	13.0
Ctt	14	11	14	15	13	11	7	11	6	13	-	-	11.5
DS28A x C.I. 9058	13	6	13	-	-	-	-	-	-	-	-	-	10.7
DS28A x Pc	11	14	9	12	-	-	-	-	-	-	-	-	11.5
DS28A x Cc	10	13	-	-	-	-	-	-	-	-	-	-	11.5
DS28A x Ctt	6	14	13	10	-	-	-	-	-	-	-	-	10.8
Pc x C.I. 9058	12	13	6	-	-	-	-	-	-	-	-	-	10.3
C.I. 9058 x Cc	7	-	-	-	-	-	-	-	-	-	-	-	7.0
C.I. 9058 x Ctt	8	9	14	12	-	-	-	-	-	-	-	-	10.8

1/ An analysis of variance showed no significant difference among entries.

variance of the data, from a completely randomized design, showed no significant difference among parents and hybrids with respect to number of young produced. From these data it appears that DS28A and C.I. 9058 exhibit a tolerance type resistance since the plants failed to reduce the reproductive capacity of the greenbug. Further, random observations made on F_2 and F_3 testcross plants revealed no apparent difference in greenbug population densities.

DISCUSSION AND CONCLUSIONS

Testing for Greenbug Resistance

Screening wheat varieties and hybrids for resistance to the greenbug is not a simple matter and a number of testing methods have been proposed (10, 13, 34). Painter and Peters (34) made a general statement that an acceptable screening method must provide for a study of many entries with a minimum of space and time, and give a reasonably accurate classification of levels of resistance with reproductibility of results. The type and level of resistance will usually dictate to some degree the method of testing. Where a high level of resistance is involved, such as that of DS28A and C.I. 9058, rigorous testing can be practiced. Both DS28A and C.I. 9058 appear to exhibit a tolerance type resistance, i.e., they can support a heavy infestation of greenbugs without apparent injury. However, some recent evidence presented by Wood (58) shows that if greenbugs are propagated for several generations on DS28A the rate of fecundity is appreciably lowered. Possibly the resistance in DS28A and C.I. 9058 may be a combination of tolerance and antibiosis.

Older susceptible wheat plants often will tolerate heavy populations for a short period, particularly if the plants are vigorous and healthy. For this reason it would seem necessary to screen for resistance while the plants are quite young. In the 1958-59 season at Stillwater all plants were infested at emergence or within 24 hours following emergence with seemingly good results. In the 1957-58 season

the F_1, F_2 and testcross populations were 5 days of age and in the 2-leaf stage when infested. This delay in infestation may partially account for the escapes that were detected the following season (see pages 32 and 35).

Under caged conditions DS28A and C.I. 9058 are usually killed by the greenbug, presumably because of the tremendous population build-up that occurs under such conditions. However, the time required to kill DS28A and C.I. 9058 is greater than for susceptible varieties. Daniels and Porter (13) used cages to cover flats during the screening period and rated the hybrids and parents as to amount of damage sustained when the majority of the susceptible parent plants were killed. Their technique gave results similar to those obtained at Stillwater where cages were not used and a different method of classification was employed. In the present study a plant was considered resistant if it was growing vigorously 35 to 45 days after infestation. Painter and Peters (34) conducted tests in a basement insectary under fluorescent lights. Their results agreed closely with those mentioned above. They graded plants as to degree of injury after approximately 2 weeks of infestation or when the maximum differences were evident between resistant and susceptible checks. Each of the above methods is probably satisfactory for screening for resistance but none is infallible. Progeny testing is the best possible safeguard against misclassification or escapes, and even this is not infallible.

Genetic Studies

A single recessive gene pair, gbgb, appears to separate the resistant varieties, DS28A and C.I. 9058, from the susceptible varieties,

Pc, Cc and Ctt. Painter and Peters (34) and Daniels and Porter (13) also report that resistance in DS28A is governed by a single gene pair, although the latter authors suspected the presence of modifying genes.

Susceptibility is not completely dominant as was shown by the F_1 hybrids having a slightly greater tolerance than the susceptible parents. F_1 hybrids involving DS28A outlived the susceptible parents by 7.6 days and those involving C.I. 9058 outlived susceptible parents by 13.9 days. The F_1 plants of C.I. 9058 crossed with Pc, Cc and Ctt were more vigorous and lived 7.1 days longer than those involving DS28A. This is partially attributed to the rapid initial spring growth type, characteristic of C.I. 9058, in the F_1 plants. Also, the infestation was slightly lower on the C.I. 9058 hybrids as attested by the susceptible parents living an average of 0.8 days longer than the same varieties among the DS28A hybrids.

That there is a lack of complete dominance of susceptibility is further supported by results obtained by Daniels and Porter (13). They found the F_1 plants to be intermediate between the parents. Painter and Peters (34), however, stated that in 2 respects, aphid fecundity and production of chlorosis, the F_1 plants showed a reaction more like the resistant then the susceptible parents. The statement regarding production of chlorosis agrees with observations made in this study. When susceptible parent plants were near death the amount of chlorosis in most F_1 plants was more nearly like that of the resistant parent. Nevertheless, a short time later the F_1 plants developed severe chlorosis and died. Aphid fecundity studies reported herein revealed no significant difference among parent and F_1 plants. It is noteworthy that greenbug resistance is recessive in wheat and dominant in barley (27).

The F_2 data of DS28A crossed with Pc, Cc and Ctt, adjusted on the basis of the F_3 reaction of resistant F_2 plants, fitted very closely a 3:1 ratio of susceptible to resistant plants. Using the sum of chi-squares for all populations a probability of .50-.70 was obtained for goodness of fit. Similar results were obtained when C.I. 9058 was crossed with Pc, Cc and Ctt. However, in the C.I. 9058 populations considerably more heterozygous F_2 plants were classed as resistant than in populations involving DS28A. The same explanation as offered for the greater tolerance of F_1 plants of C.I. 9058 over those of DS28A is offered here. Theoretically, the heterozygous F_2 plants should be of the same genetic constitution, Gbgb, as the F_1 plants.

Unselected F_3 hybrids of DS28A x Pc and testcrosses of F_1's of DS28A and C.I. 9058 to resistant and susceptible parents offer further evidence that one recessive gene pair controls resistance. The 524 F_3 lines segregated very near to a 1:2:1 ratio of susceptible: segregating: resistant. Testcrosses to the susceptible parents proved to be susceptible in all populations tested. Testcrosses of DS28A F_1 hybrids to DS28A segregated 41 susceptible to 41 resistant or an exact fit to a 1:1 ratio. Testcrosses of C.I. 9058 F_1 hybrids to C.I. 9058 segregated 40 susceptible to 58 resistant with a probability for goodness of fit to a 1:1 ratio of .10-.20 for the sum of chi-squares.

The number of days survival for susceptible plants in testcrosses as compared to the susceptible parents and F_1's agreed with expectations. Susceptible plants in testcrosses to DS28A lived an average of 20.3 days compared to 21.0 days for the F_1's (Table 7). These similar averages would be expected assuming both groups of plants had the genotype Gbgb. Theoretically then, testcrosses to the susceptible parent should be of

the genotypes GbGb and Gbgb in a 1:1 ratio and thus the average life should lie between that of the F_1 and the susceptible parents. To support this theory it is shown that these testcrosses lived an average of 16.0 days compared to 13.4 days for Pc, Cc and Ctt and 21.0 days for the F_1 plants. The same general response can be noted for testcrosses involving C.I. 9058 (Table 13).

There appeared to be no evidence for any degree of cytoplasmic inheritance in crosses of resistant and susceptible varieties. Responses from reciprocal crosses were apparently not different.

That DS28A carries the same gene pair for resistance as C.I. 9058 is evident from similar reactions obtained from F_1, F_2, F_3 and testcross hybrids of the 2 varieties when crossed with the same susceptible varieties and from crosses with each other. Hybrids of DS28A x C.I. 9058 showed no susceptible plants in F_1 and testcrosses to both parents. Four F_2 progenies from 5 F_1 plants were completely resistant while progeny from the other F_1 plant segregated approximately 11 resistant: 5 susceptible. Notes recorded for the F_1 plants in the 1956-57 season indicate all were actual crosses. This should preclude "selfing" as being a factor in the populations that failed to segregate. No reason is offered to explain the segregating population. It is difficult to visualize an outcross because of the odd ratio obtained. An outcross would undoubtedly have involved a susceptible variety since no other greenbug resistant wheats were grown in the same greenhouse during flowering time. Such as outcross would be expected to segregate 3 susceptible: 1 resistant on the basis of these studies.

Monosomic Analysis

Failure to locate the chromosome carrying greenbug resistance was a disturbing feature of this study. Initially the task appeared simple. F_1 progeny from a susceptible monosomic plant fertilized with normal pollen from DS28A would contain monosomic and disomic plants in a ratio of 3:1 (46). Monosomic F_1 progeny in the critical chromosome family should contain only the recessive resistant gene from DS28A without the incompletely-dominant allele for susceptibility of CS. Had a single gene dose been effective in causing resistance, the critical family would thus have segregated approximately 3 resistant: 1 susceptible or 3 monosomic to 1 disomic. Since all F_1 progenies were susceptible the resistance gene of DS28A is assumed to be a hemizygous-ineffective, i.e., a single gene dose is not sufficient to cause resistance. Sears (47) reported a similar case in which a single dose of the sphaerococcum gene was ineffective.

Each of the 21 F_2 populations from monosomic F_1 plants segregated very closely to a 3:1 ratio of resistant to susceptible plants. According to Sears (48) a hemizygous-ineffective recessive gene may be located by the study of F_2 populations but not by observation of F_2 ratios. The genes in the critical F_2 family should express themsleves only in the disomic segregates. Since about 1/4 of each population is disomic the critical F_2 should not differ significantly from other F_2 families in proportion of resistant segregates. In addition, resistant plants from non-critical F_2 families should contain approximately 3/4 monosomic and 1/4 disomic plants; however, only 1/4 of the resistant plants should be disomic.

The cytological data in Table 17 show no family to have all disomic

resistant plants. Four families, X, XI, XIII and XXI had as many as 50% disomics. With such small populations (4 to 6 plants for these families) a 1:1 ratio of monosomic to disomic plants may frequently occur when a 3:1 ratio is expected. No plausible explanation is offered to explain why all resistant plants from the critical family were not disomic unless there were hemizygous monosomic "escapes" in the critical F_2. This could occur but it seems unlikely since in the F_2 of DS28A crossed with Pc, Cc and Ctt only 10.4% of the plants were misclassified. However, the monosomic F_2 test was conducted in a different year and environmental conditions may have permitted more escapes. In conducting the F_2 monosomic test the resistant plants appeared to be highly resistant and the susceptible plants were dead at the conclusion of the test. No moderately resistant types were observed.

Although the critical chromosome was not identified in this study, some information regarding gene action was realized. Further, the avenues of approach to identify the chromosome carrying the gene for greenbug resistance are fewer in number. The next approach suggested is to either repeat the above F_2 study using larger populations or choose 4 or 5 disomic plants from an unselected F_2 for each of the 21 chromosomes and note the segregation in the F_3. Progeny from the critical F_2 family should be resistant. Sears (48) proposed the latter method for studies in which the F_2 are difficult to classify.

Breeding for Greenbug Resistance in Winter Wheat

Incorporating greenbug resistance from DS28A and C.I. 9058 into adapted winter wheats should present little difficulty, providing adequate facilities are available to screen for resistance. Breeding work

underway at Stillwater has resulted in the production of apparently homozygous resistant F_5 lines from the cross DS28A x Pc that are reasonably good agronomically. Both DS28A and C.I. 9058 are poorly adapted types. In addition to having a spring habit of growth they appear ultrasusceptible to leaf rust and have a very weak straw. From limited field observations these undesirable characters are evidently not linked or at least not closely linked with the gene for greenbug resistance.

In breeding for resistance it seems most desirable to screen F_2 populations and subsequently grow resistant plants to maturity. To eliminate escapes of heterozygous plants, F_3 lines from resistant F_2 plants should be tested. Concurrently, with the F_3 screening test, field plantings of F_3 lines can be made. This procedure would eliminate 3/4 of the F_2 population at first screening. An alternate procedure would be to grow F_2 space plants and test for greenbug resistance as F_3 lines. This method should require only one greenbug test since the genotypes GbGb and Gbgb should be identifiable. However, considerably more greenhouse space is required for this procedure. Also, if a concurrent field planting of F_3 is desired 4 times more material will need to be handled than for the previous method. One advantage here is that selection can be practiced within segregating (Gbgb) F_3 lines.

Of course, other methods, including the backcross method, are not precluded in breeding for greenbug resistance. The 2 methods outlined above merely provide for a rapid production of homozygous resistant lines.

Breeding for greenbug resistance may become more difficult once greenbug resistant varieties are in commercial production. What appears to be greenbug biotypes that can destroy DS28A and C.I. 9058 have already

made their appearance in greenhouse cultures. Practically nothing is known regarding the number and distribution of greenbug biotypes under field conditions. Dahms (7) collected greenbugs from wheat in southwestern Oklahoma and from oats in eastern Mississippi and found no differences between them as measured by the response of 15 varieties of small grains. Cartier and Painter (4) have reported biotypes in the species of corn leaf aphid that attack sorghums. Therefore, it is important that the wheat breeder continue to search for new and better sources of resistant germ plasm to be better prepared for what seems to be inevitable.

SUMMARY

The genetics of greenbug resistance in common wheat was studied during the period 1954-1959. The study included a genetic analysis both by conventional and by monosomic methods.

F_1, F_2, F_3 and testcross hybrids of the greenbug resistant varieties DS28A and C.I. 9058 crossed with the susceptible varieties Pc, Cc and Ctt and with each other revealed that resistance is conditioned by a single recessive gene pair, common to both resistant strains. The gene symbol gbgb was assigned.

F_1 hybrids of resistant x susceptible wheats showed susceptibility to be incompletely dominant. F_1 hybrids of DS28A and C.I. 9058 crossed with susceptible wheats lived 7.6 and 13.9 days longer, respectively, than the average of the susceptible varieties. F_2 data, adjusted on the basis of F_3 reaction, gave a good fit to a 3:1 ratio of susceptible: resistant. Reciprocal crosses responded similarly indicating an absence of cytoplasmic influence on the hereditary mechanism. Testcrosses to the resistant parents segregated approximately 1 susceptible: 1 resistant while testcrosses to the susceptible parents were susceptible.

F_1 and F_2 data of DS28A crossed with the entire monosomic series of CS failed to reveal the chromosome carrying the gene for greenbug resistance. Since no monosomic F_1 plants were resistant, the resistance gene is assumed to be hemizygous-ineffective. Why F_2 monosomic data did not disclose the critical chromosome could not be adequately explained.

It was concluded from the data presented herein and from observa-

tions of breeding nurseries that greenbug resistance can be quickly transferred from DS28A and C.I. 9058 to other strains of wheat.

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A P P E N D I X

APPENDIX

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App. Table 1.--Distribution frequency of susceptible parent and susceptible hybrids of DS28A x Pc according to number of days lived following a greenbug infestation.

Variety or cross	Total number of plants in classes[1/]																No. of plants		
	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39		Sus.	Res.	Total
DS28A	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--		0	48	48
Pc	20	16	9	3	--	--	--	--	--	--	--	--	--	--	--		48	0	48
DS28A x Pc F_1	--	--	--	5	2	2	--	1	--	1	--	--	--	--	--		11	0	11
Pc x DS28A F_1	--	--	--	--	--	--	1	5	--	--	1	--	--	--	--		7	0	7
DS28A x (DS28A x Pc F_1)	--	--	2	2	--	3	--	1	--	--	1	--	--	3	--		12	5	17
DS28A x (Pc x DS28A F_1)	--	--	4	3	1	1	--	1	1	--	--	--	--	2	--		13	12	25
Pc x (DS28A x Pc F_1)	1	2	2	10	4	1	2	--	--	--	--	--	--	1	--		23	0	23
Pc x (Pc x DS28A F_1)	2	--	2	1	--	--	--	--	--	--	--	--	--	--	--		5	0	5
DS28A x Pc F_2	5	12	11	21	11	7	2	3	3	1	2	--	--	2	--		80	37	117
Pc x DS28A F_2	16	21	21	12	12	15	2	1	6	2	3	--	--	7	--		118	37	155

1/ Classes are designated by upper limits in days lived and are inclusive.

App. Table 2.--Distribution frequency of susceptible parent and susceptible hybrids of DS28A x Cc according to number of days lived following a greenbug infestation.

Variety or cross	Total number of plants in classes[1/]															No. of plants		
	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	Sus.	Res.	Total
DS28A	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0	47	47
Cc	4	11	19	11	2	--	--	--	--	--	--	--	--	--	--	47	0	47
DS28A x Cc F_1	1	--	1	4	6	6	1	--	1	--	--	--	--	--	--	20	0	20
Cc x DS28A F_1	--	1	3	3	--	4	2	--	--	--	--	--	--	--	--	13	0	13
DS28A x (DS28A x Cc F_1)	1	2	2	1	1	3	--	--	--	--	--	--	--	--	--	10	14	24
DS28A x (Cc x DS28A F_1)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0	2	2
Cc x (DS28A x Cc F_1)	9	9	8	3	3	1	--	1	--	--	--	--	--	--	1	35	0	35
Cc x (Cc x DS28A F_1)	10	7	3	3	--	3	1	1	2	--	--	--	--	--	--	30	0	30
DS28A x Cc F_2	--	7	14	17	19	8	7	5	9	2	8	--	5	1	--	102	32	134
Cc x DS28A F_2	3	9	20	6	13	12	7	13	4	1	2	--	1	9	--	100	29	129

1/ Classes are designated by upper limits in days lived and are inclusive.

App. Table 3.--Distribution frequency of susceptible parent and susceptible hybrids of DS28A x Ctt according to number of days lived following a greenbug infestation.

Variety or cross	Total number of plants in classes[1/]															No. of plants		
	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	Sus.	Res.	Total
DS28A	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0	47	47
Ctt	20	15	4	3	1	--	--	--	--	--	--	--	--	--	--	43	0	43
DS28A x Ctt F_1	--	--	--	4	4	8	4	--	--	--	--	--	--	--	--	20	0	20
Ctt x DS28A F_1	--	--	--	--	--	3	2	1	--	--	--	--	--	--	--	6	0	6
DS28A x (DS28A x Ctt F_1)	--	--	--	1	1	2	--	--	--	--	--	--	--	--	--	4	4	8
DS28A x (Ctt x DS28A F_1)	--	--	1	--	--	--	--	--	--	--	--	--	--	1	--	2	4	6
Ctt x (Ctt x DS28A F_1)	--	5	4	1	1	--	--	1	--	--	--	--	--	--	--	12	0	12
DS28A x Ctt F_2	14	14	16	13	7	7	13	8	3	1	--	1	--	4	--	101	36	137
Ctt x DS28A F_2	22	27	16	10	7	5	9	4	8	--	2	1	--	5	--	116	43	159

1/ Classes are designated by upper limits in days lived and are inclusive.

App. Table 4.--Distribution frequency of susceptible parent and susceptible hybrids of C.I. 9058 x Pc according to number of days lived following a greenbug infestation.

Variety or cross	Total number of plants in classes[1/]															No. of plants		
	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	Sus.	Res.	Total
C.I. 9058	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0	49	49
Pc	5	23	15	6	--	--	--	--	--	--	--	--	--	--	--	49	0	49
C.I. 9058 x Pc F_1	--	--	--	1	--	4	2	3	--	--	--	--	--	3	--	13	0	13
Pc x C.I. 9058 F_1	--	--	3	--	2	1	4	--	--	--	2	--	--	--	--	12	0	12
C.I. 9058 x (C.I. 9058 x Pc F_1)	--	1	--	1	1	5	1	--	1	--	--	1	1	1	--	13	15	28
Pc x (C.I. 9058 x Pc F_1)	3	10	10	3	1	1	--	--	1	--	--	--	--	--	--	29	0	29
Pc x (Pc x C.I. 9058 F_1)	2	4	2	--	--	--	--	--	--	--	--	--	--	--	--	8	0	8
C.I. 9058 x Pc F_2	1	16	11	18	3	11	5	3	4	1	2	2	2	13	--	92	33	125
Pc x C.I. 9058 F_2	1	15	18	18	9	9	8	8	4	1	5	2	--	7	1	106	47	153

1/ Classes are designated by upper limits in days lived and are inclusive.

App. Table 5.--Distribution frequency of susceptible parent and susceptible hybrids of C.I. 9058 x Cc according to number of days lived following a greenbug infestation.

Variety or cross	Total number of plants in classes[1/]															No. of plants		
	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	Sus.	Res.	Total
C.I. 9058	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0	45	45
Cc	2	14	13	15	3	--	1	--	--	--	--	--	--	--	--	48	0	48
C.I. 9058 x Cc F_1	--	--	--	--	1	--	2	2	--	3	--	--	--	4	2	14	0	14
Cc x C.I. 9058 F_1	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	1	0	1
C.I. 9058 x (C.I. 9058 x Cc F_1)	--	--	--	--	--	2	--	3	1	--	--	--	--	4	1	11	28	39
Cc x (C.I. 9058 x Cc F_1)	1	5	2	3	1	4	1	2	1	2	--	--	1	--	--	23	0	23
Cc x (Cc x C.I. 9058 F_1)	--	--	2	3	--	4	1	--	--	--	--	--	--	--	--	10	0	10
C.I. 9508 x Cc F_2	1	16	13	14	15	10	11	5	5	2	5	1	2	21	4	125	62	187
Cc x C.I. 9058 F_2	--	6	4	9	--	10	7	7	3	2	5	--	--	7	4	64	33	97

1/ Classes are designated by upper limits in days lived and are inclusive.

App. Table 6.--Distribution frequency of susceptible parent and susceptible hybrids of C.I. 9058 x Ctt according to number of days lived following a greenbug infestation.

Variety or cross	Total number of plants in classes[1/]															No. of plants		
	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	Sus.	Res.	Total
C.I. 9058	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0	38	38
Ctt	5	29	9	3	--	--	--	--	--	--	--	--	--	--	--	46	0	46
C.I. 9058 x Ctt F_1	--	--	--	--	--	--	1	2	1	2	1	--	--	2	--	9	0	9
Ctt x C.I. 9058 F_1	--	--	--	--	2	2	4	--	--	2	--	--	--	--	--	10	0	10
C.I. 9058 x (C.I. 9058 x Ctt F_1)-	1	--	--	--	2	1	2	4	--	--	--	--	3	1		14	14	28
C.I. 9058 x (Ctt x C.I. 9058 F_1)-	--	--	--	--	2	--	--	--	--	--	--	--	--	--		2	1	3
Ctt x (C.I. 9058 x Ctt F_1)	--	4	6	3	4	1	--	--	--	--	--	--	--	--	--	18	0	18
Ctt x (Ctt x C.I. 9058 F_1)	--	1	2	2	2	1	--	--	--	--	--	--	--	1	--	9	0	9
C.I. 9058 x Ctt F_2	2	17	15	9	12	3	10	3	3	2	2	--	3	13	5	99	45	144
Ctt x C.I. 9058 F_2	5	13	16	17	6	5	4	3	4	1	1	--	--	6	5	86	37	123

1/ Classes are designated by upper limits in days lived and are inclusive.

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