

SOME ASPECTS OF GREENBUG RESISTANCE IN
SORGHUM AS RELATED TO "BLOOMLESS"
CHARACTER

By

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1971

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
MASTER OF SCIENCE
July, 1975

Thesis
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OCT 23 1975

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ACKNOWLEDGMENTS

To my major adviser, Dr. Dale E. Weibel, I express my most deep and sincere appreciation for his understanding, encouragement, and invaluable guidance throughout the course of this research and of my graduate study. I would also like to extend my appreciation for the helpful and valuable suggestions made by Dr. K. J. Starks, Dr. L. G. Morrill and Dr. L. H. Edwards as members of my graduate committee. Special thanks are offered to Dr. R. W. McNew for the valuable guidance and assistance offered on the statistical analyses of the data.

I am also grateful to the Institute of International Education and to Ing. Agr. Horacio J. Pacagnini and Ing. Agr. Ricardo A. Parodi who helped make my graduate study possible. I wish to thank the Department of Agronomy of Oklahoma State University for the use of its facilities and for the financial aid offered during my graduate work.

To Dr. Apichai Apichatabootra and his wife I am appreciative for their help and encouragement in the conducting of this research.

I wish to thank Mrs. Kathy Henslick for the cooperation and careful manner in which she typed this work.

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CHAPTER I

INTRODUCTION

Insects, as other organisms in nature, are constantly changing. Production of new mutants enabling an insect to overcome an existing source of plant resistance is not an uncommon phenomenon in the history of agriculture. The search for different sources of plant resistance is of unquestionable value to meet and quickly solve future possible insect outbreaks. Also, a better understanding of the mechanism under which plant resistance operates as well as the mode of inheritance of this character will be helpful tools in the use of this system of insect control.

When the greenbug, Schizaphis graminum (Rond.), was recognized as a major pest of sorghum, Sorghum bicolor (L.) Moench, in 1968, several studies were initiated in the search for resistance to this insect. Not long afterward, several resistant types were found and reported. Analysis of the pedigrees of these resistant types showed that most of them seemed to trace back to a common ancestor, Sorghum virgatum (Hack.), and probably involved the same genetic systems.

Bloomless sorghums, the absence of waxy material on leaves and stems, revealed little or no tolerance to greenbug damage in seedling tests. However, at the heading stage of development in the field, they have few or no greenbugs when normal plants are being damaged.

The purpose of the research herein reported was to review the

mechanism of inheritance of the bloomless trait and normal sorghum resistance to greenbug biotype "C", as well as to look for an explanation of a possible different source of resistance to greenbug in the bloomless types of sorghums.

CHAPTER II

LITERATURE REVIEW

Since 1968 when Harvey and Hackerott (13) reported the first outbreak and serious damage to sorghum, Sorghum bicolor (L.) Moench, by greenbugs, Schizaphis graminum (Rond.), in the United States, considerable effort has been directed to the study and characterization of the responsible greenbug biotype as well as to the search for resistant sorghum germplasm.

Biotype

Wood (27) reported the existence of and characterized a new form of greenbug that was able to destroy the previously resistant wheat lines 'Dickinson Sel. 28A' and 'CI 9058'. Since this form was only found in the greenhouse he called it "greenhouse strain", giving the name of "field strain" to the old common biotype. Later, these two different forms were designated biotype A and biotype B for the field and greenhouse strains, respectively (29).

Harvey and Hackerott (13) indicated that biotype "C" was responsible for the outbreak which occurred in 1968 on sorghum. Harvey and Hackerott (14) used this new biotype to test several known sources of resistance to biotype B. The result of this study showed that 'Piper Sudangrass', 'Caribou Selection' rye, and 'CI 9058/F*Bison' wheat were resistant to biotype B but susceptible to biotype C. In

this study only 'Dicktoo' barley and 'Insave F.A.' rye showed resistance to both biotype B and C.

Wood (28) characterized the three different biotypes. The criteria applied in the study included differential reaction of host plants when infested by different biotypes, and physiological differences such as different abilities to reproduce and survive while feeding on the same host plant. The feeding habits of greenbug biotypes A and B were studied by Saxena and Chada (20). In this work it was established that biotype A makes intercellular penetration of its stylets in the plant and feeds in the phloem tissues of the vascular bundles; while biotype B penetrates both intra and intercellularly and mostly feeds on the mesophyll parenchyma of the leaf. According to Wood, Chada and Saxena (29) biotype B is not morphologically or ecologically different from biotype A, however, both differ from biotype C in the following features: biotype C has similar feeding habits to biotype A but differs from A in the fact that it is able to infest either small grains or sorghum. Biotype C can reproduce and survive at higher temperatures than biotype A and B.

Techniques to Evaluate Resistance

Wood (26) described a greenhouse technique to evaluate tolerance of small grain lines to greenbugs. He planted several rows in metal flats to which a massive infestation was imposed. The flats were not covered with plastic cages. Seedlings damaged beyond recovery within two weeks were considered to be susceptible while others were rated as tolerant. In this study eight thousand wheat varieties were

evaluated. Chada (4) also reported a technique for testing the tolerance of small grains to the greenbug. The material to be tested was grown in wood flats covered with plastic cages. Uniform infestation was produced and readings were taken 10 to 14 days later. The rating was made according to the percentage of leaf area damaged. It was concluded that since the environment was well controlled differences in reaction among the plants were more likely due to heritable characteristics. Teetes et al. (24) utilized a field technique to evaluate sorghum resistance to greenbugs. To determine the tolerance and the antibiosis component of resistance they utilized small plastic cages closed over a leaf blade in which greenbugs were confined.

Nature of Resistance

Painter (17) suggested that resistance as seen in the field consists of three main components: tolerance, antibiosis, and non-preference. He also suggested that these components may be regulated by different genetic mechanisms and that different combinations of levels of these three components can lead to the same level of resistance.

Wood et al. (30) screened 263 sorghum varieties and hybrids for tolerance to biotypes A, B and C. Out of the 263 entries only one variety, Shallu Grain, SA.7536-1, survived the infestation and showed a high degree of tolerance. In this study it was also found that Shallu Grain had a definite nonpreference and antibiotic effect. Teetes et al. (24) in a field evaluation of sorghum resistance to biotype C of greenbug, found that adult plant resistance was present in several sorghum genotypes with Shallu Grain being among them. In this study tolerance appeared to be the primary mechanism of adult

plant resistance in the field. Resistant types did not influence nymphal duration but 'IS809' (one of the resistant entries) was found to negatively influence fecundity. In the same study they also analyzed F_1 crosses of resistant X susceptible lines and reported that they were similar in behavior to the resistant parents. Starks and Wood (23) studied the damage to susceptible and resistant sorghums in several growth stages. They reported that greenbug resistance in sorghum could be present in various stages of plant growth with a possible increase in resistance for the resistant types when the plants became older. They also reported that greenbug damage to sorghum appeared to be more complex than simple mechanical damage. Hackerott and Harvey (10) agreed and reported that losses in grain production were 5 grams per head for each leaf destroyed when 'Combine Kafir-60' was studied under field infestation of greenbugs. Schuster and Starks (21) studied several sorghums to determine the main component of resistance to biotype C in each of several entries. The results showed that most of the resistant types analyzed appeared to have a similar level of the three components. However, some of them showed a higher expression for one with the other two being intermediate.

Allard (1) suggested that evidence exists to indicate that the genetic mechanism of plant resistance to insects could be similar to that operating in plant resistance to disease. Under this hypothesis more than one locus with possible allelic series can be present in the host. The final reaction for resistance will depend on the interaction of the loci and alleles present in the host with those present in the insect. A mechanism of this nature could be the

explanation for the different reactions of wheat lines to biotypes A and B reported by Wood (27).

Juneja et al. (16) studied the biochemical nature of resistance to greenbug biotype C in barley. They analyzed resistant and susceptible isogenic lines and isolated benzyl alcohol as the chemical compound that was probably responsible for resistance to biotype C of greenbugs. In the same study they added benzyl alcohol to the nutritive solution in which susceptible barley seedlings were grown, and they found that seedlings became resistant by means of tolerance and antibiotic effects. They reported similar results for another part of the study in which benzyl alcohol was added to the nutritional medium in which susceptible 'Wheatland' sorghum seedlings infested with biotype C of greenbug were grown.

On the basis of seedling tests, Hackerott, Harvey and Ross (11) classified several sorghum entries as resistant, intermediate, and susceptible. In crosses of resistant X susceptible, the resistant parent and F_1 survived 100% while the F_2 segregated in a proportion that did not deviate significantly from a 9:7 ratio. The F_2 of crosses resistant x resistant did not show segregation. These findings suggested that resistance of sorghum to biotype C of greenbug, appeared to be conferred by dominant genes at more than one locus. In the same study they reported that most of the known resistant sorghums trace back to S. virgatum as a common ancestor.

Weibel et al. (25) conducted a study on the nature of the inheritance of greenbug resistance in sorghum through the evaluation of seedling damage. They found that the F_1 of susceptible x resistant crosses give an intermediate score between the parents. The information

obtained from the damage scores of the F_2 populations suggested that the inheritance of resistance was probably regulated by a single incompletely dominant factor. They concluded that breeders should not encounter much difficulty in transferring the resistant characteristic to adapted types.

Buajarern (3) studied the inheritance of greenbug resistance by scoring the damage to seedlings planted in metal flats. He concluded that resistance appeared to be conferred by an allelic series at one locus with additive, partial, or complete dominance depending on the parents involved in the crosses.

Inheritance of Greenbug Resistance in Other Species

Curtis, Schlehuber and Wood (6) studied the resistance of two strains of common wheat to biotype A of greenbug and reported that the character seemed to be regulated by the same single recessive gene pair in both strains. Gardenhire and Chada (9) studied several crosses of resistant x susceptible varieties of barley. All of the F_1 's were found to be as resistant as the resistant parent while only one of the F_2 populations reached the lower limit of probability for the monogenic inheritance hypothesis.

Smith, Schlehuber and Curtis (22) conducted a study to determine whether or not the genes for resistance of four varieties of barley were the same, and to study the inheritance of greenbug resistance in two of them. The results indicated that the four varieties contained a common gene for resistance and that a single dominant gene was responsible for the expression of the character.

Gardenhire (8) studied the inheritance of greenbug resistance in barley and possible linkage relationships with other traits. Segregation ratios from all of the crosses of resistant x susceptible supported the hypothesis of monogenic inheritance with complete dominance. No associations were found between the gene for greenbug resistance and those regulating green-seedling, powderly mildew resistance, leaf rust resistance, and orange lemma.

In a different work Gardenhire (7) investigated the genetics of greenbug resistance in oats by infesting and rating F_2 and F_3 segregating populations. He concluded that the inheritance of greenbug resistance in the oat variety 'Russian 77' (resistant parent of the study) seemed to be regulated by a single gene pair operating with partial or no dominance.

Partitioning Method of Genetic Analysis

Powers (18) proposed the partitioning method of genetic analysis. Applying this method under the hypothesis of a one gene model, the expected frequency of the F_2 population can be obtained by multiplying the frequency distributions of each parent by $\frac{1}{4}$ and that of the F_1 by $\frac{1}{2}$. Tests for validity of the hypothesized genetic model were made by comparing obtained and theoretical means, frequency distributions, and variances, respectively.

Bloomless Characteristics of Sorghums

Relationships With Other Traits

Martin (15) pointed out the superiority of sorghum over corn in regard to its ability to perform better under drought stress conditions.

Among other factors he mentioned the bloom characteristic of most sorghums, as partially responsible for the difference in drought tolerance between the two species. Ross (19) compared the yield of Combine Kafir-60 with some nearly isogenic lines carrying the bloomless character. He concluded that the bloomless lines yielded less than the normal and that breeders could look for genotypes with even heavier bloom than now exists in common types as possible sources of drought resistance.

Cummins and Dobson (5) studied the digestibility of bloom and bloomless sorghums. For this study they utilized three near isogenic lines and they found that the bloomless types had 22% higher digestibility than the bloom types when evaluated by the "in vitro dry matter digestibility" technique. Hanna, Monson, and Burton (12), applying a similar technique to that used by Cummins and Dobson (5), studied sorghum isogenic lines and found the bloomless strain to be 31% more digestible than the strain with bloom. They also pointed out that the bloomless strains lost significantly more water than the counterpart with bloom and that this could possibly make the bloomless types of sorghum less drought tolerant than the types with bloom.

Inheritance of the Trait

Ayyangar and Ponnaiya (2) while examining the world collection of sorghums found a completely bloomless strain. They crossed the bloomless strain with both heavy and sparsely bloomed types. For the cross heavy bloom x bloomless all of the F_1 's were found to have heavy bloom and the F_2 segregated into 252 plants with heavy bloom and 84 completely bloomless. A 3:1 ratio was indicated. In the second

cross, sparse bloom x bloomless, the F_1 was also found to have heavy bloom but the F_2 segregated into 108 heavy bloomed, 35 sparse bloomed and 43 bloomless plants which did not deviate significantly from the 9:3:4 proportion. These results together with the analysis of several F_3 families indicates the possibility of two alleles regulating this character with a recessive epistatic effect for one of them.

CHAPTER III

MATERIALS AND METHODS

The sorghum entries utilized in this study were: RWD3 X Weskan-4-3-1-1-2 (bloomless), Shallu Grain SA 7536-1 (resistant), and F_1 and F_2 generations derived from the cross of these lines, and RS 610 (a susceptible hybrid). A description of the different entries is given in Table I. The lines will be referred to as RWD3-Weskan and Shallu Grain hereafter.

The experiment was conducted in two greenhouses from October 1974 to March 1975, with two replications in the Agronomy greenhouse and two replications in the Entomology greenhouse. The temperature in both greenhouses was kept between 65 and 85^o F.

Four tables were utilized, each table containing one replication consisting of 10 pots of RWD3-Weskan, 10 pots of Shallu Grain, 10 pots of F_1 plants, 25 pots of F_2 plants, and 10 pots of RS610 plants. The distribution of the pots on the table was randomly determined.

Several treated seeds were planted in each pot on October 29. After the seedlings emerged and were established they were thinned to two plants in each pot. This doubled the size of the F_2 population to study segregation of bloomless and eventually insured the presence of at least one individual per pot. All pots were closely observed throughout the study, uniformly fertilized, and watered according to individual needs.

TABLE I
CHARACTERISTICS OF THE SORGHUM MATERIAL UTILIZED IN THE STUDY

Identification	Bloom or bloomless	Reaction to greenbug damage in seedling tests	Coleoptile color
Shallu Grain SA 7536-1	Bloom	Resistant	Green
RWD3 X Weskan-4-3-1-1-2	Bloomless	Susceptible	Green
F ₁	Bloom	Intermediate	Red
F ₂	Segregating	Segregating	Segregating
RS 610 (Combine Kafir-60 X Comb. 7078)	Bloom	Susceptible	Red

Biotype "C" of the greenbug cultured on susceptible sorghum was utilized to infest the experimental material.

Bloomless Segregation Study

The criterion applied to study the bloom or bloomless characteristics of the different plants was the visual evaluation of the amount of waxy material present on those parts of the plants where it is normally produced.

The plants were classified into bloom and bloomless at two different times. The first classification was done when the plants were 30 days old and the second when they were 80 or more days old. The readings were taken on the two plants of each pot and only the second readings were utilized.

Frequencies of bloom and bloomless individuals within the F_2 population were recorded and fitted to a 3:1 segregation pattern by a chi-square analysis.

Tolerance Component of Resistance Study

One of the two plants present in each pot was randomly selected and utilized for this part of the study. Considering the four replications together, the initial number of plants for each of the entries was: 40 plants of RWD3-Weskan, 40 plants of Shallu Grain, 40 plants of F_1 , 40 plants of RS 610, and 100 plants of F_2 . Some of the plants died during the course of the study.

Plastic cages, 2.5 X 2.5 X 2.5 centimeters, with cloth covered holes on top and bottom were utilized to confine ten adult apterate greenbugs on a blade of a sorghum leaf. The cages were supported with

wire loops. All cages were examined every other day and the offspring removed keeping constant the initial number of adult greenbugs until the readings were made. Because the number of insects confined within a cage was kept constant, this method was supposed to eliminate the interference of antibiosis and nonpreference effects in the infliction of damage.

Damage readings were obtained at two different ages of the plants with the same plant in each pot being utilized. The first set of cages for damage readings was attached to leaf blades when the plants were 25 to 30 days old and the second set when the plants were 45 to 50 days old. The general criterion for selecting the leaves in both sets was to choose the healthiest youngest fully extended leaf that was available at the time of infestation. The readings of each replication were taken when the section of the leaves in most of the cages on the susceptible checks were severely damaged or dead. The number of days between infestation and reading for all replications and both sets of damage readings are given in Table II.

The damage readings were made following a scale of six classes (1 to 6) in which 1 represented no damage and 6 represented those leaves that were dead or almost dead in that area included in the cage.

For the first set of damage readings the area of leaf included in the cages was rather constant for the different plants in a replication and for the different replications. However, when the damage readings for the second set were taken, variability in the area of leaf included in the cage due to differential plant growth rate was present in considerable magnitude. In order to diminish a possible source of bias,

TABLE II
 NUMBER OF DAYS BETWEEN INFESTATION AND
 READING FOR ALL REPLICATIONS
 ON BOTH SETS OF READINGS

Set	I	II	III	IV
First	17	16	17	17
Second	17	16	22	25

the readings were corrected to an area of leaf equivalent to the average area of leaf blades confined to the different cages of the particular replication that was being read.

With regard to the analysis of the data collected in this part of the study, frequency distributions for the percentage of individuals within each damage class were constructed for the different entries for both sets of readings. The experiment was considered a randomized complete block with four replications with each table being a replication. The two sets of readings were analyzed as repeated readings on time following a split plot scheme. Unbalanced classes were present because of the initial difference in number of individuals within each entry and because of some missing individual plant readings. Analysis of variance by the method of fitting constants was applied and therefore the F values obtained could be biased. Careful interpretation of values near significance levels should be done. Two different analysis were completed. The first one included each of the entries as a main treatment and the purpose was to study the

average damage score of entries and sets, and the possible interaction between them. The second analysis only considered the F_2 population split into two groups, bloom and bloomless individuals. These two groups comprised the main treatment. Bloom-bloomless groups, sets of readings and their corresponding interactions were considered. The main purpose of the second analysis was to investigate within the F_2 individuals a possible relationship between the bloom and bloomless characteristic and tolerance to damage.

To study the possible mechanism of inheritance of the damage component of resistance, the partitioning method of genetic analysis as proposed by Powers (18) was applied. Under this method, if the character is regulated by one major effective factor pair, the theoretical mean and frequency distribution of F_2 is obtained by the following equation:

$$F_2 (P_1 \times P_2) = \frac{1}{4}(P_1 + P_2) + \frac{1}{2}F_1 (P_1 \times P_2)$$

the test of the hypothesis of one major effective pair of alleles was made by comparison of theoretical and observed frequency distributions, variances and means.

Nonpreference Component of Resistance Study

This resistance component was studied at three different ages of the plants with two different methods being used. The F_2 population was not included in the study.

Seedling Test

Six plastic pots 10-inch in diameter were utilized. In each of the pots the four entries were planted near the edge equally spaced in

a random pattern. Five treated seeds per entry were planted and after emergence they were thinned to one seedling per entry. Seven to ten days after emergence 40 selected apterate adult greenbugs were released near the center of each pot and the pots were covered with a cylindrical plastic cage with cloth covered holes. The number of adults per seedling were recorded four days after releasing and expressed as the percentage of the total greenbugs recovered within the pot. The experiment was analyzed as a completely randomized design and the entry means were tested using the LSD criterion.

Adult Stage Test

Two tests were conducted on older plants. The first test included RWD3-Weskan, Shallu Grain, and the F_1 when the plants were 45 to 60 days old. The second test included RWD3-Weskan, Shallu Grain, the F_1 and RS610 when the plants were 70 to 75 days old. Seven replications were completed on both experiments.

To run these tests pots of the different entries were placed together so that the terminal 10 centimeters of the healthiest and newest leaf from each plant could be enclosed within a 12.5 X 12.5 X 5 centimeter plastic cage. The cage had a cloth covered hole on the top. The leaves were distributed as evenly and uniformly as possible so that greenbugs had equal access to them. Forty adult apterate greenbugs were released near the center of the plastic cage to which all the leaves were converging. The cages were closed and reopened four days later when the counts were made. The number of adults per leaf was recorded and expressed for each entry as a percentage of the

total number recovered within the cage. The experiments were analyzed as completely randomized designs and the entry means were tested using the LSD criterion.

CHAPTER IV

RESULTS AND DISCUSSION

Bloomless Segregation Study

Readings were taken at two different ages of the plants. Close observation of the material within the first 30 days of age suggested that the production of bloom may begin as early as 15 to 20 days after emergence. However, since some differences were found between the first and the second readings, the second readings were utilized for analysis.

All the Shallu Grain plants were considered to have bloom. None of the RWD3-Weskan plants showed the presence of bloom. The F_1 plants all had bloom and apparently there was no difference between the degree of bloom of Shallu Grain and F_1 plants. The F_2 population was classified into 149 bloom and 45 bloomless plants. A single gene model was tested by chi-square and found to fit with a probability between .50 and .75.

These results indicated that the bloomless characteristic seemed to be regulated by a single pair of genes. Furthermore, since the F_1 was comparable to the bloom parent it could be concluded that the bloom condition was completely dominant. These data are in agreement with the findings of Ayyangar and Ponnaiya (2) and apparently did not involve the sparse bloom condition described by these workers. However, it could be possible for the sparse bloom condition to be involved if

the bloom and sparse bloom plants of a 9:3:4 ratio were combined resulting in a 3:1 ratio for bloom and bloomless.

Figure 1 shows in a schematic way how the alleles that regulate the bloomless condition are assumed to be operating under the hypothesis of one major effective pair.

Tolerance Component of Resistance Study

Figures 2 to 6 show the percent of individuals within each damage class for the different entries and for the first set of readings. In Figures 7 to 11 the same information is given for the second set of readings. For all of the entries of the study in each of the two sets, the frequency distributions given in the figures represent the sum of all the readings obtained for that entry from the four replications.

The highest average reading in both sets was obtained from the distribution of the RS610 entry, a result that was expected since this genotype was known to be highly susceptible. The Shallu Grain parent distributions in both sets gave the lowest average readings. The readings that made up the distributions of RWD3-Weskan were closer to the readings of RS610 than to those of Shallu Grain. F_1 distributions were located between those of the parents, however, some degree of overlapping of F_1 and parental distributions occurred. F_2 readings were scattered across the length of the scale, however, a clear tendency for higher frequencies in the damage classes intermediate to the parental distributions can be seen.

Environmental effects were known to be present and could be the explanation for the variation encountered among readings in nonsegregating entries.

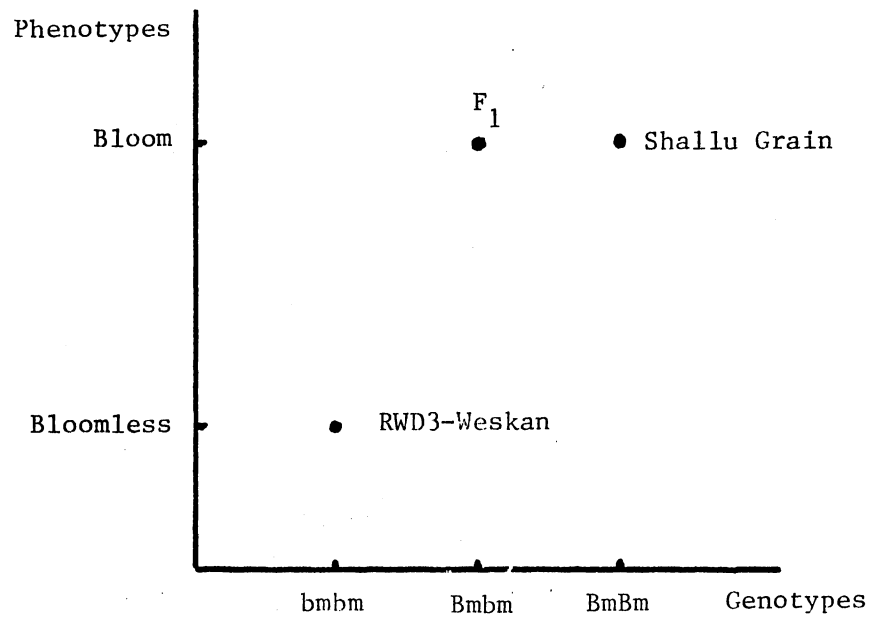


Figure 1. Possible Mode of Operation of Bloom and Bloomless Alleles.

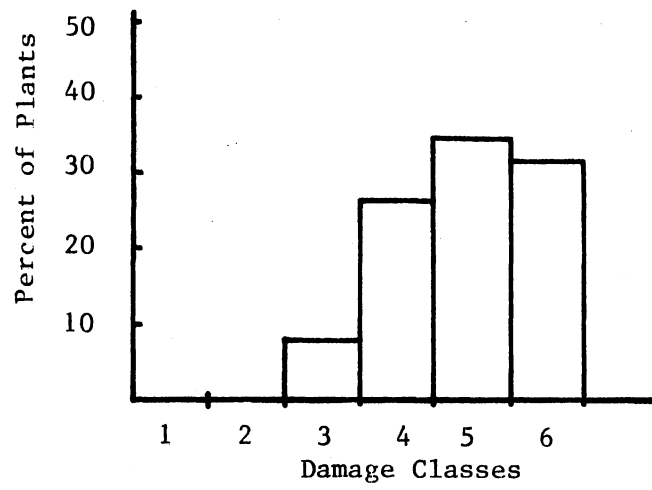


Figure 2. Frequency Distribution of Plants of RWD3-Weskan in Damage Classes for the First Set of Readings.

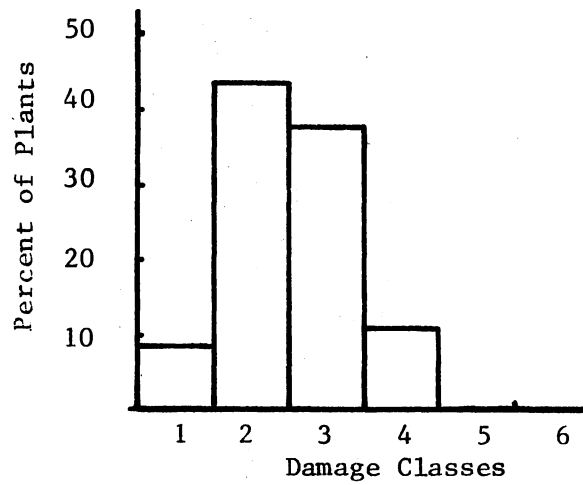


Figure 3. Frequency Distribution of Plants of Shallu Grain in Damage Classes for the First Set of Readings.

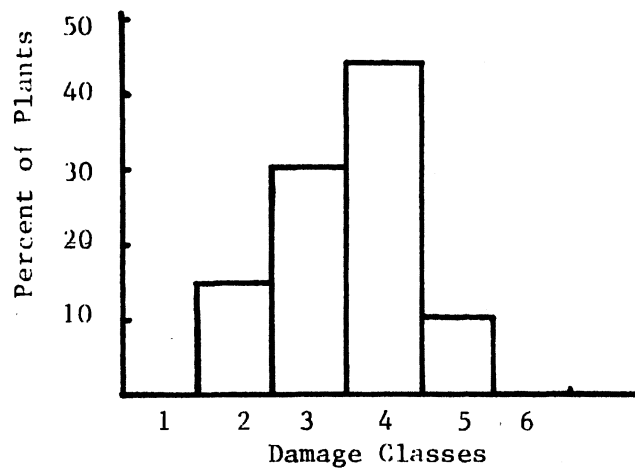


Figure 4. Frequency Distribution of Plants of F_1 from RWD3-Weskan X Shallu Grain in Damage Classes for the First Set of Readings.

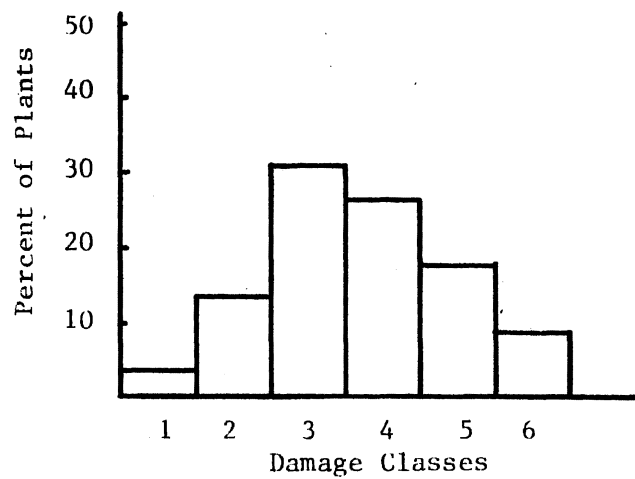


Figure 5. Frequency Distribution of Plants of F_2 from RWD3-Weskan X Shallu Grain in Damage Classes for the First Set of Readings.

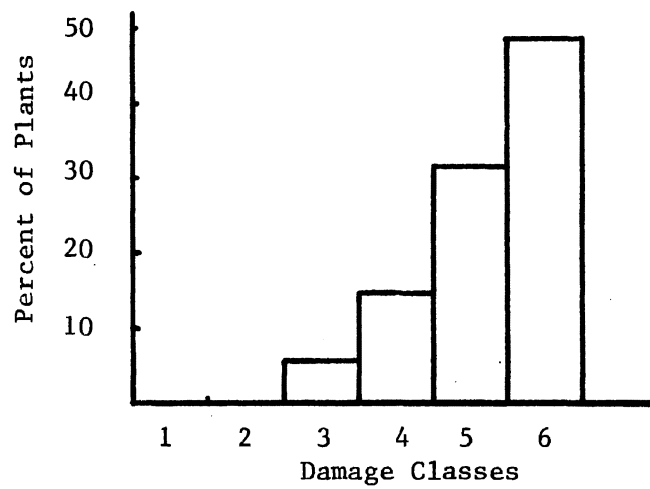


Figure 6. Frequency Distribution of Plants of RS610 in Damage Classes for the First Set of Readings.

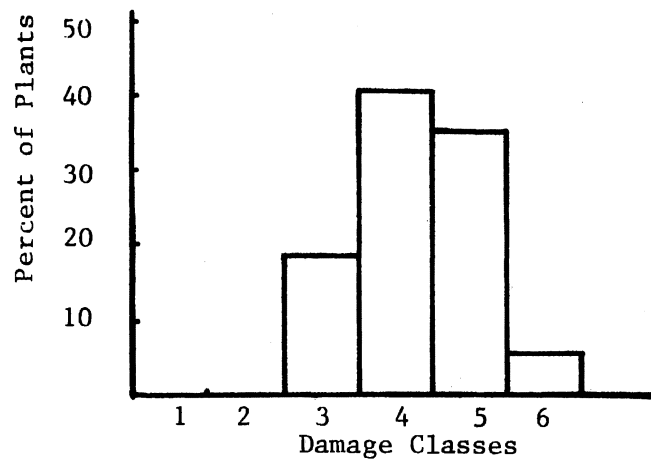


Figure 7. Frequency Distribution of Plants of RWD3-Weskan in Damage Classes for the Second Set of Readings.

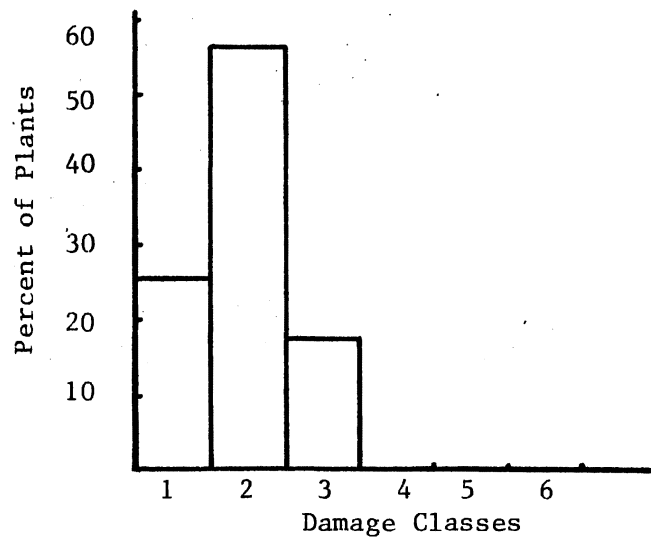


Figure 8. Frequency Distribution of Plants of Shallu Grain in Damage Classes for the Second Set of Readings.

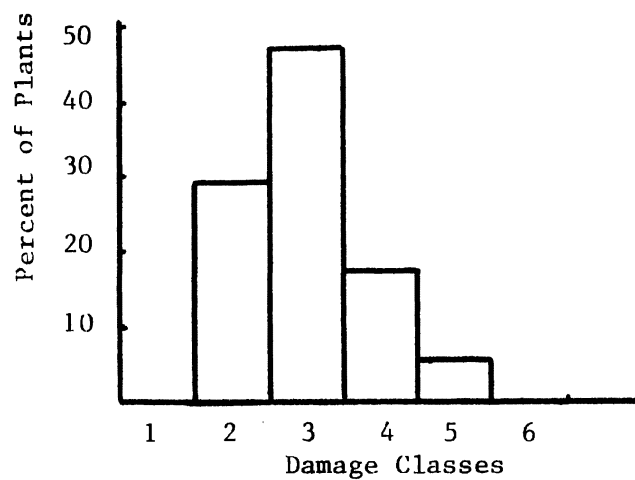


Figure 9. Frequency Distribution of Plants of F_1 from RWD3-Weskan X Shallu Grain in Damage Classes for the Second Set of Readings.

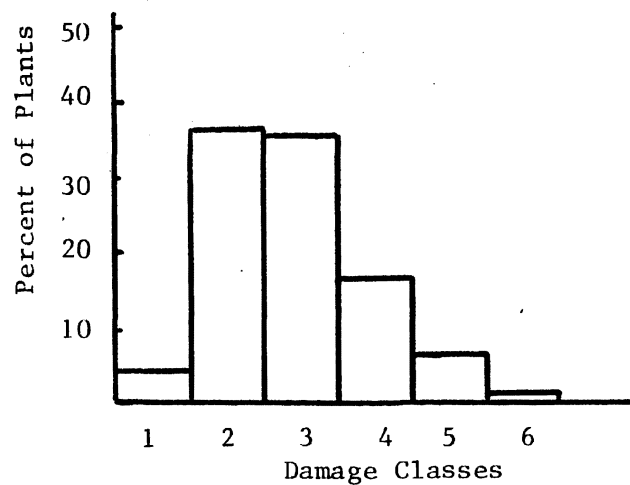


Figure 10. Frequency Distribution of Plants of F_2 from RWD3-Weskan X Shallu Grain in Damage Classes for the Second Set of Readings.

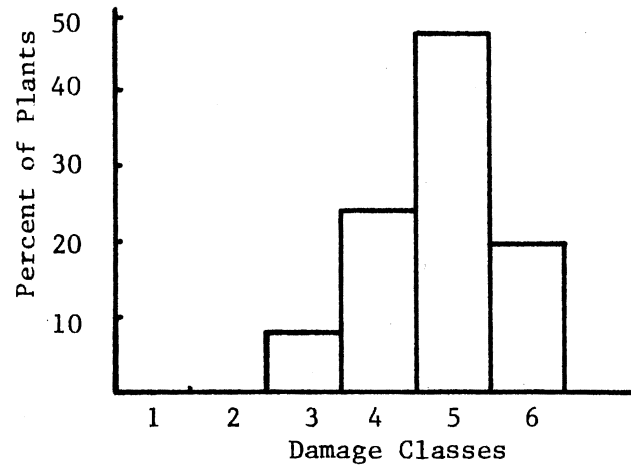


Figure 11. Frequency Distribution of Plants of RS610 in Damage Classes for the Second Set of Readings.

An estimate of the environmental effect plus the variation introduced by the experimental technique can be obtained by pooling the observed variation of the parents, F_1 , and susceptible check because they were composed of genetically uniform material.

Table III shows the analysis of variance when all the entries were considered. The significance of the F value for replications when averaged over the sets can be explained by environmental effects. The presence of F_2 segregating populations in each replication could also account for part of these differences. The highly significant F value for entries indicated that there were real differences among them when considering both sets of readings together. The highly significant F value for sets means that the average of all readings for the second set was significantly lower than the average of all the readings for the first set. Also, means for all entries in the second set were lower than means for all entries in the first set. However, the F value for entry X set interaction was not significant.

The significant difference between the two sets of damage readings may have been the result of a failure of the experimental technique to produce equal damage to the larger area of leaf confined within the cages for the second set of readings. An increased tolerance to greenbug damage with the increased age of the plants was another possibility. Starks and Wood (23) found an increase in resistance with the age of the plants, but it was only for the resistant types. The present work showed no entry x set interaction which indicated that both resistant and susceptible types increased their tolerance to damage with age in comparable amounts, if indeed, there was an increase in resistance. Means and variances for each of the entries

TABLE III
ANALYSIS OF VARIANCE FOR DAMAGE
SCORE OF ALL ENTRIES

Source	df	SS	MS	F
Replication	3	10.39	3.46	4.02*
Entry	4	358.08	89.52	104.09**
Error a	12	10.35	0.86	-
Set	1	28.76	28.76	21.62**
Entry X Set	4	2.11	0.53	0.40
Error b	15	19.97	1.33	-

* Significant at the 0.05 level of probability.

** Significant at the 0.01 level of probability.

within each set as well as the overall means for both sets are shown in Table IV.

The position of the mean for RWD3-Weskan in the second set of readings suggested that tolerance to damage may not be the component of resistance responsible for the behavior of bloomless sorghums in the field at heading stage under natural greenbug infestations. F_1 and F_2 means in both sets of readings were located somewhere between the parental means with a slight tendency of being closer to the Shallu Grain parent mean.

F_2 distributions on both sets showed the largest variances of all the entries. This was expected since variation among individuals due to genetic segregation was likely to be present in the F_2 populations. The variances of all the entries in the second set were smaller than in the first. F_2 variances decreased more than variances of the other entries. This can be explained by the higher frequency of individuals in the lower part of the scale for the second set of readings. The rest of the entries also showed smaller values for the variances in the second set of readings.

Table V shows the analysis of variance for damage scores when the F_2 populations were split into bloom and bloomless subgroups and these subgroups considered as the main treatments.

The nonsignificant F value for subgroups indicated a lack of correlation of the bloomless characteristic with the tolerance component of damage and therefore the bloom - bloomless characteristic seems to be inherited independently from the genetic factor or factors that regulate the tolerance component of damage. However, this interpretation implies the following assumptions: a) no epistatic

TABLE IV
 MEANS AND VARIANCES OF DAMAGE SCORE FOR ALL
 ENTRIES IN BOTH SETS OF READINGS

Sorghum Entry	First Set		Second Set	
	Mean	Variance	Mean	Variance
RWD3-Weskan	4.89	0.91	4.27	0.70
Shallu Grain	2.51	0.65	1.92	0.44
F ₁	3.50	0.79	3.00	0.75
F ₂	3.67	1.54	2.87	1.02
RS610	5.23	0.83	4.80	0.75
All entries together	3.91		3.17	

TABLE V
 ANALYSIS OF VARIANCE FOR DAMAGE SCORE OF BLOOM AND
 BLOOMLESS SUBGROUPS WITHIN F₂ POPULATIONS

Source	df	SS	MS	F
Replication	3	8.37	2.79	2.03
Subgroup	1	0.42	0.42	0.31
Error a	3	4.11	1.37	
Set	1	25.06	25.06	28.47**
Subgroup X Set	1	1.01	1.01	1.15
Error b	6	5.27	0.88	-

** Significant at the 0.01 level of probability.

effects have introduced bias into the results, b) the experiment included enough individuals within each subgroup to give a good estimation of the true mean damage, and c) the design and the analysis were good enough to test the hypothesis of independent inheritance of these two traits.

The significant F value for sets and the absence of significance for subgroup X set interaction can be interpreted as in the analysis including all the entries (Table IV).

Inheritance of Tolerance Component of Resistance

Frequency distributions of the damage scores for the F_2 populations for the two sets of readings may be found in Tables VI and VII. On the hypothesis of one major effective factor pair, the theoretical frequency distributions, means, and variances for the F_2 population for both sets of readings were derived by applying the partitioning method of genetic analysis, and compared with the observed data by chi-square. The probability values of both chi-square tests fell within the region of acceptance, and the observed means and variances did not deviate greatly from their respective theoretical values. Therefore, the hypothesis of one major effective factor pair may be accepted. From the position of the F_1 and F_2 means with respect to the means of the parents (Table IV) it can be concluded that the single gene may operate with partial or no dominance; therefore, assuming no interallelic interactions, additive gene action should account for the level of resistance in a particular genotype. Figure 12 shows the way in which the alleles regulating tolerance to damage are assumed to be operating. These results are in agreement

TABLE VI
OBSERVED AND EXPECTED F₂ FREQUENCY DISTRIBUTIONS, MEANS, AND
VARIANCES FOR THE FIRST SET OF DAMAGE READINGS

F ₂ Population	Damage Classes						\bar{X}	S ²
	1	2	3	4	5	6		
Observed	3	13	30	26	17	8	3.67	1.54
Expected*	1.97	17.76	25.64	30.83	13.14	7.66	3.60	1.49

$\chi^2 = 4.4604$ Probability between .25 and .50

*Derived using Powers (18) Partitioning Method of Genetic Analysis.

TABLE VII

OBSERVED AND EXPECTED F_2 FREQUENCY DISTRIBUTIONS, MEANS, AND
 VARIANCES FOR THE F_2 SECOND SET OF DAMAGE READINGS

F_2 Population	Damage Classes						\bar{X}	S^2
	1	2	3	4	5	6		
Observed	4	36	35	16	6	1	2.87	1.02
Expected*	6.28	28.23	32.10	18.59	11.49	1.32	3.05	1.33

$$\chi^2 = 6.2949 \text{ Probability between } .25 \text{ and } .50$$

* Derived using Powers (18) Partitioning Method of Genetic Analysis.

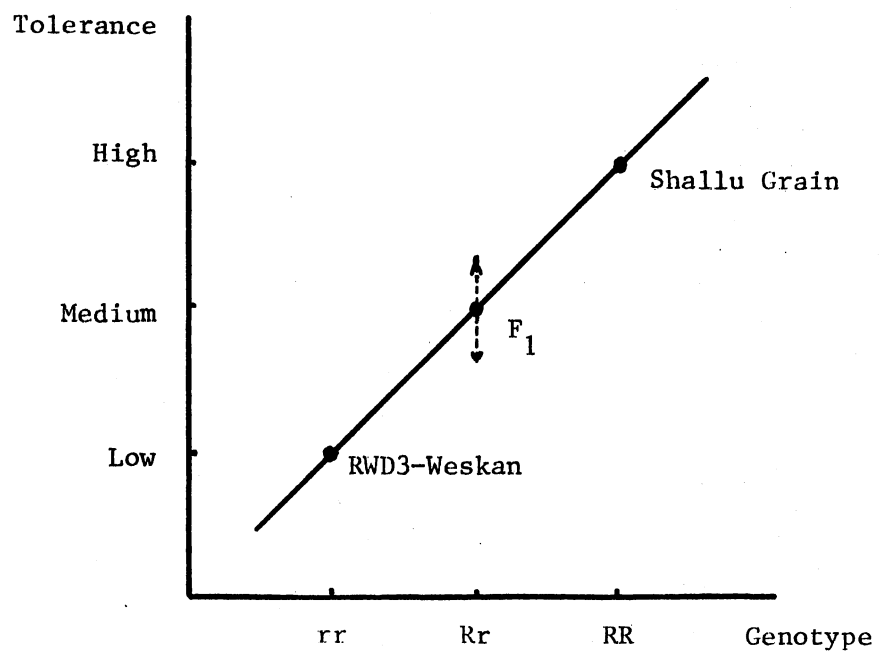


Figure 12. Possible Mode of Operation of the Alleles Regulating Tolerance to Damage.

with those reported by Weibel et al. (25) and could also be in agreement with the findings reported by Buajarern (3). However, since only crosses of two parents were utilized in the present study, the presence of an allelic series could not be detected.

Alternative hypothesis for number of genes involved and type of gene action could also explain the F_2 distribution patterns found in each set of readings. The F_2 distribution for the first set could be the result of the action of two or more genes working in additive fashion without epistatic or dominant effects. However, the sensitivity of the partitioning method when applied to a genetic design such as the one utilized in this study, is not sufficient to distinguish between the alternatives of one or more than one gene. Backcrosses as well as analysis of further generations would be needed to test this alternative hypothesis.

The F_2 distribution for the second set of readings could be compared to either a 3:1 or 9:7 ratio depending on where the separation of the different genotypes is assumed to be. However, the position of the F_1 in relation to its parents would not support the 3:1 ratio. The second ratio would not be different from the results reported by Hackerott and Harvey (11). Under the hypothesis of more than one gene regulating this trait, the assymetry of the F_2 distribution for the second set of readings could be explained also by multiplicative gene action under which the addition of any new allele for tolerance would produce an increase that could be described by a geometric progression. However, the position of the F_1 and F_2 means with respect to their parents does not support this theory.

If tolerance to damage is regulated by one gene pair, the

differences between the means of RWD3-Weskan and RS610 could be explained by the presence of different alleles of a series as proposed by Buajarern (3).

Nonpreference Component of Resistance Study

In the searching for an explanation of the behavior of bloomless types of sorghum under natural greenbug infestation in the field at heading stage, the nonpreference component of resistance was investigated at three different growth stages (ages of the plant) and the results compared.

Table VIII shows the means for each entry expressed in units of percent of the total greenbugs recovered for tests at three ages of the plants.

Seedling Test

Shallu Grain showed high nonpreference which is in agreement with data reported by Schuster and Starks (21) and Wood et al. (30). The F_1 showed a low to intermediate nonpreference being significantly lower than RWD3-Weskan. The mean of RWD3-Weskan indicated that at the seedling stage this bloomless type of sorghum showed little nonpreference. It was not significantly different from the mean of RS610.

Adult Stage Tests

The similarity of the means in this test suggested some kind of increased nonpreference of the bloomless entry compared to the results at the seedling stage. However, the variability among the readings of this test was higher than that among the readings of the seedling test,

TABLE VIII
NONPREFERENCE COMPONENT OF RESISTANCE STUDIES

Sorghum Entry	Seedling Stage	\bar{X} percentage of greenbugs per seedling	
		45-50 days	65-70 days
Shallu Grain	9.6	30.7	19.3
RWD3-Weskan	32.6	32.5	22.1
F ₁	16.6	36.4	22.4
RS610	41.3	-	35.4
LSD _{0.05}	10.02		9.36

and no significant differences were indicated.

The results of the nonpreference test when the plants were 65 to 70 days old are also shown in Table VIII. By applying the LSD criterion, means could be put into two groups. Shallu Grain, RWD3-Weskan and their F_1 were in one and RS610 in the other group. These results showed again the high nonpreference of Shallu Grain even though it was not significantly lower than the other entries of its group. The mean for the bloomless entry was significantly lower than that for RS610 which suggested a higher nonpreference for the bloomless entry at 65-70 days of age than at the seedling stage. The F_1 showed a level of nonpreference equal to Shallu Grain at 65-70 days of age, while in the seedling stage it did not.

CHAPTER V

SUMMARY AND CONCLUSIONS

A bloomless line (RWD3-Weskan) and a line with resistance to greenbugs (Shallu Grain), their F_1 , F_2 and a susceptible check (RS610) were utilized to study a possible relationship between the bloomless character in sorghum and resistance to biotype C of the greenbug.

The inheritance of the bloomless characteristic was studied followed by the study of two of the three components of host plant resistance to insects: tolerance to damage, and nonpreference. Tolerance was tested at two stages of plant development by confirming and keeping constant a number of adult greenbugs in plastic cages closed over leaf blades. Readings were taken when the susceptible check was dead or badly injured. A scale of 1 to 6 with the lower values indicating tolerance was utilized to score the damage. Nonpreference was studied at three different ages of the plants by releasing adult apterate greenbugs so that they had equal access to the entries.

From the analysis of the collected information it was possible to derive the following conclusions:

1. The bloomless characteristic, for the entries utilized in this study, appeared to be the recessive condition of a single pair of alleles operating with full level of dominance for the presence of bloom.

2. The average damage score of the bloomless entry in both sets of readings suggested that tolerance is not the component of resistance responsible for the observed behavior of this material in the field.

3. The similarity of the means for damage scores for bloom and bloomless groups of F_2 individuals suggested that the genetic factors responsible for the expression of bloom and bloomless were inherited independently from those regulating the expression of tolerance to damage. (This finding also gives additional support for the inference made in point 2).

4. Tolerance to damage appeared to be regulated by a single pair of alleles with partial or no dominance.

5. Bloomless plants seemed to increase their nonpreference with increasing age.

Even though further information was considered necessary to fully explain the behavior of the bloomless sorghums in the field, a nonpreference effect or perhaps a combination of nonpreference and antibiotic effects can be proposed to account for the resistance to biotype C of the greenbug shown in the field.

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