GREENBUG RESISTANCE IN WHEAT GERMPLASM

LINES CI 17881-17886

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INTRODUCTION

The three parts of this dissertation are separate and complete manuscripts. Part I appears in Crop Science 25:686-688. Part II has been submitted to Euphytica for publication. Part III is to be submitted to the Journal of Economic Entomology.

PART I

BIOTYPE E GREENBUG RESISTANCE IN WHEAT STREAK MOSAIC VIRUS-RESISTANT WHEAT GERMPLASM LINES

BIOTYPE E GREENBUG RESISTANCE IN WHEAT STREAK MOSAIC VIRUS-RESISTANT WHEAT GERMPLASM LINES

ABSTRACT

A new source of biotype E greenbug [Schizaphis graminum (Rondani)] resistance was identified in greenhouse screening tests from a group (CI 17881-17886) of wheat (Triticum aestivum L.) germplasm lines previously released as resistant to wheat streak mosaic virus (WSMV). The germplasm release statement from the South Dakota Agric. Exp. Stn. identified the pedigree of these lines as CI 15092/T. speltoides// 'Fletcher' (CI 13985) /3/ 5*'Centurk' (CI 15075). Our objective was to determine the parental source of the greenbug resistance and to quantify the components of resistance. The particular T. speltoides accession used in the cross was unknown; however it appeared to be the donor of the resistance because the other parents were susceptible to biotype E in greenhouse tests. CI 17882 and CI 17885 exhibited the highest levels of resistance. The resistance in these lines is a new source that can be exploited in the development of greenbug-resistant wheat germplasm. New sources of greenbug resistance are needed because of the periodic occurrence of new biotypes.

Additional index words: *Schizaphis graminum* (Rondani), Wheat streak mosaic virus, *Agropyron intermedium* (Host) Beauv., *Triticum aestivum* L. em Thell, *T. speltoides* (Tausch) Gren. ex Richter.

INTRODUCTION

New biotypes of the greenbug [Schizaphis graminum (Rondani)] have been a great hindrance to the development of greenbug-resistant wheat (Triticum aestivum (L.) cultivars. 'Dickinson' selection 28A (DS28A, CI 13833) wheat provided resistance to biotype A, but not to biotypes B, C, and E which subsequently developed. Biotype B was noted in 1958 (Wood, 1961) and predominated in the southern Great Plains until it was replaced by biotype C. Biotype C attacks grain sorghum (Sorghum bicolor L. Moench) as well as small grains and was discovered in 1968 (Harvey and Hackerott, 1969). 'Amigo,' CI 17609, a wheat germplasm line released by Sebesta and Wood (1978), has a single dominant resistance gene derived from rye (Secale cereale L. cv. Insave FA) and confers resistance to biotypes A, B, and C. The latest greenbug biotype, designated as "E", was discovered in 1980 when Amigo and advanced breeding lines having Amigo-derived resistance showed susceptible reactions to greenbugs collected near Bushland, TX (Porter et al., 1982).

Prior to the discovery of biotype E, an amphiploid of T. turgidum/T. tauschii ('Largo', CI 17895) reported by Joppa et al. (1980), and amphiploids of T. durum/T. tauschii reported by Harvey et al. (1980) were shown to have T. tauschii-derived biotype C resistance. Subsequent testing has shown that both of these sources also provide resistance to biotype E (Porter et al., 1982; Martin et al., 1982).

Because of the greenbug's history of biotypes, it is important that additional sources of resistance to virulent biotypes are identified.

Since the discovery of biotype E, many wheat lines and relatives have been evaluated for greenbug resistance at Stillwater, OK, by USDA-ARS and Oklahoma State University researchers. Resistance to biotype E was identified recently in a group of wheat germplasm lines that were previously shown to have resistance to wheat streak mosaic virus (WSMV) (Wells et al., 1982). These WSMV-resistant wheat lines (CI 17881-17886), all from the cross CI 15092/T. speltoides//'Fletcher' (CI 13985)/3/5* Centurk' (CI 15075), were released by Wells et al. in 1982. The present work reports tests conducted to determine the parental source of the greenbug resistance and to determine the components (antibiosis, tolerance, nonpreference) and levels of greenbug resistance in these lines. These resistance components are discussed in detail by Horber (1980) and Painter (1951).

MATERIALS AND METHODS

Many wheat lines have been evaluated in the greenhouse using the methods described by Starks and Burton (1977) in an attempt to identify new sources of greenbug resistance. It was during this routine testing that greenbug resistance was discovered in the WSMV-resistant germplasm lines. Four of the lines (CI 17882-17885) were classified as resistant, and two (CI 17881 and CI 17886) were classified as susceptible to biotype E. To determine the parental source of resistance, from 38 to 47 plants each of CI 15092, Fletcher, and Centurk were tested along with CI 17882 for their reaction to biotype E greenbugs in greenhouse tests.

Three tests using biotype E were then conducted to quantify the components of resistance. Each of these tests measures a different parameter associated with resistance, and thus they provide a more detailed characterization of resistance than does the intial screening test. Checks used in the tests were biotype E-resistant Largo, biotype C-resistant Amigo, and Centurk, a susceptible check. Largo was not included in the antibiosis test due to insufficient seed supply. Greenbugs used in the tests were from greenhouse cultures that are checked periodically to confirm biotype identity.

Antibiosis Test

The greenbug's reproductive capacity on the host was used to measure antibiosis. Seeds of the six germplasm lines, Amigo, and Centurk were planted separately in 7.6-cm diam pots, and seedlings were thinned to one seedling per pot. Individual plants were infested at the one-leaf stage by placing ca. five adult greenbugs on each seedling

with a fine, moistened brush. Each plant was then covered with a 6-cm diam x 30-cm high plastic cage with cloth-covered ventilation holes. As soon as newborn nymphs were observed, the adults were removed leaving five nymphs on each plant. These nymphs were allowed to mature, and when the new adults began reproducing, all but one were removed. The total number of progeny produced by an adult female greenbug on an individual plant was determined by counting and removing nymphs daily until the female stopped producing offspring ca. 20 to 25 days later. The test was conducted in a growth chamber at a constant temperature of 24±1°C with a 16-h light period. A randomized complete block design with 10 replications (pots) was used, and the mean number of progeny produced on each entry was calculated.

Tolerance Test

This test measured the effect of greenbug feeding on growth of the seedlings. Seedlings of the six germplasm lines and Amigo, Centurk, and Largo were infested in the one-leaf stage with 15 adult greenbugs, and as a check to indicate normal growth, another such set of plants was left uninfested. The height of all plants was recorded on the day of infestation. Pots, cages, and methods of infestation used were the same as those previously described. There was one plant per replication (pot) and five replications in a randomized complete block design. Greenbugs were added or removed as needed to maintain 15 per plant. Ten days after infestation, plant heights were recorded. Growth of infested and uninfested plants of the same entry was compared, and mean percentage of normal growth was calculated. Also, infested plants were

visually rated for feeding damage by using a rating scale of 1 = no damage to 6 = dead or dying plant. Susceptible plants were severely stunted and yellow. The test was conducted in a greenhouse during May, when temperatures ranged from 21 to 26 C.

Nonpreference Test

This test measured the insect's host selection over the array of entries. The nine entries were randomized with one plant of each entry in a circular pattern ca. 3 cm from the edge of a 30.5-cm diam pot. When the plants were in the one-leaf stage, 65 adult greenbugs were released in the center of each pot, and the pots were covered with plastic cages similar in design but larger than those previously described. The number of greenbugs on each plant was recorded 48 h later, and the mean number of greenbugs on plants of each entry was determined. The test had seven replications (pots) and was also conducted in a greenhouse during May.

A separate analysis of variance (ANOVA) was calculated for data from each of the three tests, and the least significant differences (LSD) at the 0.05 level were used to compare the means.

RESULTS AND DISCUSSION

In the test to determine the parental source of resistance, all plants of CI 17882 were resistant, while all plants of CI 15092, Fletcher, and Centurk were susceptible. Thus, the resistance was assumed to have been derived from T. speltoides. The identity of the particular T. speltoides accession used is unknown, but subsequent tests have indicated greenbug resistance in several T. speltoides lines (J.A. Webster and O.G. Merkle, unpublished data). Wheat germplasm lines CI 17882 and CI 17885 were significantly greater in levels of antibiosis, tolerance, and nonpreference than Amigo and Centurk (Table 1). The mean number of nymphs/adult produced on CI 17882 and CI 17885 were 32.2 and 29.7, compared with 60.7 and 59.9 on Amigo and Centurk, respectively. Means of percentage normal growth of infested plants (followed by damage ratings in parentheses) of CI 17882 and CI 17885 were 57.0 (1.2) and 64.8 (1.6), compared with 27.7 (4.4) and 32.9 (5.0) for Amigo and Centurk, respectively. In the nonpreference test, CI 17882 and CI 17885 were the least preferred. On the basis of results from all tests, CI 17882 and CI 17885 exhibited the highest levels of resistance of the six lines (CI 17881-17886) examined.

CI 17884 was significantly more tolerant than Amigo and Centurk, but its levels of antibiosis and nonpreference were not significantly different. CI 17883 appeared moderately resistant in the initial screening test; however, its levels of antibiosis, tolerance, and nonpreference were not significantly different from Amigo or Centurk. CI 17881 and CI 17886 did not perform significantly better than Amigo or

Centurk in any of the tests. Amigo also manifested susceptible responses similar to Centurk, indicating that the test greenbugs were biotype E as defined by Porter et al. (1982). Largo was not included in the antibiosis test. The antibiosis level of Largo is not particularly high according to Starks et al. (1983) and Webster and Inayatullah (1984), but it is significantly higher in antibiosis than the standard susceptible wheat checks. In our test, Largo exhibited a high level of tolerance, but the nonpreference component was not significantly different from Amigo or Centurk. Results of nonpreference tests are largely a function of the entries included. Starks et al. (1983) showed in a test with different entries that the nonpreference component of Largo was high, but Wood et al. (1974) stated that nonpreference by greenbugs was probably the least important of the three resistance components in a test with 'Gaucho' (CI 15323) triticale.

One of the parents of these lines, CI 15092, is a 42-chromosome wheat line that has a disomic substitution for resistance to WSMV obtained from Agropyron intermedium (Host) Beauv., and the six derived lines (CI 17881-17886) have variable amounts of A. intermedium chromatin (Wells et al., 1982). Translocated segments of chromosomes from alien species often carry deleterious genes along with the desired resistance genes, so the recovery of high-yielding good agronomic types from crosses involving such material may be difficult. Nevertheless, CI 17882 has been included in crosses in an attempt to widen the genetic base of greenbug resistance in wheat. Use of several sources of biotype E resistance in breeding programs may reduce genetic vulnerability, which is an important consideration because of the frequent occurrence

of new biotypes.

Currently, genetic studies are in progress to determine the inheritance of this new source of greenbug resistance. It appears that WSMV and greenbug resistance are closely associated since during the process of backcrossing (to Centurk) and selecting for WSMV resistance, greenbug resistance was maintained in homogeneous form in three of the lines: CI 17882, CI 17884, and CI 17885. This is interesting since WSMV and greenbug resistance genes were apparently contributed by different parents. Probably the simplest hypothesis to explain the apparent linkage is that there was a crossover event between the T. speltoides chromosome carrying the greenbug resistance genes and the chromosome having the A. intermedium segment such that resultant progeny had greenbug and WSMV resistance genes located on the same chromosome. Segregating populations produced for the inheritance study will be used to determine if the genes are linked. Irradiation techniques were used in the development of CI 17881-17886 (Wells et al., 1982), so it cannot be ruled out that greenbug resistance is a result of induced mutation. However, the recent discovery of greenbug-resistant T. speltoides accessions (J.A. Webster and O.G. Merkle, unpublished data) would suggest that the resistance was derived from T. speltoides.

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Table 1. Resistance response of wheat genotypes to biotype E greenbugs.

Entry	Antibiosis (nymphs/ adult)	Nonpreference (adults/ plant)	Tolerance	
			% of normal plant ht.	Damage rating
CI 17881	61.7	9.0	31.7	4.6
CI 17882	32.2	3.4	57.0	1.2
CI 17883	47.4	7.0	44.2	4.0
CI 17884	46.6	4.7	56.9	1.4
CI 17885	29.7	2.4	64.8	1.6
CI 17886	68.7	5.8	42.3	5.4
Amigo(S)	60.7	7.0	27.7	4.4
Centurk (S)	59.9	6.5	32.9	5.0
Largo (R)	ND	6.2	73.3	1.2
$\bar{x}$	50.9	5.8	47.9	3.2
LSD 0.05	17.7	2.7	19.0	1.0

Means of antibiosis, nonpreference, and tolerance tests are averages of 10, 7, and 5 replications, respectively. Rating scale: 1 = no damage to, 6 = dead or dying plants. ND = No data.

R = resistant to biotype E; S = susceptible to biotype E.

PART II

INHERITANCE OF GREENBUG RESISTANCE IN CI 17882 AND ITS RELATIONSHIP WITH WHEAT STREAK MOSAIC VIRUS RESISTANCE

INHERITANCE OF GREENBUG RESISTANCE IN CI 17882 AND ITS RELATIONSHIP WITH WHEAT STREAK MOSAIC VIRUS RESISTANCE

ABSTRACT

Genetic studies were conducted to determine the inheritance of biotype E greenbug resistance in CI 17882 (CI 15092/*T. speltoides*// Fletcher/3/5*Centurk), a wheat germplasm line previously released as resistant to wheat streak mosaic virus (WSMV). In addition, the association of greenbug and WSMV resistance in CI 17882 was examined. Results indicated that biotype E greenbug resistance in CI 17882 is conditioned by a single dominant gene that is not linked with the WSMV resistance gene.

Additional index words: Triticum speltoides, Triticum aestivum, Schizaphis graminum, insect biotypes, host plant resistance.

INTRODUCTION

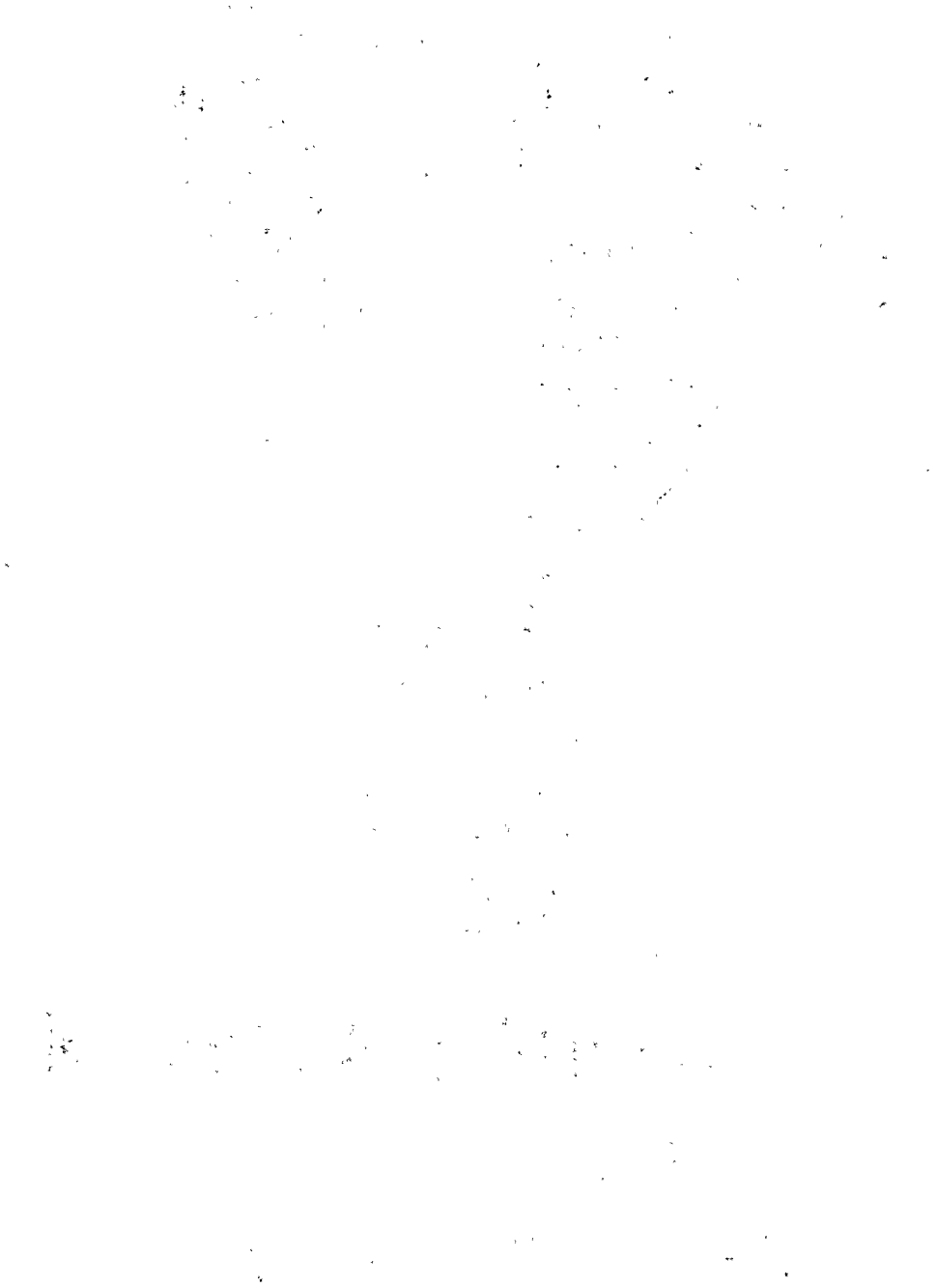
The greenbug, Schizaphis graminum (Rondani) is a serious pest of wheat, Triticum aestivum L. em Thell., in the southern Great Plains. The periodic occurrence of new virulent biotypes has made the development of greenbug-resistant wheat cultivars difficult. 'Dickinson' Selection 28A (DS 28A, CI 13833) a hexaploid selection from a durum germplasm 'Dickinson No. 485' (CI 3707), has a recessive gene that confers resistance to biotype A (1), but not to biotypes B(12), C(2), and E(6), that subsequently developed. 'Amigo' (CI 17609) a wheat germplasm line released by Sebesta and Wood in 1978 (7) has a single dominant gene located on wheat chromosome 1A (3) derived from 'Insave F.A.' rye (Secale cereale L.) that provides resistance to biotypes A, B, and C. In 1980, it was discovered that Amigo and advanced breeding lines having Amigo derived resistance were susceptible to infestations of greenbugs collected in Texas (6). This latest greenbug variant was designated as biotype E. Resistance to biotype E, derived from T. tauschii (Coss.) Schmal., has been identified in amphiploids of T. turgidum/T. tauschii ('Largo', CI 17895) (4) and T. durum/T. tauschii (CI 17959) (5). Greenbug resistance in Largo is inherited as a single dominant gene (4) located on chromosome 7D (3). Preliminary data indicate that different genes condition resistance in Largo and CI 17959 (Unpublished data, J.M. Tyler, J.A. Webster, and E.L. Smith).

Additional sources of biotype E resistance are being sought to broaden the genetic base of greenbug resistance in wheat. Resistance to biotype E was identified in a group (CI 17881-17886) of wheat germplasm

lines (9) that had previously been released by Wells et al. (11) as resistant to wheat streak mosaic virus (WSMV). The lines are from the cross CI 15092/ T. speltoides//'Fletcher' (CI 13985)/3/5*'Centurk' (CI 15075). Tests measuring the components of greenbug resistance (antibiosis, tolerance, nonpreference) revealed that CI 17882 and CI 17885 exhibited the highest levels of resistance; CI 17883 and CI 17884 showed low to moderate resistance, and CI 17881 and CI 17886 were classified as susceptible (9). In that study the T. speltoides (Tausch) Gren. ex Richter parent, was determined by deduction to be the donor of the greenbug resistance since the other three parents, CI 15092, Fletcher and Centurk were uniformly susceptible to biotype E greenbugs. The particular T. speltoides accession used in the cross is unknown. Subsequent tests have indicated greenbug resistance in several T. speltoides lines (Unpublished data J.A. Webster, and O.G. Merkle). The WSMV-resistant parent, CI 15092, is a 42-chromosome wheat line that has a disomic substitution from Agropyron intermedium (Host.) Beauv., and CI 17881-17886 have variable amounts of A. intermedium chromatin (11). Although WSMV and greenbug resistance were apparently contributed by different parents it appeared that WSMV and greenbug resistance were associated. This was hypothesized because during the process of backcrossing (to Centurk) and selecting for WSMV resistance, greenbug resistance was maintained in CI 17882, CI 17884, and CI 17885.

Research reported here was conducted to determine the inheritance of greenbug resistance in CI 17882 and to investigate the association of WSMV and greenbug resistance. CI 17882 was selected from the group of six lines for the study because it had the highest level of greenbug

resistance.



MATERIALS AND METHODS

Inheritance of Greenbug Resistance

CI 17882 was crossed with the greenbug susceptible culivars, 'TAM 105' (CI 17826) and 'Newton' (CI 17715). CI 17882 plants used in crosses were confirmed to be homozygous for biotype E greenbug resistance by progeny testing. Reactions of plants from F1, F2, F3, and backcross generations of both crosses to biotype E infestations provided phenotypic ratios which were used to estimate the mode of inheritance of greenbug resistance. Data from the F2, F3, and backcross generations were tested by the Chi-square goodness of fit test. Checks included in the tests were biotype C resistant Amigo, biotype E resistant Largo, the susceptible parents TAM 105 and Newton, and the resistant parent CI 17882.

Plants were evaluated for greenbug resistance using methods similar to those described by Starks and Burton (8). The F1, F2, F3, and backcross seeds and seeds of checks were planted in rows in uncaged greenhouse flats containing a 3:1:1 soil, peat moss, sand mix. When the seedlings were in the one leaf stage (ca. 4 to 8 cm in height) they were infested with biotype E greenbugs at the rate of 10 to 15 per plant. Reinfestations were made as needed to maintain proper greenbug numbers. Greenbugs used were from greenhouse cultures that are checked periodically to confirm biotype identity. About two weeks after infestation susceptible plants were chlorotic and stunted. Most of the susceptible plants eventually died. Resistant plants maintained their green color and showed little or no damage. Only resistant F2 plants

were saved to derive F3 families. Greenbug tests were conducted in the fall in a greenhouse with no supplemental lighting, and with temperatures ranging from 18 to 25 C.

Association of WSMV and Greenbug Resistance

To examine the association of WSMV resistance and greenbug resistance in CI 17882, 16 F3 families from each cross, from the greenbug inheritance study were evaluated for WSMV resistance. The 32 F3 families were derived from greenbug resistant F2 plants that had not been evaluated for WSMV resistance. A standard linkage test that requires evaluation of testcross or F2 plants for both traits was not done because it is not feasible to test a seedling for reaction to greenbugs and WSMV. Both test procedures severely weaken susceptible seedlings, and even the resistant seedlings become stressed which may result in invalid susceptible readings in the second test. Reactions of F3 families were used to identify the genotypes of F2 plants for both traits. If an unusually large number of parental types are observed, linkage would be suspected. Parental types in the F2 would be manifested in the F3 as families showing the same response to greenbugs and WSMV (resistant, segregating, or susceptible for both traits). Since only greenbug resistant F2 plants were selected, one would expect that each F3 family would be either resistant for both traits, or segregating for both traits if the genes are closely linked. A chi-square test for independent inheritance of two genes was done.

Progenies from the crosses TAM 105/CI 17882 and Newton/CI 17882 were evaluated for WSMV resistance. The parents, F1 and F2 plants, and

the 32 F3 families from those crosses were included in the test. There were 25 seeds per row planted in flats containing sterilized soil. A susceptible parent and the resistant parent, and seven rows of progenies from the genetic populations were planted in each flat. The test was conducted in the fall in a greenhouse under the conditions described previously.

Plants were inoculated with WSMV at the 2 to 3 leaf stage. Inoculum was prepared from infected plants grown in a greenhouse. Equal weights of water and fresh leaf tissue from infected plants were placed in a blender and the leaf tissue was ground. The mixture was then strained and celite abrasive was added to the liquid. A commercial paint gun attached to an air compressor was used to spray the plants with inoculum. The celite abrasive damaged the leaf tissue allowing entry of the virus into the test plants.

WSMV symptoms on susceptible plants were first noticed about one week after inoculation. Symptoms appeared as yellowish-green chlorotic streaks on newly developed leaves. Plants within each F3 line were scored as resistant or susceptible.

RESULTS AND DISCUSSION

Inheritance of Greenbug Resistance

Reactions of parent, F1, F2, check, and backcross plants and F3 families from the crosses TAM 105/CI 17882 and Newton/CI 17882 are shown in Table 1. All plants of the susceptible parents TAM 105 and Newton were susceptible and all CI 17882 plants were resistant. The resistant reactions of all Largo plants and susceptible reactions of all Amigo plants confirmed that the test greenbugs were biotype E. Resistant reactions of all F1 plants from both crosses indicated complete dominance of greenbug resistance in CI 17882. Complete dominance was also indicated by the backcross data where the ratio of resistant to susceptible plants from the crosses Newton/2/Newton/CI 17882 and TAM 105/2/TAM 105/CI 17882 gave a close fit to the 1:1 hypothesis.

The numbers of resistant and susceptible F2 plants for both crosses suggested a 3 resistant:1 susceptible ratio which indicates that greenbug resistance in CI 17882 is conferred by a single dominant gene. Segregation of F3 families from resistant F2 plants in both crosses suggested a 1 resistant:2 segregating ratio which also indicates a single dominant gene.

Results of this genetic study show that greenbug resistance in CI 17882, apparently derived from T. speltoides, is simply inherited. Resistance is also simply inherited in those cases documented; in the hexaploid wheat DS 28A, Insave F.A. rye, and T. tauschii. Single gene traits are easily handled in breeding programs, and transfer of greenbug resistance in CI 17882 to adapted wheat genotypes should be possible.

Since major genes conferring greenbug resistance have been identified in relatives of common wheat, and genetic-cytogenetic techniques allow interspecific and in some cases intergeneric crosses, it is important to continue research on wheat relatives in an attempt to identify new sources of greenbug resistance. This research is especially important because of the frequent occurrence of greenbug biotypes.

Association of WSMV and Greenbug Resistance

After performing a heterogeneity chi-square test (Table 2, footnote), information from both crosses was pooled. Reactions of parent, F1, F2 plants, and F3 families to WSMV infection are shown in Table 2. All CI 17882 plants showed resistant reactions, whereas all TAM 105 and Newton plants were susceptible. Reactions of F1 plants indicated that WSMV resistance in CI 17882 is incompletely dominant. Reactions of F2 plants to WSMV infection strongly suggest a 3 resistant:1 susceptible ratio which indicates that CI 17882 has a single dominant gene for resistance to WSMV. These results are consistent with those of Wang and Liang (10). They reported that WSMV resistance in CI 15092, the donor of WSMV resistance in CI 17882, is conditioned by a major dominant gene derived from A. intermedium and that full expression of resistance requires a complementary dominant gene located on a wheat chromosome. In our study, no attempt was made to distinguish different levels of resistance within the resistance class. The plants were classified as either resistant or susceptible.

Of the 32 F3 families tested with WSMV, 14 were resistant and 18 segregated for reaction to biotype E greenbug (Table 3). Of those

families, 5 were resistant, 22 segregated, and 5 were susceptible for reaction to WSMV (Table 2) approaching a 1:2:1 pattern (P = .10-.20). A 1:2:1 segregation pattern of F3 families is expected for a trait controlled by a single gene if the F3 families are derived from F2 plants selected at random. The implication is that selection of greenbug resistant F2 plants was essentially random selection for WSMV resistance therefore suggesting that the two genes assort independently. The observed numbers of F2 plants of each genotype, and the expected numbers if the genes are not linked are shown in Table 3. The expected values are based on a 1:2:1 hypothesis for WSMV reaction and a 1:2 hypothesis for greenbug reaction. The chi-square value of 6.34 with 5 degrees of freedom (P = .20-.30) indicated independent inheritance of the two genes.

CONCLUSIONS

These results indicate that the genes controlling greenbug and WSMV resistance in CI 17882 are not linked. Ideally, more F3 families would have been evaluated, but unfortunately this was not feasible because the WSMV test procedures are laborious and tedious.

The absence of linkage was not totally unexpected because the genes for greenbug and WSMV resistance were apparently derived from different parents (9). However, the fact that three of the six lines (CI 17881-17886) are homogeneous for greenbug resistance despite no selection for greenbug resistance in the backcross scheme is difficult to explain if there is no linkage. But, we believe there are two plausible explanations. First, a very low probability event may have occurred by chance, i.e., the greenbug resistance gene was carried by chance through the backcrosses. Secondly, the greenbug resistance gene may have enhanced the expression of the WSMV resistance gene. If this is so, researchers who developed these lines may have consistently selected WSMV resistant plants (after inoculation) that carried the greenbug resistant gene. If the greenbug gene or genes linked to it modified the effect of the WSMV gene, greenbug resistance may have been indirectly selected in the backcross procedure.

It may be difficult to extract high yielding good agonomic types that have greenbug and/or WSMV resistance derived from CI 17882 because germplasm lines that have wild species in their parentage often carry many deleterious genes along with the desired resistance genes. Observation of progenies having WSMV resistance derived from CI 17882 suggest that the WSMV gene is linked to undesirable genes. However, it

should be possible to isolate progenies that have the greenbug gene but not the WSMV gene, since results of this study indicate that the two are not linked. Thus, if little T. speltoides (the apparent donor of greenbug resistance) chromatin is carried in CI 17882, there is a chance of deriving agronomically acceptable greenbug resistant progenies from CI 17882.

ACKNOWLEDGEMENT

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LIST OF TABLES

Table 1. Reaction of Parent, F1, F2, and backcross plants and F3 families from the crosses TAM 105/CI 17882 and Newton/CI 17882 to biotype E greenbug infestation.

Cultivar, line or cross	Generation	Res.[+]	Seg.	Sus.	Hypothesis	X^2	P
Amigo		0		83			
Largo		96		0			
TAM 105		0		108			
Newton		0		123			
CI 17882		166		0			
TAM 105/CI 17882	F_1	42		0			
	F_2	459		137	3:1	1.28	.20-.30
	F_3	31	49		1:2	1.05	.30-.50
	Backcross	16		18	1:1	0.11	.70-.90
Newton/CI 17882	F_1	34		0			
	F_2	421		133	3:1	0.29	.50-.70
	F_3	29	48		1:2	0.64	.30-.50
	Backcross	19		22	1:1	0.22	.50-.70

[+]Res. = resistant, Seg. = segregating, Sus. = susceptible

Table 2. Reaction of Parent, F_1, and F_2 plants and F_3 families from the crosses TAM 105/CI 17882 and Newton/CI 17882 to WSMV infection.

Cultivar, line or cross	Generation	Res.[+]	Seg.	Sus.	Hypothesis	X^2	P
TAM 105		0		45			
Newton		0		67			
CI 17882		107		0			
TAM 105/CI 17882							
Newton/CI 17882							
Crosses pooled[‡]	F_1	14		4			
	F_2	33(19+14)		9(4+5)	3:1	0.28	.50-.70
	F_3	5(1+4)	22(12+10)	5(3+2)	1:2:1	4.50	.10-.20

[+]Res. = resistant, Seg. = segregating, Sus. = susceptible

[‡]Numbers in parenthesis are the numbers of plants from each cross, TAM 105/CI 17882 and Newton/CI 17882, respectively. Heterogeneity chi-square values and corresponding P values for pooling F_2 and F_3 data are 0.44 (P = .50-.70) and 1.50 (P = .30-.50), respectively.

Table 3. Distribution of F2 genotypes from the crosses TAM 105/CI 17882 and Newton/CI 17882 for reaction to biotype E greenbugs and WSMV.

Genotype[+]	Number of F_2 plants		X^2	P
	Observed	Expected[‡]		
GgWw	13	10.66		
GGWW	2	2.66		
GGWw	9	5.33		
GGww	3	2.66		
GgWW	3	5.33		
Ggww	2	5.33	6.34	.20-.30

[+]G and g indicate alleles conferring greenbug resistance and susceptibility, respectively. W and w indicate alleles conferring WSMV resistance and suseptibility, respectively.

[‡]Expected numbers if the genes are inherited independently, based on 1:2:1 and 1:2 patterns for WSMV and greenbug reaction, respectively, giving a 4:1:2:1:2:2 expected pattern.

F_2 plant genotypes were confirmed by F_3 progenies.

PART III

EXPRESSION OF GREENBUG RESISTANCE IN THE HETEROZYGOUS CONDITION IN F1 WHEAT PLANTS

EXPRESSION OF GREENBUG RESISTANCE IN THE HETEROZYGOUS CONDITION IN F1 WHEAT PLANTS

Abstract

Resistance of F1 wheat plants to biotype E greenbugs was evaluated on basis of response of infested seedlings and grain yield. Biotype E resistant CI 17882 was crossed with susceptible hard red winter wheat 'Chisholm' (P.I. 486219) to generate F1 heterozygous genotypes. CI 17882 (CI 15092/T. speltoides// 'Fletcher'(CI 13985/3/5*'Centurk'(CI 15075)) has a single dominant gene for greenbug resistance derived from T. speltoides. Seedling tolerance (% of normal plant height) of infested resistant and F1 genotypes was measured. Greenbug reproduction on the parental and F1 genotypes was also measured. A grain yield test was conducted to determine yield loss in greenbug infested F1 plants. Results showed that greenbug reproduction was higher on the F1 genotype than on the resistant genotype, but significantly lower than that on the susceptible parent. Seedling tolerance of the F1 plants to greenbug infestations was not significantly different from that of the resistant parent. Grain yield loss in infested F1 plants was not significantly different from that of the resistant parent. The results indicated that hybrid wheat breeders need to include only one greenbug resistant parent in hybrid combinations, if resistance is derived from CI 17882.

Additional index words: Triticum aestivum, Schizaphis graminum, hybrid wheat, Triticum speltoides.

INTRODUCTION

The greenbug, Schizaphis graminum (Rondani), is a serious pest of wheat, Triticum aestivum L., and other small grains in the central and southern plains of the United States. Severe outbreaks can cause significant losses to wheat producers. The Oklahoma Agricultural Extension Service estimated that the 1976 greenbug outbreak cost Oklahoma wheat growers $80 million (Starks and Burton, 1977). Insecticides can be used to control greenbug infestations, however resistant wheat cultivars would be a more efficient and economical means of control. Since the 1950's wheat breeders and entomologists in the region have attempted to develop greenbug resistant wheat cultivars. These efforts however have been thwarted by the periodic occurrence of new virulent greenbug biotypes. Since much effort continues to be invested in the development of resistant cultivars, it is important to document protection provided by different genes conferring resistance. For information on the nature and number of genes in wheat germplasm that confer greenbug resistance, see Tyler et al. (1985). Furthermore, with the advent of hybrid wheat, it is appropriate to determine the effectiveness of resistance genes in single allelic dose in F1 heterozygotes.

The effectiveness of the genes for resistance can be measured in terms of the amount of grain yield loss of infested plants having the resistance gene. Burton et al. (1985) showed in their field study, which involved several levels of biotype C greenbug infestation, that a homozygous resistant genotype sustained significantly less yield

reduction than did a susceptible genotype.

The effect of resistant genotypes on greenbug reproduction may also be an important aspect of protection. Reproductive levels influence population densities and it has been shown that the grain yield of resistant genotypes is effected significantly by greenbug population levels (Burton et al., 1985). Reproduction of greenbugs has been used to measure the antibiosis of resistant genotypes and it is known that different resistance sources provide different levels of antibiosis (Starks et al., 1983). Abdel-Malek et al. (1966) reported very similar rates of greenbug reproduction on heterozygous F1 and homozygous resistant parental plants having resistance derived from 'Dickinson' selection 28A (CI 13833). However, this is not unexpected because their data suggested that Dickinson does not have a strong antibiosis component. For resistance sources that have a high antibiosis component the results may be different. Abdel-Malek et al. (1966) did not measure grain yield response in their study.

There has not been a comprehensive study of the host-plant insect interaction of F1 wheat plants heterozygous for a major resistance gene and greenbugs, which includes tests of seedling tolerance, greenbug reproduction, and grain yield response. This would be pertinent information to hybrid wheat breeders. Also, there have been no published studies in which yield losses due to biotype E (the latest biotype) infestations in susceptible, resistant, or heterozygous wheat genotypes were measured. Therefore, the objectives of this study were to compare the seedling and grain yield responses of biotype E greenbug infested F1 heterozygous wheat plants having resistance derived from T.

speltoides, to that of plants of the homozygous resistant parent.

MATERIALS AND METHODS

Heterozygous genotypes were generated by crossing CI 17882, which is resistant to biotypes C and E of the greenbug, with the greenbug susceptible hard red winter wheat cultivar 'Chisholm' (PI 486219). CI 17882 (CI 15092/*T. speltoides*//'Fletcher'(CI 13985)/3/5*'Centurk'(CI 15075)) has a single dominant gene (J.M. Tyler, J.A. Webster and E.L. Smith unpublished data) for greenbug resistance from *T. speltoides* (Tyler et al., 1985). Biotype E greenbugs were used in all tests. Greenbugs were from greenhouse cultures that are checked periodically to confirm biotype identity. References pertaining to greenbug biotypes were reported by Webster and Inayatullah (1985).

Seedling Tests

Greenbug reproduction on F1 plants was compared to that on the parents, Chisholm and CI 17882. Seeds of the three genotypes were planted separately in 7.6 cm diameter pots, and seedlings were thinned to one seedling per pot. Individual plants were infested at the one-leaf stage by placing five adult greenbugs on each seedling with a fine, moistened brush. Each plant was then covered with a 6 cm diameter x 30 cm high plastic cage with cloth-covered ventilation holes. As soon as newborn nymphs were observed, the adults were removed, leaving five nymphs on each plant. These nymphs were allowed to mature, and when the new adults began reproducing all but one were removed. The total number of progeny produced by an adult female greenbug on an individual plant was determined by counting and removing nymphs daily until the female stopped producing offspring ca. 20-25 days later. A randomized

complete block design with 7 replications (pots) was used and the mean number of progeny produced on each wheat genotype was calculated.

A tolerance test measuring the effect of greenbug feeding on the growth of the seedlings was also conducted. CI 17882 and F1 seedlings were infested in the one-leaf stage with 15 adult greenbugs, and as a check to indicate normal growth, another set of plants was left uninfested. The height of all seedlings was recorded on the day of infestation. Pots, cages, and methods of infestation used were the same as those previously described. There was one plant per replication (pot) and 6 replications in a randomized complete block design. Greenbugs were added or removed as needed to maintain 15 per plant. Ten days after infestation, plant heights were recorded. Growth of infested and uninfested plants of the same genotype was compared, and mean percentage of normal growth (height) was calculated.

A separate analysis of variance was calculated for data from the tolerance and reproduction tests, and the least significant differences (LSD) at the 0.05 level were used to compare the means.

Grain Yield Test

This test was designed to evaluate the effect of greenbug infestation on grain yield of the three genotypes. It has been established that seedling infestations cause a greater reduction in yield of susceptible and resistant genotypes than do later infestations (Burton et al., 1985; Kieckhefer and Kantack, 1980). Twenty-four seedlings per genotype of the three genotypes were grown in a greenhouse flat containing Soil. There were 4 rows of 6 plants each for each

genotype, with the rows arranged randomly within the flat. Plants were infested in the 2-leaf stage with 10 greenbugs per plant. The infestation was done in a greenhouse under natural light with temperatures ranging from 19 to 26C. Twice each day greenbugs were dispersed over the flat to prevent buildup on the susceptible parent. Eight days after infestation the plants were sprayed with malathion to kill the greenbugs. At that time there were about 30 greenbugs per plant. Another set of plants was grown in another flat and was left uninfested to serve as a check. The flats were kept together and both were caged with rectangular cages similar to those previously described. Ten days after the greenbugs were killed all plants were placed in a cold room (5±2°C) for vernalization. Six weeks later plants were transplanted into a greenhouse soil bed. Plants were spaced 14 cm apart in rows that were 25.4 cm apart. A liquid nutrient solution (Peters Co. soluble fertilizer 15-15-15) was applied to the plants 2 days after transplanting and again when the plants were beginning to joint. Sulphur dust was used to control foliar pathogens. No disease or nutrient deficiency symptoms were noticed during the growth and development of the plants. Uninfested and infested plants of the three genotypes provided 6 treatment combinations (entries). Four plants of an entry were placed consecutively in a row and this constituted a plot. The plots were arranged in a randomized complete block design, and there were 6 replications. Measurements of total grain yield were made on a plot basis. Means were calculated for each entry. Analysis of variance was done on the data and LSD at the 0.05 level was used to compare the means.

RESULTS AND DISCUSSION

Greenbug Reproduction

The mean number of nymphs/adult produced on the F1 genotype was significantly greater than that produced on the resistant parent (Table 1). This suggests that greenbug populations could increase more rapidly on F1 hybrids than on pure-line cultivars that are homozygous for greenbug resistance. Although greenbug reproduction on the F1 was nearly twice that on the resistant parent, it was only about one third of that on the susceptible parent (Table 1). In view of that comparison, the antibiosis expressed by the F1 genotype may be at a practical usable level even though it is significantly less than that expressed by the resistant parent.

The ultimate contribution of this difference in reproductivity to grain yield loss in F1 genotypes is probably not easily assessed. Reproductive rate is only one factor determining population density. All factors (such as climate, migration, parasites etc.) should be considered. Knowledge concerning the relative contribution of antibiosis to plant protection is presently not available. This information would allow for a more accurate estimate of which levels of antibiosis are usable.

Seedling Tolerance

Results of the tolerance test are shown in Table 1. The infested seedlings of the resistant parent did not differ significantly in percentage of normal growth from those of the infested F1 seedlings.

This suggests that during fall infestations seedling damage of F1 plants would be similar to that of homozygous resistant plants. This is an important point, because fall infestations of seedling wheat have a greater impact on wheat yields than do spring infestations (Burton et al., 1985).

Grain Yield Test

Grain yield of infested and uninfested plots of the three genotypes is shown in Table 2. The duration of the greenbug infestation was only 8 days, however this resulted in a significant difference in the grain yield between infested and uninfested Chisholm plants. This is consistent with other reports of significant wheat yield reduction due to short periods (10 days) of greenbug infestations (Burton et al., 1985; Kieckhefer and Kantack, 1980). Grain yield of the resistant parent CI 17882 was not significantly affected by the infestation. The yield of the infested F1 plants was not significantly less than that of the uninfested F1 plants.

These results indicated that the resistance gene in single dose in the F1 plants was very effective in preventing grain yield losses due to greenbug infestation. This suggests that hybrid wheat breeders need include only one greenbug resistant parent in their hybrid combinations, which is desirable since it would reduce the time and effort invested in parental line development. However, these results apply only to the resistance source used in this study. Other sources of resistance may react differently in F1 genotypes. Furthermore, the level and duration of infestation used in this study was not severe. It would be

interesting to evaluate the effectiveness of F1 genotypes subjected to more severe greenbug infestations.

The data indicated that the F1 genotype (heterozygote) was as effective as the resistant parent (homozygote) in preventing yield losses. This was attributed to the increased seedling vigor of the F1 plants that was observed during the study. The F1 seedlings appeared more vigorous than those of either parent. It is postulated that the decreased expression of resistance of the F1 plants (as evidenced by the increased greenbug reproduction on them) was more than compensated for by their generally increased vigor. Seedling vigor is likely an important aspect of protection when fall greenbug infestations occur.

Results of this study indicated that biotype E greenbug resistance in CI 17882, which is derived from T. speltoides, should provide a usable level of resistance in heterozygous F1 genotypes. It is recommended that hybrid wheat breeders evaluate the effectiveness of other resistance genes in F1 genotypes before using them in a breeding program.

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Table 1. Seedling response of wheat genotypes to biotype E greenbugs

Genotype	Reproduction nymphs/adult (antibiosis)	Percentage of normal plant height (tolerance)
Chisholm (S)	62.7	ND
CI 17882 (R)	10.3	54.6
Chisholm/CI 17882 F1	19.5	47.0
LSD 0.05	5.8	19.3

ND = No data.

S = Susceptible, R = resistant

Table 2. Mean yield of biotype E greenbug infested and uninfested plots of three wheat genotypes.

Genotype	Grain yield (g)		Differences between infested and uninfested plots
	uninfested plots	infested plots	grams
Chisholm (S)	53.3	44.5	8.8 *
CI 17882 (R)	26.3	23.2	3.1 NS
Chisholm/CI 17882 F1	56.1	54.1	2.0 NS

S = susceptible, R = resistant.

* , NS, indicate significant and nonsignificant according to LSD procedure at P = 0.05. LSD at 0.05 level = 8.2 grams

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