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# Complementarity of genes for resistance to greenbug [*Schizaphis graminum* (Rondani)], biotype E, in sorghum [*Sorghum bicolor* (L.) Moench]*

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**Summary.** Gene complementarity among various sources of resistance to greenbug biotype E was assessed. Analysis of the $F_2$ generation of crosses between susceptible and resistant parents (mating 1) and among sources of resistance (mating 2) suggested that resistance in sorghum to greenbug biotype E was complexly inherited and, to some extent, dependent on the nature of both the resistant and susceptible parents. Positive transgressive segregation in the $F_2$ generations of both matings was found to be due to effective plus factors, contributed by both parents in a cross, which complemented each other. The number of plus factors ranged from one to two in the susceptible parents and from two to five in the resistant parents of mating 1, and from one to five in the parents of mating 2. The consistently significant reciprocal effects shown by Sarvasi and PI264453 indicated that these sources had major factors for resistance in their cytoplasms, which were expressed in all their crosses. The results from this study indicated that the sources of resistance complemented each other to give increased number of $F_2$ segregates with increased resistance. Thus, it should be possible to increase and diversify resistance of sorghum to greenbug biotype E by accumulating different, effective plus factors from various sources through recurrent selection.

**Key words:** Transgressive segregation – Epistasis – Frequency distribution – Castle-Wright formula – Number of effective factors

## Introduction

One of the major economic pests of sorghum in the USA is the greenbug [*Schizaphis graminum* (Rondani)]. This aphid has been a destructive pest of sorghum [*Sorghum bicolor* (L.) Moench.] since 1968 when biotype C developed (Harvey and Hackerott 1969; Hackerott and Harvey 1971; Teetes and Johnson 1973). Since then, sorghum breeders have attempted to genetically manipulate exotic resistant germ plasm to develop agronomically acceptable, insect-resistant, high-yielding hybrids. Resistant hybrids have several advantages. They are economical for the producer; they are specific to the target species; they leave no harmful residue in foods or in the environment; and they are compatible with biological, chemical, and other control methods.

By 1980, at least 90% of the sorghum acreage in the US was planted to resistant hybrids. Then, biotype E developed and overcame the majority of the known sources of resistance within sorghum germ plasm (Porter et al. 1982). Greenbug resistance of sorghum had been reported by many researchers to be simply inherited and incompletely dominant (Boozaya-Angoon 1983; Hackerott et al. 1983; Teetes 1975; Weibel et al. 1972). Recently (Dixon et al. 1990), 12 new exotic sources of resistance to greenbug biotype E, including the four sources previously resistant to biotype C, have been identified. To effectively utilize these new sources in a breeding program and diversify the resistance when transferred into elite materials, it is essential to compare the genetics of resistance among various sources. By combining genes that relate to different sources and/or mechanisms, we may identify epistatic interactions such that higher levels of resistance can be developed to protect sorghum from a future biotype change. The specific objectives of this study were: (1) to determine if genes for resistance to

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greenbug biotype E combine complementarily in crosses, and (2) to investigate if whole plant resistance is influenced by reciprocal effects.

## Materials and methods

### *Genetic material*

Seven sources of resistance (IS2388, Sarvasi, PI264453, PI220248, PI229828, N50735, and N43172) and three inbred lines (Redlan, Wheatland, and Tx2536) of sorghum susceptible to greenbug biotype E were used as parents in this study. All possible crosses, including reciprocals, were made between the susceptible lines and the sources of resistance (mating 1) and among the sources of resistance (mating 2). The parents and $F_2$ generations from the matings were evaluated for plant resistance to greenbug biotype E in a greenhouse, using the flat screening technique (Starks and Burton 1977). The greenhouse was kept at an average temperature of about 30 °C and a photoperiod regime of 14 h.

### *Design and management of experiments*

The sorghum entries were grown in a randomized complete block with six replications in galvanized metal flats (35.6 × 50.8 × 9.53 cm) with a soil mixture. Each flat had ten equidistant rows of about 25 plants per row; five rows wer assigned to the test entries and were alternated with rows of a susceptible check, Rex 16−6. All entries were uniformly infested with five greenbugs per plant at the two-leaf stage (about 9 days after planting). Greenbug biotype E of various ages, cultured on a susceptible commerical hybrid (NC+ 630-X), was used. The greenbugs were allowed to feed, develop, and reproduce until the susceptible check rows were dying; this typically took between 11 and 14 days. Then, whole plant resistance was measured by visually rating individual plants on a scale from 1 to 9, representing the percentage of damage incurred: 1 = 0−10; 2 = 11−20; 3 = 21−30; 4 = 31−40; 5 = 41−50; 6 = 51−60; 7 = 61−70; 8 = 71−80; and 9 = 81 to death of the plant.

### *Statistical analysis*

A positive transgressive segregate was defined as an $F_2$ progeny rated at least one damage class lower than the average damage class of the better parent. The average damage score of a parent or a cross was defined as the summation of the product of the frequency count and the value of the damage class, divided by the total number of plants evaluated. The frquency distribution of the $F_2$ generation was used to determine the relative percentage of transgressive segregates. The number of independently segregating, effective factor pairs was estimated by using the Castle-Wright formula (Castle 1922; Wright 1968). Lawrence and Frey (1976) argued that the range of $F_2$ segregates was a more appropriate estimate of $(\bar{P}_1-\bar{P}_2)$, when the parents did not represent the genotypic extremes for the segregating loci. Therefore, the range between the extreme $F_2$ segregates ($R$) was used, instead of the parental range. In this study, the variance of each $F_2$ from a cross contained some nonadditive genetic variance and, hence, the formula used (Lawrence and Frey 1976) to estimate the minimum number of effective factors ($n$) is represented as:

$$\tilde{N}=\frac{R^2}{8\sigma_g^2},$$

where $R$ = range of the $F_2$ segregates in the cross and $\sigma_g^2$ is the genetic variance. Thus, the number of factors affecting a trait contributed by each parent in a cross was estimated.

The number of favorable factors in the poorer parents was calculated as:

$$\tilde{n}=\frac{(\bar{X}^b-\bar{X}_{p1})+(\bar{X}_{p2}-\bar{X}_w)}{2}\times\frac{\tilde{N}}{R},$$

where $\tilde{n}$ = number of plus (favorable) factors contributed by the poor parent, $X_b$ = score of the best segregate of the cross, $X_{p1}$ = score of the better parent of the cross, $X_{p2}$ = score of the poor paent of the cross, and $X_w$ = score of the poorest $F_2$ segregate of the cross. The number of favorable factors in the better parent was obtained by subtraction, and because the number of factors estimated was the minimum, the number was approximated to the next largest integer.

The ANOVA statistics ($df=R-1$) of the Cochran-Mantel-Haenzel Chi-square were used to determine significant differences in the distribution of $F_2$ scores among the various sources of resistance, and to test for reciprocal differences in the $F_2$ distribution of the crosses.

## Results and discussion

The resistant parents used in this study did not represent the genotypic extremes, but showed intermediate levels of resistance to greenbug biotype E (Dixon et al. 1990). The range was between 4.5 for both PI229828 and N43172 and 6.2 for Sarvasi (Table 1). If a score of 1 to 6 is considered resistant, then Sarvasi would be classified as susceptible. The susceptible lines Redlan, Wheatland, and Tx2536, as expected, were in the susceptible range. The range of the sources of resistance was only 1.7, yet with a few exceptions, the segregating $F_2$ generations resulting from resistant-by-susceptible crosses (mating 1) and from resistant-by-resistant crosses (mating 2) showed no tendency to fall into distinct classes (Tables 1 and 2).

Transgressive segregation was observed in $F_2$ progenies of both mating 1 (Table 3) and mating 2 (Table 4). Only positive transgressive segregates (at least one damage score lower than the better parent) are shown. Crosses involving Sarvasi, the poorest of the resistant sources, had the highest frequency of transgressive segregates for both the resistant-by-susceptible and the resistant-by-resistant crosses. A high frequency of positive transgressive segregates was found in crosses of Redlan with N50735 and PI220248. The frequency of transgressive segregates was generally higher in the $F_2$ progenies of crosses between the susceptible and resistant parents, when the resistant parents were used as females. There were a number of reciprocal differences in the frequency of transgressive segregates in mating 2 (Table 4). The crosses among resistant parents generally had a higher frequency of positive transgressive segregates than the crosses between susceptible and resistant parents.

The presence of transgressive segregation in this study constituted further evidence for multiple-factor control for resistance, which involved different alleles in different parents and was cumulative for degree of resistance. The Castle-Wright formula was used to estimate the mini-

**Table 1.** Frequency distributions of damage scores, sample sizes (*N*), and average damage scores (ADS) of parents and $F_2$ progenies of crosses and reciprocals of susceptible-by-resistant sorghum genotypes

| | Damage score | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | *N* | ADS |
| *Parent* | | | | | | | | | | | |
| IS2238 | – | – | – | – | 73 | 47 | 3 | – | – | 123 | 5.4 |
| Sarvasi | – | – | – | – | – | 86 | 23 | 1 | – | 110 | 6.2 |
| PI264453 | – | – | – | 14 | 85 | 17 | 1 | – | – | 117 | 5.0 |
| PI220248 | – | – | 1 | 2 | 49 | 73 | – | – | – | 125 | 5.6 |
| PI229828 | – | 1 | 4 | 60 | 59 | 1 | 1 | – | – | 126 | 4.5 |
| N50735 | – | – | – | 3 | 85 | 25 | – | – | 1 | 114 | 5.2 |
| N43172 | – | – | 2 | 61 | 61 | – | 1 | 1 | – | 126 | 4.5 |
| Redlan | – | – | – | – | – | 1 | 25 | 94 | 6 | 126 | 7.8 |
| Wheatland | – | – | – | – | – | – | – | 74 | 56 | 130 | 8.4 |
| Tx2536 | – | – | – | – | – | – | 12 | 95 | 6 | 113 | 7.9 |
| *Cross* | | | | | | | | | | | |
| Redlan x IS2238 | – | 1 | 2 | 12 | 34 | 53 | 11 | – | 58 | 171 | 6.7 |
| Redlan x Sarvasi | – | – | 2 | 7 | 41 | 111 | 23 | 1 | 9 | 194 | 6.0 |
| Redlan x PI264453 | – | – | – | – | – | 25 | 7 | 30 | 90 | 152 | 8.2 |
| Redlan x PI220248 | – | 1 | 2 | 7 | 15 | 22 | 3 | – | 64 | 114 | 7.4 |
| Redlan x PI229828 | – | – | 5 | 17 | 46 | 66 | 36 | 12 | 52 | 234 | 6.5 |
| Redlan x N50735 | – | 5 | 3 | 8 | 22 | 22 | 4 | 2 | 59 | 125 | 6.9 |
| Redlan x N43172 | – | – | 1 | 23 | 28 | 75 | 19 | 19 | 99 | 264 | 7.0 |
| Wheatland x IS2238 | – | – | – | – | 8 | 34 | 16 | 22 | 54 | 134 | 7.6 |
| Wheatland x Sarvasi | – | – | 1 | 7 | 14 | 22 | 6 | 1 | 80 | 131 | 7.7 |
| Wheatland x PI264453 | – | – | – | – | – | – | – | – | – | – | – |
| Wheatland x PI220248 | – | 4 | 4 | 10 | 53 | 61 | 11 | 1 | 35 | 179 | 6.1 |
| Wheatland x PI229828 | – | – | – | – | 11 | 41 | 53 | 29 | 30 | 164 | 7.2 |
| Wheatland x N50735 | – | – | 6 | 10 | 35 | 30 | 5 | – | 92 | 178 | 7.2 |
| Wheatland x N43172 | – | – | – | 5 | 8 | 64 | 36 | 10 | 70 | 193 | 7.3 |
| Tx2536 x IS2238 | – | – | – | 1 | 5 | 20 | 20 | 7 | 73 | 126 | 8.0 |
| Tx2536 x Sarvasi | – | – | – | – | 19 | 33 | 17 | 20 | 79 | 168 | 7.6 |
| Tx2536 x PI264453 | – | – | – | – | – | 7 | 14 | 8 | 16 | 45 | 7.7 |
| Tx2536 x PI220248 | – | – | – | – | 18 | 66 | 50 | 6 | 16 | 156 | 6.6 |
| Tx2536 x PI229828 | – | – | 4 | 7 | 34 | 82 | 58 | 9 | 10 | 204 | 6.2 |
| Tx2536 x N50735 | – | – | 1 | 5 | 47 | 40 | 8 | 1 | 75 | 177 | 7.0 |
| Tx2536 x N43172 | – | – | – | – | – | 7 | 14 | 8 | 16 | 45 | 7.7 |
| *Reciprocals* | | | | | | | | | | | |
| IS2238 x Redlan | – | – | – | – | 4 | 23 | 23 | 12 | 66 | 128 | 7.9 |
| IS2238 x Wheatland | – | – | – | – | 12 | 13 | 13 | 5 | 79 | 122 | 8.0 |
| IS2238 x Tx2536 | – | – | – | 3 | 6 | 36 | 11 | 15 | 26 | 97 | 7.1 |
| Sarvasi x Redlan | – | – | – | 2 | 13 | 31 | 18 | 2 | 34 | 100 | 7.1 |
| Sarvasi x Wheatland | – | 1 | 8 | 11 | 17 | 26 | 11 | 3 | 64 | 141 | 7.0 |
| Sarvasi x Tx2536 | 2 | 1 | 5 | 13 | 23 | 44 | 5 | 2 | 10 | 105 | 5.6 |
| PI264453 x Redlan | – | – | 2 | 3 | 21 | 72 | 17 | 7 | 28 | 150 | 6.5 |
| PI264453 x Wheatland | – | 1 | 2 | 8 | 8 | 34 | 4 | 3 | 40 | 100 | 7.0 |
| PI264453 x Tx2536 | – | – | – | 11 | 13 | 31 | 7 | 6 | 32 | 100 | 6.8 |
| PI220248 x Redlan | – | – | 4 | 13 | 10 | 14 | 13 | 9 | 25 | 88 | 6.7 |
| PI220248 x Wheatland | – | – | – | 1 | 5 | 15 | 5 | 3 | 71 | 100 | 8.2 |
| PI220248 x Tx2536 | – | – | – | – | 4 | 21 | 29 | 6 | 2 | 28 | 90 | 6.7 |
| PI229828 x Redlan | – | 2 | 2 | 9 | 16 | 30 | 5 | 1 | 54 | 119 | 7.0 |
| PI229828 x Wheatland | – | – | 3 | 8 | 16 | 21 | 22 | 7 | 29 | 106 | 6.8 |
| PI229828 x Tx2536 | – | – | 1 | 3 | 33 | 48 | 12 | 3 | 22 | 122 | 6.3 |
| N50735 x Redlan | – | – | 1 | 9 | 13 | 16 | 2 | – | 2 | 43 | 5.4 |
| N50735 x Wheatland | – | – | – | 5 | 20 | 33 | 21 | 8 | 27 | 114 | 6.8 |
| N50735 x Tx2536 | – | – | – | – | – | 3 | 8 | 2 | 55 | 68 | 8.6 |
| N43172 x Redlan | – | – | – | 2 | 12 | 72 | 47 | 15 | 10 | 158 | 6.6 |
| N43172 x Wheatland | – | 2 | 2 | 7 | 28 | 73 | 29 | 2 | 24 | 167 | 6.3 |
| N43172 x Tx2536 | – | – | – | 1 | 6 | 44 | 20 | 4 | 30 | 105 | 7.0 |

**Table 2.** Frequency distributions of damage scores, sample sizes (*N*), and average damage scores (ADS) of $F_2$ progenies of crosses among resistant sorghum parents

| | Damage score | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | *N* | ADS |
| *Cross* | | | | | | | | | | | |
| IS2238 × Sarvasi | – | 2 | 7 | 12 | 22 | 14 | 5 | 2 | 37 | 101 | 6.4 |
| IS2238 × PI264453 | – | – | – | 1 | – | 2 | 8 | 3 | 72 | 86 | 8.7 |
| IS2238 × PI220248 | – | – | – | 1 | 18 | 25 | 12 | 7 | 34 | 97 | 7.1 |
| IS2238 × PI229828 | – | – | – | 5 | 18 | 53 | 22 | 4 | 11 | 113 | 6.3 |
| IS2238 × N50735 | – | – | – | 3 | 15 | 58 | 30 | 6 | 7 | 119 | 6.4 |
| IS2238 × N43172 | – | – | 1 | 3 | 16 | 45 | 22 | 6 | 7 | 100 | 6.3 |
| Sarvasi × PI264453 | – | – | 6 | 16 | 28 | 40 | 22 | 4 | 56 | 172 | 6.7 |
| Sarvasi × PI220248 | – | 3 | 5 | 12 | 17 | 51 | 29 | 9 | 21 | 147 | 6.3 |
| Sarvasi × PI229828 | – | 6 | 3 | 9 | 17 | 47 | 9 | 2 | 8 | 101 | 5.7 |
| Sarvasi × N50735 | – | – | – | 7 | 11 | 18 | 13 | 9 | 42 | 100 | 7.3 |
| Sarvasi × N43172 | – | – | – | – | 18 | 6 | 13 | 11 | 46 | 94 | 7.6 |
| PI264453 × PI229828 | – | 2 | 5 | 12 | 19 | 15 | 6 | 1 | 30 | 90 | 6.4 |
| PI264453 × N50735 | – | – | – | 7 | 15 | 31 | 13 | 7 | 27 | 100 | 6.8 |
| PI264453 × N43172 | – | 7 | 16 | 16 | 26 | 25 | 8 | 6 | 11 | 115 | 5.3 |
| PI220248 × PI229828 | – | 6 | 10 | 17 | 24 | 39 | 17 | 2 | 11 | 126 | 5.5 |
| PI220248 × N50735 | – | 3 | 8 | 9 | 12 | 19 | 14 | 9 | 32 | 106 | 6.6 |
| PI220248 × N43172 | – | – | 5 | 28 | 46 | 41 | 6 | 1 | 8 | 135 | 5.4 |
| PI229828 × N50735 | – | 2 | 6 | 8 | 21 | 63 | 5 | 2 | 3 | 110 | 5.6 |
| PI229828 × N43172 | 3 | 7 | 7 | 9 | 16 | 35 | 17 | 4 | 8 | 106 | 5.5 |
| N50735 × N43172 | – | – | 1 | 2 | 7 | 61 | 17 | 2 | 10 | 100 | 6.4 |
| *Reciprocals* | | | | | | | | | | | |
| Sarvasi × IS2238 | 1 | 14 | 12 | 18 | 62 | 59 | 2 | – | – | 168 | 4.9 |
| PI264453 × IS2238 | – | 6 | 27 | 33 | 69 | 90 | 3 | – | 5 | 233 | 5.0 |
| PI220248 × IS2238 | – | – | – | 2 | 19 | 71 | 42 | 19 | 28 | 181 | 6.8 |
| PI229828 × IS2238 | – | – | 5 | 13 | 44 | 68 | 23 | 6 | 23 | 182 | 6.1 |
| N50735 × IS2238 | – | – | – | 10 | 27 | 60 | 31 | 5 | 13 | 146 | 6.2 |
| N43172 × IS2238 | – | – | – | – | 9 | 55 | 19 | – | – | 83 | 6.1 |
| PI264453 × Sarvasi | 9 | 8 | 9 | 29 | 49 | 48 | 6 | – | 9 | 167 | 4.9 |
| PI220248 × Sarvasi | – | – | – | 3 | 29 | 30 | 12 | 49 | 71 | 194 | 7.5 |
| PI229828 × Sarvasi | – | 4 | 10 | 22 | 25 | 34 | 6 | 1 | 8 | 110 | 5.2 |
| N50735 × Sarvasi | – | – | – | 27 | 91 | 89 | 63 | 27 | 83 | 380 | 6.6 |
| N43172 × Sarvasi | – | 7 | 20 | 31 | 36 | 45 | 4 | – | 44 | 187 | 5.7 |
| PI229828 × PI264453 | – | 4 | 6 | 52 | 54 | 50 | 3 | 1 | 15 | 185 | 5.2 |
| N50735 × PI264453 | – | 1 | 2 | 9 | 25 | 34 | 16 | 3 | 20 | 110 | 6.3 |
| N43172 × PI264453 | – | – | 1 | 10 | 39 | 60 | 20 | 4 | 1 | 135 | 5.8 |
| PI229828 × PI220248 | – | – | 10 | 42 | 50 | 51 | 23 | 3 | 1 | 180 | 5.3 |
| N50735 × PI220248 | – | – | 11 | 49 | 57 | 110 | 61 | 5 | 51 | 344 | 6.1 |
| N43172 × PI220248 | – | – | – | 4 | 20 | 57 | 16 | 2 | 32 | 131 | 6.7 |
| N50735 × PI229828 | 1 | 10 | 40 | 63 | 45 | 34 | 8 | 3 | 6 | 210 | 4.6 |
| N43172 × PI229828 | – | – | 2 | 13 | 33 | 60 | 23 | 4 | 53 | 188 | 6.7 |
| N43172 × N50735 | – | – | – | 8 | 33 | 77 | 31 | 5 | 30 | 184 | 6.4 |

mum number of effective factors segregating in the $F_2$ generation of each cross. If the difference in the variance between the $F_2$ progenies and the pooled variance of the parents used as an estimate of experimental error did not exceed 0.6, the number of effective plus factors contributed by both parents in a cross was not estimated. Lawrence and Frey (1976) suggested that reduced frequency of transgressive segregates for a trait in $F_2$ progenies of some crosses could result from linkages. The lack of $F_2$ variance or reduced $F_2$ variance of some susceptible-by-resistant and resistant-by-resistant crosses also could be due to minor differences or no differences in their genes and gene actions.

The minimum number of effective factors segregating for resistance ranged from 2 to 7 (Table 3) in the $F_2$ progenies resulting from the susceptible-by-resistant crosses, and from 3 to 9 for the resistant-by-resistant crosses. In the majority of both crosses, the range between the extreme $F_2$ genotypes for each cross was far greater than the range between the parents (data not shown), which suggested that both parents in these matings were contributing factors for resistance to their progenies. From one to

**Table 3.** Percentages of transgressive segregates with damage scores at least one class better than the better parent, number of plus factors for resistance contributed by both parents, and Chi-square values for reciprocal differences in $F_2$ progenies of crosses including reciprocals between susceptible lines and sources of resistance in sorghum to greenbug, biotype E

| | Cross | | | Reciprocal | | | Chi-square |
|---|---|---|---|---|---|---|---|
| | Frequency % | Parent 1 | Parent 2 | Frequency % | Parent 1 | Parent 2 | |
| Redlan × IS2238 | 8.8 | 2 | 4 | 0.0 | + | + | 25.05** |
| Redlan × Sarvasi | 25.6 | + | + | 15.0 | + | + | 30.93** |
| Redlan × PI264453 | 0.0 | + | + | 3.3 | + | + | 59.45** |
| Redlan × PI220248 | 8.8 | 2 | 3 | 19.3 | 1 | 2 | 6.25* |
| Redlan × PI229828 | 2.1 | 2 | 5 | 3.4 | 1 | 3 | 3.60 |
| Redlan × N50735 | 12.8 | 1 | 2 | 23.2 | + | + | 32.15** |
| Redlan × N43172 | 0.4 | 1 | 4 | 0.0 | + | + | 5.25* |
| Wheatland × IS2238 | 0.0 | + | + | 0.0 | + | + | 4.67* |
| Wheatland × Sarvasi | 16.8 | 2 | 3 | 26.3 | + | + | 5.45* |
| Wheatland × PI264453 | – | – | – | 11.0 | 1 | 3 | – |
| Wheatland × PI220248 | 10.0 | 2 | 5 | 1.0 | + | + | 61.01** |
| Wheatland × PI229828 | 0.0 | + | + | 2.8 | 1 | 4 | 3.22 |
| Wheatland × N50735 | 9.0 | 1 | 2 | 4.4 | 2 | + | 2.49 |
| Wheatland × N43172 | 0.0 | + | + | 2.4 | + | + | 20.82** |
| Tx2536 × IS2238 | 0.8 | + | + | 3.1 | + | + | 16.43** |
| Tx2536 × Sarvasi | 11.3 | + | + | 42.0 | + | + | 58.51** |
| Tx2536 × PI264453 | 0.0 | + | + | 11.0 | 1 | + | 18.17** |
| Tx2536 × PI220248 | 0.0 | + | + | 4.4 | 1 | + | 0.44 |
| Tx2536 × PI229828 | 2.0 | + | + | 0.8 | + | + | 0.41 |
| Tx2536 × N50735 | 3.4 | 1 | 3 | 0.0 | + | + | 48.25** |
| Tx2536 × N43172 | – | + | + | 0.0 | + | + | – |

+ Indicates little or no genetic variance observed
*, ** $P \leq 0.05$ and 0.01 respectively

**Table 4.** Percentages of transgressive segregates with damage scores at least one class better than the better parent, number of plus factors for resistance contributed by both parents, and Chi-square values for reciprocal differences in $F_2$ progenies of crosses including reciprocals among sources of resistance in sorghum

| | Cross | | | Reciprocal | | | Chi-square |
|---|---|---|---|---|---|---|---|
| | Frequency % | Parent 1 | Parent 2 | Frequency % | Parent 1 | Parent 2 | |
| IS2238 × Sarvasi | 18.8 | 1 | 2 | 26.7 | + | + | 32.42** |
| IS2238 × PI264453 | 1.2 | + | + | 28.4 | + | + | 145.29** |
| IS2238 × PI220248 | 1.0 | 3 | 3 | 1.1 | + | + | 2.65 |
| IS2238 × PI229828 | 0.0 | + | + | 2.7 | + | + | 1.44 |
| IS2238 × N50735 | 2.5 | + | + | 6.8 | + | + | 0.61 |
| IS2238 × N43172 | 1.0 | + | + | 0.0 | + | + | 1.87 |
| Sarvasi × PI264453 | 12.8 | 2 | 2 | 33.0 | 4 | 5 | 38.51** |
| Sarvasi × PI220248 | 13.6 | 4 | 5 | 1.5 | 4 | 5 | 24.73** |
| Sarvasi × PI229828 | 7.9 | + | + | 12.7 | + | + | 3.98* |
| Sarvasi × N50735 | 7.0 | 2 | 2 | 7.1 | 2 | 3 | 9.37** |
| Sarvasi × N43172 | 0.0 | 2 | 3 | 14.4 | 1 | 2 | 41.57** |
| PI264453 × PI220248 | – | + | + | – | + | + | – |
| PI264453 × PI229828 | 7.8 | 2 | 2 | 5.4 | + | + | 16.90** |
| PI264453 × N50735 | 7.0 | 3 | 3 | 10.9 | 5 | 5 | 5.03* |
| PI264453 × N43172 | 20.0 | 2 | 2 | 0.7 | + | + | 4.75* |
| PI220248 × PI229828 | 14.2 | 3 | 4 | 5.6 | + | + | 0.70 |
| PI220248 × N50735 | 18.8 | 2 | 2 | 17.4 | + | + | 3.27 |
| PI220248 × N43172 | 3.7 | + | + | 0.0 | + | + | 35.33** |
| PI229828 × N50735 | 7.3 | + | + | 24.3 | + | + | 25.02** |
| PI229828 × N43172 | 16.0 | 3 | 3 | 1.1 | 3 | 3 | 17.73** |
| N50735 × N43172 | 0.0 | + | + | 0.0 | + | + | 0.19 |

+ Indicates little or no genetic variance observed
*, ** $P \leq 0.05$ and 0.01 respectively

two plus factors (Table 3) from the susceptible parents and from two to five plus factors from the resistant parents were contributed to the $F_2$ progenies of the susceptible-by-resistant crosses.

A range of one to five plus factors was contributed to the $F_2$ progenies by both parents involved in the resistant-by-resistant crosses (Table 4). For these types of matings, the resistant parents contributed a wider range of potentially independent plus (favorable) factors to their progenies. In a majority of the cases, a reciprocal effect was reflected in the differential number of plus factors contributed by the parents. The greatest difference was seen in crosses involving Sarvasi, PI264453, and PI220248.

Reciprocal differences in the mean distribution of damage scores in the $F_2$ progenies were significant for many crosses between the susceptible and resistant parents and among the sources of resistance (Tables 3 and 4). From the susceptible-by-resistant crosses, IS2238, Sarvasi, PI264453, and N43172 consistently showed significant reciprocal effects but PI229828 did not, suggesting that the factor contributing to the reciprocal effect was absent in PI229828. From the resistant-by-resistant crosses, only Sarvasi and PI264453 consistently showed significant reciprocal effects, indicating that some major factor(s) in these two sources of resistance was expressed in all of their crosses. The factor in IS2238 contributing to the reciprocal effects when crossed with the susceptible parents was not expressed when it was crossed with the resistant parents, except Sarvasi and PI264453. N43172 showed significant reciprocal effects in all of its crosses, except with IS2238. In crosses among the sources of resistance, PI220248 did not show any reciprocal effect, except with those already shown to have some contributing factors for reciprocal effects. The reciprocal effects of PI220248, N50735, and N43172 in crosses with the susceptible parents could have been due to maternal effects resulting from small differences in seed size. Overall, the results seemed to indicate that Sarvasi and PI264453 had major factors in their cytoplasm controlling resistance, and IS2238 had a factor contributing to cytoplasmic-by-genic interaction that was expressed only in crosses with susceptible parents.

Significant differences among the seven sources of resistance were manifested in the mean distribution of $F_2$ progeny damage scores, when these sources were crosses

**Table 5.** Chi-square values for differences in the mean distribution of damage scores of $F_2$ progenies of seven sources of resistance when crossed to each of three susceptible lines of sorghum

| Resistant sources | Female | | |
|---|---|---|---|
| | Redlan | Wheatland | Tx2536 |
| | Chi-square | | |
| IS2238 vs. Sarvasi | 11.47** | 0.07 | 6.79** |
| IS2238 vs. PI264453 | 40.74** | – | 12.82** |
| IS2238 vs. PI220248 | 6.22** | 37.51** | 3.93* |
| IS2238 vs. PI229828 | 0.45 | 5.67* | 12.67** |
| IS2238 vs. N50735 | 0.84 | 3.03 | – |
| IS2238 vs. N43172 | 2.05 | 2.33 | – |
| Sarvasi vs. PI264453 | 105.99** | – | 0.26 |
| Sarvasi vs. PI220248 | 33.63** | 32.89** | 27.54** |
| Sarvasi vs. PI229828 | 8.07** | 5.19* | 43.43** |
| Sarvasi vs. N50735 | 15.65** | 3.23 | 7.25** |
| Sarvasi vs. N43172 | 25.25** | 2.52 | – |
| PI264453 vs. PI220248 | 13.15** | – | 42.77** |
| PI264453 vs. PI229828 | 52.73** | – | 61.43** |
| PI264453 vs. N50735 | 23.74** | – | 11.45** |
| PI264453 vs. N43172 | 26.88** | – | – |
| PI220248 vs. PI229828 | 10.21** | 22.94** | 5.22* |
| PI220248 vs. N50735 | 2.02 | 15.09** | 3.42 |
| PI220248 vs. N43172 | 1.41 | 24.33** | – |
| PI229828 vs. N50735 | 2.40 | 0.01 | 11.71** |
| PI229828 vs. N43172 | 4.68* | 0.45 | – |
| N50735 vs. N43172 | 0.13 | 0.23 | – |

*, ** $P \leq 0.05$ and 0.01, respectively

to each of the susceptible lines Redlan, Wheatland, and Tx2536 (Table 5). The expressivity of resistance in some cases was influenced by the nature of the female parent. Damage scores and other results indicated that IS2238, N50735, and N43172 differed only by minor genes, which were influenced by the specific cross. All other sources differed from each other in various degrees of resistance because of cytoplasmic genes or minor genes in the nucleus, which were expressed differently in specific susceptible-by-resistant or resistant-by-susceptible crosses.

## Conclusions

The results suggested that resistance in sorghum to greenbug biotype E was complexly inherited and to some extent dependent on the nature of both the resistant and susceptible parents. Positive transgressive segregation in the susceptible-by-resistant crosses indicated that both parents were contributing favorable factors towards resistance. Positive transgressive segregation observed for mating 2 can be explained by different arrays of plus factors in the various sources that complemented each other to enhance resistance. The results from this study indicated that IS2238, N43172, and N50735 were similar in the expression of their resistance in crosses and only differed by minor genes, which were influenced by the specific cross. Sarvasi, PI264453, PI220248, and PI229828 differed from all other sources by up to five effective factors, with the most favorable factors seen in crosses that involved Sarvasi, PI264453, and PI220248.

Sarvasi and PI264453 consistently showed significant reciprocal effects when crossed with both susceptible and other resistant parents because of some major factor(s) in their cytoplasms. The reciprocal effect in IS2238 was expressed only when it was crossed to the susceptible parents (Redlan, Wheatland and Tx2536). N43172 showed significant reciprocal effects in all of its crosses except with IS2238. PI229828 did not show any significant reciprocal effect when crosses with the susceptible parents. Generally, it showed reciprocal effects with those sources of resistance that appeared to have some major contributing factors for reciprocal effects.

The sources of resistance complement each other to give increased number of $F_2$ segregates with increased resistance. Thus, it should be possible to increase and diversify resistance of sorghum to greenbug biotype E by accumulating different, effective plus (favorable) factors into elite sorghum germ plasm through recurrent selection.

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