A STUDY OF ANTIBIOSIS AND NONPREFERENCE MECHANISMS OF GREENBUG RESISTANCE OF "BLOOMLESS" SORGHUM

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A STUDY OF ANTIBIOSIS AND NONPREFERENCE

MECHANISMS OF GREENBUG RESISTANCE

OF "BLOOMLESS" SORGHUM

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CHAPTER I

INTRODUCTION

Grain sorghum, *Sorghum bicolor* (L.) Moench, one of the major cereal crops in the world, was severely attacked by the greenbug, *Schizaphis graminum* (Rondani), in 1968 on the Great Plains of the United States. In 1974, the greenbug demonstrated a resistance to the organophosphate chemicals used to control the greenbug on sorghum. Thus, the discovery and utilization of plant resistance to the greenbug is a major device to control the greenbug.

Resistant sources of sorghum to greenbugs have been reported and utilized in the production of greenbug resistant hybrids. Another source of resistance has been discovered in connection with the "bloomless" characteristic of sorghum. A bloomless sorghum is one which lacks the presence of bloom, the white, powdery appearing substance found on the surface of the leaves and stems. The purpose of this study was to investigate antibiosis and nonpreference mechanisms of resistance to the greenbug in bloomless sorghums using near-isogenic bloom and bloomless lines.

CHAPTER II

LITERATURE REVIEW

Grain Sorghum, *Sorghum bicolor* (L.) Moench, is a major cereal crop, ranking fourth in acreage to wheat, corn, and rice in the world (34). It is a basic food in many parts of Asia and Africa and a major feed grain and forage crop in the United States (17).

Grain sorghum is one of the four major groups of sorghum. The other groups are the sorgos, the broomcorns, and the grass sorghums. The grain sorghums are divided into 7 smaller groups, of which the groups kafir, milo, feterita, and hegari have contributed most of the germplasm for the development of grain sorghums in the United States. Most new grain cultivars have come from crosses between kafirs and milos and the development of new hybrids has generally been from selections from the kafirs, milos, hegaris, and feteritas in milo type cytoplasm (34).

Biotypes of the Greenbug

The greenbug, *Schizaphis graminum* (Rondani), was first reported on sorghum in 1863 by Passerini in Italy (33). In 1968, Harvey and Hackerott (12) reported serious damage to sorghum by the greenbug in seven states. Prior to 1968, greenbugs were considered pests of small grains and not of sorghum in the United States. The greenbugs attacking sorghum appeared similar to those attacking wheat, but differed morphologically and ecologically. This greenbug was classified as a new biotype-Biotype C. The greenbugs attacking wheat are classified as Biotypes A and B. Wood et al. (38) differentiated the biotypes in this manner:

> Biotype A. The original greenbug to which resistance has been developed in wheat, barley, and oats, but which does not occur in Southwestern grain fields now. Dickinson Sel. 28A wheat and wheat hybrids containing this germ plasm are resistant to Biotype A, but all wheats are susceptible to Biotypes B and C. 'Will' barley maintains resistance to Biotype A . . . Feeding is in the phloem sieve-tube of the leaf vascular bundle.
>
> Biotype B. Dickinson Sel. 28A and all other wheats and wheat hybrids are susceptible, but Will barley maintains resistance to it. This greenbug is not morphologically or ecologically different from Biotype A, but both A and B differ from Biotype C with this respect. Feeding is in the parenchyma of the leaf, in contrast to the phloem feeding by Biotypes A and C.
>
> Biotype C. This greenbug infests and damages small grains and sorghums. All wheats and wheat hybrids are susceptible, but Will barley maintains resistance to it. It is morphologically and ecologically different from Biotypes A and B. It is much lighter in color; the cornicles are yellowish green with no blackening (one-third of distal end black in A and B), tips not expanded, and wrinkles are present throughout their entire length (wrinkles present on basal portions only for Biotypes A and B) . . . Development and reproduction rates on nearly mature sorghum plants are about 5 times greater than for Biotypes A and B on similar plants; about ten percent are males, and eggs deposited inside cages, whereas, no males have been observed in Biotypes A and B; and development takes place in the field at temperatures as high as 110 degrees Fahrenheit, whereas Biotypes A and B leave small grains when temperatures reach 80 to 85 degrees Fahrenheit.

Harvey and Hackerott (12) indicated that Biotype C preferred sorghum and sudangrass more than did Biotype B, which preferred barley, wheat, and rye. Sudangrass was highly resistant to Biotype B but not to Biotype C.

Mechanisms of Resistance

According to Painter (22), there are three mechanisms of resistance in plants. They are as follows:

> Tolerance is a basis of resistance in which the plant shows an ability to grow and reproduce itself or to repair injury to a marked degree in spite of supporting a population approximately equal to that damaging a susceptible host.
>
> Antibiosis is used in its usual sense as the tendency to prevent, injure, or destroy (insect) life . . . the effects take the form of reduced fecundity, decreased size, abnormal length of life, and increased mortality.
>
> Nonpreference is used to denote the group of plant characters and insect responses that lead to or away from the use of a particular plant or variety, for oviposition, for food, or for shelter, or for combinations of the three.

Greenbug Resistance in Small Grains

In 1961, Wood (36) found that wheat lines Dickinson Sel 28A and CI 9058 were resistant to the greenbug Biotype A but susceptible to the Biotype B. In 1969, Wood et al. (38) reported the Dickinson Sel 28A wheat to be resistant to the greenbug Biotype A but not to Biotypes B and C. Will barley was found to have resistance to all three biotypes of the greenbug. Harvey and Hackerott (11) found 'Dicktoo' barley and 'Insave F.A.' rye to be resistant to both biotypes B and C.

Wood et al. (40) reported the 'Gaucho' (CI 15323) triticale to be resistant to the Biotype C. Gaucho is a cross with the 'Chinese Spring' wheat and the Insave F.A. rye. Insave F.A. rye displayed all three mechanisms of resistance and the Gaucho triticale displayed the tolerance and antibiosis mechanisms of resistance. Sebesta and Wood (unpublished), using the Gaucho triticale, transferred the resistance to wheat.

Greenbug Resistance in Grain Sorghum

In 1969, Wood et al. (39) reported a sorghum variety, SA 7536-1 (Shallu Grain), to be resistant to the greenbug. It demonstrated high tolerance to all three greenbug biotypes. The reproduction of the greenbug Biotype C was decreased nearly 90 percent and longevity was decreased by 15 days. It also demonstrated the nonpreference mechanism of resistance. Also in 1969, Hackerott and Harvey (9) found resistance in tunisgrass, *Sorghum virgatum* (Hack.) Staph., cross (KS30). Tolerance appeared to be the major component of resistance. Using seedlings, the resistance appeared to be controlled by dominant genes at more than one locus. The F_1 of a resistant x susceptible cross survived 100 percent, whereas the F_2 segregated survival in a 9 to 7 ratio. They indicated that the reduction in survival and reproduction of adult greenbugs suggested antibiosis and/or nonpreference. Wood (37) indicated that antibiosis was reflected in the decreased fecundity of greenbugs on Shallu Grain.

Hackerott and Harvey (8) reported that grain yields are reduced as leaves are destroyed by the greenbug. Reduction in grain yield was caused by reduced seed size and numbers of seeds per head. The greenbugs did not reduce the yield of the resistant KS30.

Weibel et al. (35), using the resistant varieties Shallu Grain, PI 264453, and IS809, reported an intermediate score between resistant and susceptible parents. The score, however, was closer to the resistant parent. Data from the F_2 populations indicated that the inheritance of resistance was probably controlled by a single incompletely dominant factor.

Buajarern (3) in 1972 indicated that resistance appeared to be conferred by genes at one locus with an indication of an allelic series at that locus. Gene actions appeared to be additive and either partially or completely dominant depending on the parents and crosses involved.

Starks et al. (26) indicated that levels of resistance varied considerably among cultivars and that cultivars had different types of resistance. The variety IS809 demonstrated high antibiosis, Shallu Grain demonstrated high tolerance, and 'Piper' demonstrated non-preference. Resistance seemed to be controlled by simple gene action.

Johnson et al. (15), using the resistant lines IS809, Shallu Grain, and KS30 under natural infestations, reported that the resistance in these and their F_1 hybrids was due to tolerance.

Schuster and Starks (25) used 10 selections that had previously shown resistance to determine the components of host plant resistance. All varieties indicated low preference by both the alate and apterate greenbugs. Some varieties were highly nonpreferred. Antibiosis was also a resistance factor in some selections. The average number of progeny per adult was lower than the susceptible check on all varieties indicating some antibiosis in all the varieties. In some selections, the average weight of the nymphs were lower and the time until reproduction started was lengthened. Plant height differences between infested and uninfested plants of each entry and plant-injury ratings indicated that tolerance may be the main component of resistance of PI 264453. Five of the selections--PI 229828, IS809, Shallu Grain, PI 302178, and PI 226096--indicated comparatively high degrees of all three resistance components.

Teetes et al. (31) studied greenbug nonpreference and antibiosis mechanisms on resistant and susceptible sorghums. The resistant lines PI 264453, IS809, KS30, and SA 7536-1 demonstrated nonpreference and the F_1 hybrids of susceptible x resistant lines also demonstrated nonpreference but to a lesser degree. In antibiosis studies, duration of stadia was increased, where progeny per adult, adult longevity, and length of reproduction period were decreased for greenbugs reared on resistant sorghums. Honeydew excretion by aphids on resistant sorghums was generally less than on susceptible sorghums, indicating reduced feeding.

Teetes et al. (32) reported the resistant lines IS809, KS30, and SA 7536-1 (Shallu Grain) to be less infected with greenbugs than susceptible lines in the field. An 'in the field' determination of antibiosis indicated that adults reared on IS809 produced fewer offspring per day than those reared on the other sorghum lines. Tolerance appeared to be the primary mechanism of resistance.

Harvey and Hackerott (13) indicated that infestations of seedlings by the greenbug reduced grain and forage yields of a susceptible grain sorghum, but did not reduce the yields of the homozygous resistant line or the heterozygous F_1. The F_1, however, tended to be injured more than the resistant parent. Greenbug feeding caused reduced tillering and plant height and delayed maturity more in susceptible than resistant sorghums. Seed weights were not affected.

Starks and Wood (27) indicated that greenbug resistance in sorghum can be present in various stages of plant growth and that greenbug injury to sorghum is more complex than mechanical damage. The collapse of greenbug populations on the resistant IS809 before flowering suggested that plant maturation may adversely affect the greenbug.

Maunder et al. (19) suggested that there may be a lack of sufficient resistance at an early stage of growth in resistant varieties. A stunting effect was evident when plants were inoculated with greenbugs when plants were 2.5 centimeters high or less in both resistant and susceptible lines. Maunder (18) also obtained results indicating the presence of two or more genes for resistance. In using a hybrid having female resistance to the greenbug from Shallu Grain and male resistance from KS30, the susceptible x resistant cross displayed more resistance than the resistant x susceptible cross.

Bloomless Grain Sorghum

A bloomless sorghum is one which lacks the presence of bloom, a white, powdery appearing waxy substance found on the surface of the leaves and stems. Ayyanger and Ponnaiya (2) in 1941 reported an African variety Vigage to be bloomless. When crossed with a bloom variety, the F_1 plants were all bloom and the F_2 gave a 3 to 1 ratio of bloom to bloomless plants. When crossed with a sparse bloom plant, the F_1 plants were all bloom and the F_2 segregated into a 9:3:4 ratio of bloom, sparse bloom, and bloomless. This suggested the possibility of 2 genes regulating the bloom character. Peiretti (23) in 1975 obtained results which indicated that the bloomless characteristic was regulated by a single pair of genes with the bloom condition being completely dominant.

Ross (24) compared the yields of normal bloom Combine Kafir-60 and near-isogenic lines carrying the bloomless trait and found the bloomless lines to be significantly lower in yield.

Cummins and Dobsin (6) studied in vitro dry matter digestibilities of three near-isogenic sorghum lines differing in the bloom and bloomless characteristic. They found digestibilities to be 22% higher on the bloomless type compared to the bloom type, suggesting that the bloom reduced the digestibilities. Hanna et al. (7) reported isogenic lines of bloomless sorghum to be 31 percent more digestible than its bloom counterpart according to in vitro dry matter disappearance tests. They suggested that the bloom-covered sorghum was more drought tolerant than the bloomless sorghum because of slower water loss through the leaves.

Chatterton et al. (5) measured net carbon dioxide and water vapor exchanges in isogenic lines of bloom and bloomless sorghums. They found the mean net carbon dioxide exchange rate for bloomless lines to be 18 percent higher than for bloom lines. The overall mean transpiration rate was 26 percent higher in bloomless than in bloom lines. They concluded that bloom acted as a barrier and modified gas exchange properties. They suggested that lower yields in bloomless sorghums are results of lower gas exchange ratios.

Greenbug Resistance in Bloomless Sorghum

Recently, the bloomless sorghums were found to show some degree of resistance to the greenbug. Peiretti (23) indicated that the bloomless plants seemed to increase in the nonpreference mechanism of resistance as the plants increased in age. Tolerance did not appear to be a component of resistance in the bloomless sorghum. Amini (1) reported that in a segregating F_2 population of bloom and bloomless plants, the bloom plants exhibited the same degree of tolerance as the bloomless plants, indicating that the resistance mechanism in bloomless plants was not tolerance. The bloomless sorghums in nonpreference tests displayed an increase in nonpreference with an increase in the age of the plants. The bloomless plants were not significantly different from the resistant IS809 (bloom type) in nonpreference at 50 and 70 days of age. Amini also indicated that the bloomless type of resistance and the normal type of resistance are regulated by independent genetic factors, and they can be combined.

CHAPTER III

METHODS AND MATERIALS

Sorghum Entries

Three near-isogenic bloom and bloomless pairs of lines were studied to investigate the antibiosis and nonpreference mechanisms of greenbug resistance in bloomless sorghums. They were Martin bloom and bloomless, RWD3 x Weskan bloom and bloomless, and RCK-60 bloom and bloomless. Also included were BOK8 as the susceptible check and Shallu Grain as the resistant check. Shallu Grain has been found to possess all three mechanisms of resistance (39). The seed for all entries was obtained from the Oklahoma State University sorghum breeding program. A list of the sorghum entries is given in Table I.

Antibiosis Study

The near-isogenic lines of bloom and bloomless sorghum were used to compare the daily rate of reproduction of the greenbug. This study was conducted at three different growth stages of the plant. Each growth stage was a period of 20 days. They were as follows:

> Growth Stage 1. The stage of plant growth from 30 to 50 days of age. It consisted of the period from the sixth leaf stage to the tenth leaf stage at which the plants were from approximately 8 inches to 18 inches in height.
>
> Growth Stage 2. The stage of plant growth from 55 to 75 days of age. It consisted of the preboot and boot stages of the plant.

TABLE I

LIST OF SORGHUM ENTRIES WITH IDENTIFYING BLOOM OR BLOOMLESS CHARACTERISTIC

Sorghum Entry	Characteristic
BOK8 (susceptible)	Bloom
RWD3 x Weskan-4-3-1-1-2-2	Bloom
RWD3 x Weskan-4-3-1-1-2-2	Bloomless
Martin	Bloom
Martin	Bloomless
RCK-60	Bloom
RCK-60	Bloomless
Shallu Grain, SA 7536-1 (resistant)	Bloom

Growth Stage 3. The stage of plant growth from 80 to 100 days of age. It consisted of the stages from head emergence to the hard dough stage of the plant.

All plants were grown in 8-inch pots in the greenhouse. There were 24 pots in each replication consisting of eight varieties at each of three growth stages. There were a total of 10 replications on five tables with two replications on each table. Replications were randomly placed on the tables and the randomized block design was used for the pots in the replications.

For growth stage 1, small 3-inch x 12-inch clear plastic cylinder cages were placed over the plant to confine the greenbugs to the plant. For growth stages 2 and 3, the greenbugs were placed in small hinged 1-inch x 1-inch x ½-inch clear plastic cages that were clamped over the leaf blade of the plant. These smaller cages were mounted on a wire platform which was attached to a bamboo supporting stick in every pot. The cylinder cages had screened holes in the top and on the sides to provide ventilation. The smaller cages had screened holes in the lid of the cage. Both types of cages were made of cellulose nitrate (4).

Greenbugs of the Biotype C were obtained from ARS, Entomology Department at Oklahoma State University. To adapt the greenbugs to the different sorghum entries, five adult greenbugs were placed on each plant 20 days before the counting period. After two days, the adults were removed and three of their offspring were left on the plant. After these greenbugs reached the adult stage and produced offspring, they were removed from the plant and two of their offspring were left on the plant. These two offspring, after reaching the adult stage, were the two greenbugs from which their offspring were counted through the course of the counting period.

During the counting period, the offspring from the two adult greenbugs were counted and removed daily. The offspring from both greenbugs were counted together and the number was recorded for that particular plant for that day. The offspring were removed daily for the entire counting period. All data were analyzed according to the number of offspring from both greenbugs.

Culture plants infested with greenbugs were maintained for all entries to supply greenbug substitutions for injured, missing, or alate (winged) greenbugs in the cages. Alate greenbugs were removed because they have a lower rate of reproduction than the apterous (nonwinged) greenbugs (14). The greenbugs on the culture plants were adapted to the varieties in the same manner as those on the test plants.

Because of the large number of observations required, the ten replications were not grown simultaneously. Three replications were planted on February 20; three more replications were planted 20 days later on March 11; and four more were planted 20 days later on March 31. These three planting dates were designated as seasons 1, 2, and 3 respectively. A diagram showing the relationship of seasons and growth stages is shown in Figure 1.

Beginning June 10, temperatures in the greenhouse were over 110 degrees Fahrenheit during the day. Greenbug reproduction is stopped at these temperatures and the plants reportedly show increased resistance with increased temperatures (21). This eliminated the growth stage 3 on seasons 2 and 3. Consequently, seven replications of the entries were planted on June 11 making a total of 56 plants. These were grown to the age for growth stage 3 before greenbugs were applied for observations. The same procedure described earlier was

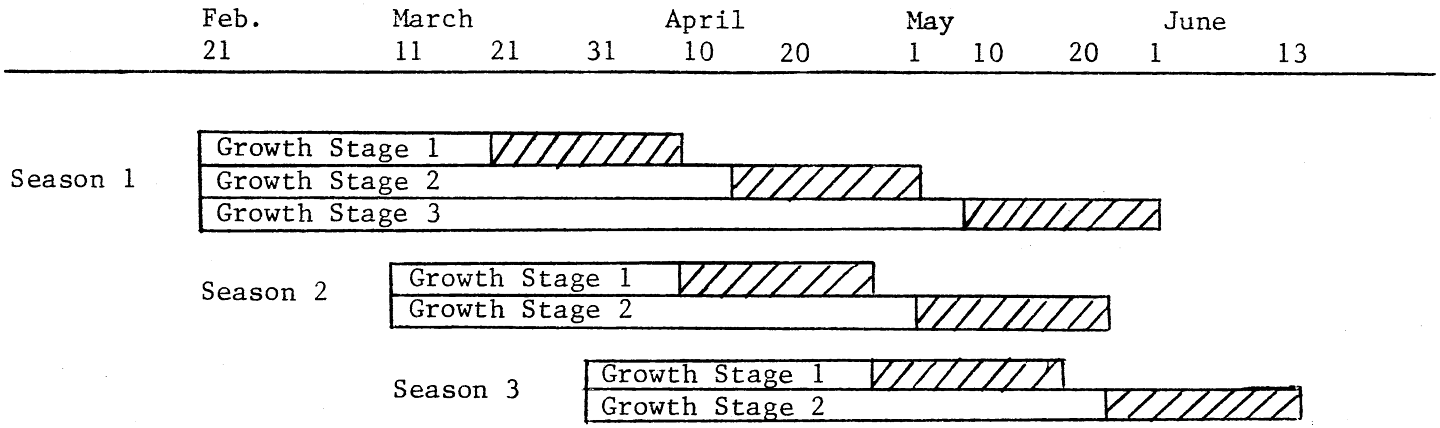

Figure 1. Diagram of Growth Stages and Counting Periods ( ) in seasons 1, 2, and 3.

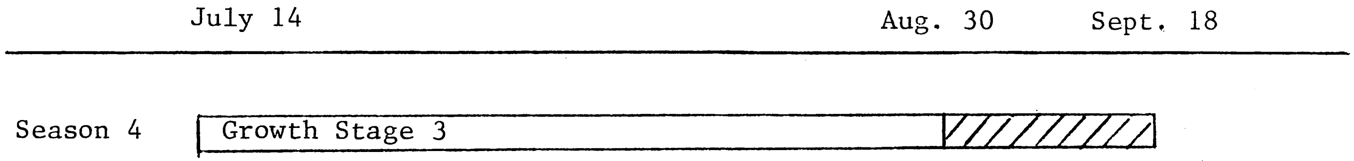

Figure 2. Diagram of Growth Stage 3 and Counting Period ( ) in Season 4.

followed for this planting which was designated as season 4 and contained only growth stage 3. A diagram of season 4 is given in Figure 2.

The daily mean number of offspring produced for the two adult greenbugs was recorded for each sorghum entry over the 20 day counting period for each season. Days in which the greenbugs were incapable of producing offspring were not included in calculating daily means. In every season, the means from the replications for every sorghum entry at each growth stage were averaged together.

An analysis of variance was used to test for differences among varieties and among growth stages and to test for variety x growth stage interactions. When differences were significant (.05 level of probability), differences between individual varieties were tested using the LSD criterion. Differences were considered significant at the .05 level of probability.

Nonpreference Study

The nonpreference mechanism of resistance was studied using a paired experiment at three different ages of the sorghum plants. Each of the eight sorghum entries was paired with each of the other entries to determine the degree of nonpreference between them. There was a total of 28 pairs for each of the three different ages of the plant. The three ages of the plants were 10 days (seedling), 40 days, and 60 days of age.

Ten-day Study

The 28 sorghum pairs were planted in 4-inch pots in the greenhouse on August 27. There was one pair per pot with the entries planted approximately 1½ inches apart. Each pair was replicated five times with replications on different tables. The randomized block design was used for pots in replications. Eight days after emergence, ten adult greenbugs were placed between the two entries in each pot and the plants were covered with small 3-inch x 12-inch clear plastic cylinder cages. After four days, the number of adult greenbugs on each plant was recorded.

Forty- and Sixty-day Studies

The 28 sorghum plant pairs were planted in 8-inch pots in the greenhouse on July 14. One pair was planted in each pot with the entries approximately four inches apart. This study was replicated five times and the randomized block design was used for pots in replications. After 40 days, clear 2½-inch x 2½-inch x ½-inch plastic cages were mounted on wooden platforms and placed between the two entries in each pot. The bottommost healthiest leaves of approximately the same age in a pair were placed side by side in the cage. Ten adult greenbugs were placed on the bottom of the cage and the cage was closed. After two days, the cages were opened and the number of greenbugs on each leaf was recorded. Twenty days later, the same procedure was followed for the 60-day study on the same plants.

Analysis of Data for Nonpreference

The mean for a variety in a pair at each growth stage was the average number of greenbugs on that variety from the five replications of that pair. Two analyses were used on the nonpreference data.

Individual "t" Tests. Differences between the means in each pair were calculated, and individual "t" tests were used to determine significant differences between the means for each pair of sorghum entries at each age of the plant.

Least Squares Analysis. A least squares analysis of variance was obtained for each age of the plant. The analysis was conducted on the basis of one member of the pair being the variety considered and the other member of the pair being a competitor to the first. Each of the varieties was considered first by averaging the number of greenbugs on that variety when it was compared with the other varieties. It was considered second as a competitor to the other varieties by averaging the number of greenbugs on the other varieties when they were compared with that particular variety. These averages for the varieties and competitors were the least squares means which was obtained from the least squares analysis. The varieties were ranked according to their least squares means and compared by testing differences among pairs of least squares means. Differences between least squares means in the pairs were tested by individual LSD values for each pair.

CHAPTER IV

RESULTS AND DISCUSSION

Antibiosis Study

The data were analyzed according to seasons and not combined from one season to another.

Season 1

Table II gives the daily means for the number of offspring for the sorghum entries at each growth stage for season 1. The analysis of variance for season 1 is given in Table III.

There was a significant difference between growth stages when considering the average mean for all the entires in each growth stage. Growth stages 1 and 2 were not significantly different from each other, but both were significantly different from growth stage 3. In growth stage 3, the greenbugs were producing a near normal amount of offspring (three to five per day) (14). Temperatures in the greenhouse during this period were around optimum for greenbug reproduction (41). The lower rate of reproduction in growth stage 2 was attributed to environmental conditions. Cloudy weather during almost all of the period lowered temperatures below optimum for greenbug reproduction and reduced lighting in the greenhouse. In growth stage 1, the lower rate of reproduction was attributed to the occurrence of an unusually high

TABLE II

SEASON 1. AVERAGE NUMBER OF OFFSPRING PER DAY FROM TWO ADULT GREENBUGS

Growth stage	BOK8	RCK-60		Martin		RWD3 x Weskan		Shallu Grain	$\bar{x}$
		bloom	bloom-less	bloom	bloom-less	bloom	bloom-less		
1	6.1	6.1	3.4	5.6	4.5	5.3	4.2	2.7	4.7
2	5.0	4.4	5.7	4.2	4.7	5.1	4.7	3.4	4.6
3	6.9	6.5	6.5	6.5	4.9	6.4	5.4	5.1	6.0
$\bar{x}$	6.0	5.6	5.2	5.4	4.7	5.6	4.8	3.7	

TABLE III

ANALYSIS OF VARIANCE FOR DAILY MEANS
IN SEASON 1

Source	d.f.	MS	F
Replications	2	1.630	
Growth stages	2	11.804	8.253*
Error a	4	1.430	
Variety	7	4.334	2.617*
Growth stage x variety	14	1.802	1.088
Error b	42	1.656	

*Significant at the .05 level of probability.

number of alate (winged) greenbugs. Alate greenbugs have a lower rate of reproduction than apterous greenbugs (21).

The F value for differences in the sorghum varieties on the rate of reproduction of the greenbug was significant at the .05 level of probability. An LSD of 1.2 was used to test differences between varieties when averaged over the three growth stages. There was no significant difference between the near-isogenic bloom and bloomless sorghums. However, the rate of reproduction was lower on the bloomless sorghum than on the bloom sorghum in each pair. There was no difference between the resistant Shallu Grain and either the Martin or RWD3 x Weskan bloomless sorghums, but there was a significant difference between the resistant Shallu Grain and the bloom-type sorghums. The susceptible BOK8 was not significantly different from the bloom-type sorghums, but it was significantly different from the bloomless sorghums except RCK-60 bloomless. This gives indication of the Martin bloomless and RWD3 x Weskan bloomless being intermediate between the bloom-type sorghums and the resistant Shallu Grain on the rate of reproduction of the greenbug.

In growth stages 1 and 3, the bloomless varieties were lower than their bloom counterparts except for RCK-60 bloomless in growth stage 3 which was equal to the RCK-60 bloom. In growth stage 2, the daily means were higher for Martin bloomless and RCK-60 bloomless than for their near-isogenic bloom entries. This occurrence was attributed partly to environmental conditions and partly to chance since the differences between the near-isogenic bloom and bloomless sorghums were not great.

There was no significant growth stage x variety interaction indicating no difference between the varieties over growth stages.

Season 2

Table IV gives the daily means for the sorghum entries at each growth stage in season 2. The analysis of variance for season 2 is given in Table V.

There was a significant difference in growth stages 1 and 2 during season 2. Growth stage 1 was grown during the same period of time that growth stage 2 of season 1 was grown. This smaller rate of reproduction in growth stage 1 was again attributed to environmental conditions. Growth stage 2 was grown during a time of higher temperatures, normal lighting, and more optimum conditions for greenbug reproduction.

The F value for testing a difference due to varieties was significant at the .01 level of probability. An LSD of 1.0 was used to test differences between the sorghum varieties when averaged over growth stages. In all three near-isogenic pairs, the rate of reproduction of the greenbug was lower on the bloomless sorghums when compared with their near-isogenic bloom sorghums. There was no significant difference between the near-isogenic bloom and bloomless entries except for Martin bloomless which was significantly lower than Martin bloom. The Martin bloomless was not significantly different from the resistant Shallu Grain. The rate of reproduction was about the same for both the bloom and bloomless RCK-60.

There were no significant differences between any of the entries in growth stage 1 including the resistant check on the rate of reproduction of the greenbug. This occurrence was attributed to the

TABLE IV

SEASON 2. AVERAGE NUMBER OF OFFSPRING FROM TWO ADULT GREENBUGS

Growth stage	BOK8	RCK-60		Martin		RWD3 x Weskan		Shallu Grain	$\bar{x}$
		bloom	bloom-less	bloom	bloom-less	bloom	bloom-less		
1	4.2	4.5	4.3	4.4	4.1	4.5	4.9	3.4	4.3
2	6.6	5.9	5.9	7.2	5.5	8.4	6.6	4.7	6.35
$\bar{x}$	5.4	5.2	5.1	5.8	4.7	6.4	5.6	4.1	5.3

TABLE V

ANALYSIS OF VARIANCE FOR DAILY MEANS IN SEASON 2

Source	d.f.	MS	F
Replications	2	2.538	
Growth stages	1	51.634	76.776**
Error a	2	.673	
Variety	7	3.235	4.307**
Growth stage x variety	7	1.308	1.742
Error b	28	.751	

**Significant at the .01 level of probability.

environmental effects. In growth stage 2, the reproduction rates on bloomless sorghums were significantly lower than those on the bloom sorghums for the Martin and RWD3 x Weskan entries. The bloomless sorghums, however, were not significantly different from the susceptible BOK8 check.

There was no significant growth stage x variety interaction in season 2. Differences between the near-isogenic bloom and bloomless Martin and RWD3 x Weskan sorghums were larger during growth stage 2 than in growth stage 1. But these differences cannot be attributed to increased resistance in the plant at later growth stages because of the environmental effects in growth stage 1.

Season 3

Table VI gives the daily means for the sorghum entries at each growth stage in season 3. The analysis of variance for daily means is given in Table VIII.

The average rate of reproduction for all varieties in growth stage 1 was less than that of growth stage 2 but the difference was not significant. There were four cloudy days during the 20 day counting period in growth stage 1. In growth stage 2, the temperatures were rising above optimum for greenbug reproduction during the last five days of the counting period. The rate of reproduction declined during these five days.

The F value for testing a difference due to varieties was significant at the .01 level of probability. When the varieties were averaged over growth stages, the rate of reproduction of the greenbug was lower on the bloomless sorghums than on their near-isogenic bloom

TABLE VI

SEASON 3. AVERAGE NUMBER OF OFFSPRING PER DAY FROM TWO ADULT GREENBUGS

Growth Stage	BOK8	RCK-60		Martin		RWD3 x Weskan		Shallu Grain	$\bar{x}$
		bloom	bloom-less	bloom	bloom-less	bloom	bloom-less		
1	5.6	4.7	5.4	4.8	5.7	5.8	4.6	3.1	5.0
2	6.5	6.0	5.2	7.1	5.6	5.0	4.8	4.1	5.5
$\bar{x}$	6.1	5.4	5.3	5.9	5.7	5.4	4.7	3.6	

TABLE VII

SEASON 4. AVERAGE NUMBER OF OFFSPRING PER DAY FROM TWO ADULT GREENBUGS

Growth stage	BOK8	RCK-60		Martin		RWD3 x Weskan		Shallu Grain	$\bar{x}$
		bloom	bloom-less	bloom	bloom-less	bloom	bloom-less		
3	5.9	5.1	5.6	5.7	6.5	5.2	5.8	5.3	5.6

TABLE VIII

ANALYSIS OF VARIANCE FOR DAILY MEANS
IN SEASON 3

Source	d.f.	MS	F
Replications	3	1.395	
Growth stages	1	10.540	5.639
Error a	2	1.869	
Variety	7	4.926	4.570**
Growth stage x variety	7	1.826	1.694
Error b	35	1.078	

**Significant at the .01 level of probability.

TABLE IX

ANALYSIS OF VARIANCE FOR DAILY MEANS
IN SEASON 4

Source	d.f.	MS	F
Replications	6	1.413	
Variety	7	1.532	1.032
Error	41	1.485	

counterparts. None of the differences between the isogenic pairs were significant at the .05 level of probability. The reproduction rate on RWD3 x Weskan bloomless was not significantly different from that on the resistant Shallu Grain, where those of the other sorghum entries were, and it was significantly different from that on the susceptible BOK8.

In growth stage 1, the rates of reproduction of the greenbug on the bloomless lines of RCK-60 and Martin were higher than those of the bloom lines. This occurrence was attributed to chance. In growth stage 2, the rates of reproduction of the bloomless lines were lower than those of their respective bloom lines, but not significantly lower.

Season 4

Table VII gives the daily means for the sorghum entries. Only growth stage 3 was studied in this season. The analysis of variance for season 4 is given in Table IX.

There was no significant difference among varieties at the .05 level of probability. In the three near-isogenic pairs, the rates of reproduction of the greenbug were higher on the bloomless lines than on their near-isogenic bloom lines. The rate of reproduction of the greenbug on the resistant Shallu Grain was higher than that on RCK-60 bloom and RWD3 x Weskan bloom.

During this growth stage, the plants were severely infested with the two-spotted spider mite. All plants were mottled and light green in color and some of the plants died before the counting period ended. The occurrence of higher rates of reproduction on the bloomless varieties and the occurrence of a high rate of reproduction on the resistant Shallu Grain was attributed to damage to the plant from the spider mite.

In all seasons except season 4, the rate of reproduction of the greenbug was lower on the bloomless sorghums than on their respective near-isogenic bloom sorghums. The differences, however, were not significant at the .05 level of probability. The reproduction rate on Martin bloomless was significantly different from that on Martin bloom in season 2. There were larger differences between the reproduction rates on the near-isogenic bloom and bloomless lines at later growth stages, but these differences were not significant. Differences in plant resistance to the greenbug from one growth stage to another could not be separated from differences in environmental conditions. Differences in growth stages were attributed to environmental conditions.

Nonpreference Study

Individual "t" Tests

The differences between the means (average number of greenbugs) in each pair of sorghum entries for the nonpreference study of 10-day old plants are given in Table X. There was a significant difference between the means in only one pair of sorghum entries in the 10-day old study. The resistant Shallu Grain was significantly different from the RCK-60 bloomless at the .05 level of probability. The number of greenbugs on the resistant Shallu Grain was always lower than when paired with each of the other entries. When the near-isogenic bloom

TABLE X

DIFFERENCES BETWEEN MEANS IN EACH PAIR FOR THE NONPREFERENCE STUDY ON 10-DAY OLD PLANTS

Variety	RWD3 x Weskan		RCK-60		Martin		Shallu Grain
	bloom	bloom-less	bloom	bloom-less	bloom	bloom-less	
BOK8	-0.8[1/]	-3.3	-1.2	-2.0	-3.2	0.5	1.4
RWD3 x Weskan bloom		-0.6	-0.8	-2.0	-2.0	0.6	4.0
RWD3 x Weskan bloomless			-2.0	0.8	-1.0	-3.2	0.6
RCK-60 bloom				0.7	1.2	-1.0	0.8
RCK-60 bloomless					0.2	-3.0	4.0*
Martin bloom						0.4	3.4
Martin bloomless							2.4

[1/] The mean of the variety at the top of the column is subtracted from the mean of the variety at the beginning of the row.

*Significant at the .05 level of probability.

and bloomless entries were paired, the bloomless entries had lower means than their respective bloom entries except for the RWD3 x Weskan pair. The differences between the pairs were small.

There is no indication in this analysis of the presence of the nonpreference mechanism of greenbug resistance in the bloomless sorghums when the plants were 10 days of age.

The differences between the means in each pair of sorghum entries for the study when the plants were 40 days of age are given in Table XI. There was a significant difference between the means of one pair of sorghum entries in this age group. The mean of the RWD3 x Weskan bloom was significantly lower than that of the RCK-60 bloom.

All of the bloomless entries had lower means when compared with their near-isogenic bloom entries. All of the bloomless entries had lower means when compared with the susceptible BOK8 and when compared with the other bloom entries except for one pair in which the Martin bloomless had a higher mean than the RWD3 x Weskan bloom. The resistant Shallu Grain always had a lower mean when paired with the other entries.

There was an indication in this analysis of the presence of the nonpreference mechanism of greenbug resistance in the bloomless sorghums at 40 days of age.

The differences between the means in each pair of sorghum entries for the study when the plants were 60 days of age are given in Table XII. The mean of the resistant Shallu Grain was significantly lower than that of the RCK-60 bloomless. None of the other differences between means were significant.

TABLE XI

DIFFERENCES BETWEEN MEANS IN EACH PAIR FOR THE NONPREFERENCE STUDY ON 40-DAY OLD PLANTS

Variety	RWD3 x Weskan		RCK-60		Martin		Shallu Grain
	bloom	bloom-less	bloom	bloom-less	bloom	bloom-less	
BOK8	2.0[1/]	1.3	0.6	0.2	-1.0	3.0	3.4
RWD3 x Weskan bloom		2.0	-2.2*	2.0	-2.8	-1.8	2.0
RWD3 x Weskan bloomless			-4.3	-1.8	-2.2	3.5	3.0
RCK-60 bloom				2.8	1.8	2.8	0.4
RCK-60 bloomless					-1.4	-0.3	0.4
Martin bloom						1.6	1.0
Martin bloomless							2.2

[1/] The mean of the variety at the top of the column is subtracted from the mean of the variety at the beginning of the row.

*Significant at the .05 level of probability.

TABLE XII

DIFFERENCES BETWEEN MEANS IN EACH PAIR FOR THE NONPREFERENCE STUDY ON 60-DAY OLD PLANTS

Variety	RWD3 x Weskan		RCK-60		Martin		Shallu Grain
	bloom	bloom-less	bloom	bloom-less	bloom	bloom-less	
BOK8	0.5[1/]	1.0	2.4	0.4	1.8	-3.6	1.2
RWD3 x Weskan bloom		0.0	0.0	-1.0	1.2	-0.5	2.25
RWD3 x Weskan bloomless			-1.8	0.2	-0.6	-0.4	-1.2
RCK-60 bloom				-1.0	2.6	-2.6	0.3
RCK-60 bloomless					0.6	2.4	4.0*
Martin bloom						-1.6	2.5
Martin bloomless							3.4

[1/] The mean of the variety at the top of the column is subtracted from the mean of the variety at the beginning of the row.

*Significant at the .05 level of probability.

The resistant Shallu Grain always had a lower mean when compared with the other entries in this age group except when compared with RWD3 x Weskan bloomless. There was no difference between the means of RWD3 x Weskan bloom and bloomless. The means for the RCK-60 bloomless and Martin bloomless entries were higher than their respective near-isogenic bloom entries. The RWD3 x Weskan bloomless entry always had a lower mean when compared with the other entries except when compared with RCK-60 bloomless.

There was no indication in this analysis of the presence of the nonpreference mechanism of greenbug resistance in the bloomless sorghums when the plants were 60 days of age. The plants at this age, however, were severely infested with the two-spotted spider mite. Some of the plants were stunted and some were dead at the time of counting because of the spider mite infestation. Consequently, the presence of the nonpreference mechanism of greenbug resistance could not be detected in the damaged sorghum.

Least Squares Analysis

The least squares analysis of variance was computed to obtain least squares means for the varieties to rank them accordingly. In the analysis, there were no significant differences among the replications or among the pairs of sorghum entries.

The least squares means for the varieties at 10 days of age are ranked from highest to lowest in Table XIII. The average number of greenbugs, when averaged over its competitors, was lowest on the resistant Shallu Grain and highest on the Martin bloom. In comparing the least squares means using the LSD for each pair of means, there is a significant difference between the means of the Martin bloom and both the BOK8 and Shallu Grain. The least squares mean for the resistant Shallu Grain is significantly different from that of all the varieties except BOK8 and RWD3 x Weskan bloom. The least squares means of the Martin bloomless and RCK-60 bloomless entries were slightly lower than those of their respective bloom entries where that of RWD3 x Weskan bloomless was higher than that of RWD3 x Weskan bloom. The susceptible BOK8 was ranked next to the resistant Shallu Grain.

There was no indication in this analysis of the nonpreference mechanism of greenbug resistance in the bloomless plants at 10 days of age. However, the plants were small when infested, and after 4 days of infestation with 10 adult greenbugs, most of them were wilted at the time of greenbug counting. The comparatively low ranking of the

TABLE XIII

LEAST SQUARES MEANS FOR VARIETIES AT 10 DAYS OF AGE

Variety	Least squares means[1/]
Martin bloom	5.593 a
Martin bloomless	5.327 ab
RCK-60 bloom	5.280 ab
RCK-60 bloomless	5.274 ab
RWD3 x Weskan bloomless	4.967 ab
RWD3 x Weskan bloom	4.727 abc
BOK8 (susceptible)	4.388 bc
Shallu Grain (resistant)	3.936 c

[1/] Means followed by a common letter are not significantly different at the .05 level of probability.

susceptible BOK8 suggests the possibility that damages to the plants by the greenbugs were great enough to repel the greenbugs from the plants for feeding.

The least squares means for varieties when the plants were 40 days of age are ranked in Table XIV.

TABLE XIV

LEAST SQUARES MEANS FOR VARIETIES AT 40 DAYS OF AGE

Variety	Least squares mean[1/]
RCK-60 bloom	5.328 a
BOK8 (susceptible)	5.169 a
Martin bloom	4.946 a
RWD3 x Weskan bloom	4.859 a
RCK-60 bloomless	4.537 a
RWD3 x Weskan bloomless	4.282 a
Martin bloomless	4.254 a
Shallu Grain (resistant)	4.184 a

[1/]Means followed by a common letter are not significantly different at the .05 level of probability.

None of the least squares means for varieties were significantly different among the varieties using the LSD criterion. However, all three bloomless entries were ranked lower than the bloom entries, indicating the presence of the nonpreference mechanism of greenbug resistance in the bloomless varieties at this age of the plant. Some of the plants were infested with the two-spotted spider mite, but infestation was light.

The least squares means for varieties when the plants were 60 days of age are ranked in Table XV.

TABLE XV

LEAST SQUARES MEANS FOR VARIETIES AT 60 DAYS OF AGE

Variety	Least squares mean[1/]
Martin bloomless	5.605 a
RCK-60 bloomless	5.217 a
BOK8 (susceptible)	4.956 ab
RCK-60 bloom	4.938 ab
RWD3 x Weskan bloom	4.895 ab
RWD3 x Weskan bloomless	4.665 ab
Martin bloom	4.637 ab
Shallu Grain (resistant)	4.032 b

[1/] Means followed by a common letter are not significantly different at the .05 level of probability.

The resistant Shallu Grain is again ranked the lowest of the entries. The Martin bloomless and RCK-60 bloomless entries were ranked higher than their respective bloom entries. RWD3 x Weskan bloomless was lower than RWD3 x Weskan bloom. There was a significant difference between the least squares means of Martin bloomless and the resistant Shallu Grain.

There is no indication in this analysis that the nonpreference mechanism of greenbug resistance is present in the bloomless sorghums at this age of the plant. However, the plants were severely infested with spider mites which affected the plants by stunting and death in some cases. Thus, the presence of nonpreference might not be detected because of damage to the plants by the spider mite.

In both analyses, there is indication of the nonpreference mechanism of greenbug resistance when the plants are 40 days of age. The nonpreference mechanism seems to increase as the age of the plant increases from 10 to 40 days of age. However, the differences between the bloom and bloomless varieties were small and not significant in either analysis. A further increase in the nonpreference mechanism of resistance to the greenbug as the age of the plant increased from 40 to 60 days was not detectable possibly because of damage to the plants by the spider mite.

Also, Wood and Starks (41), in determining optimum temperatures for greenbug reproduction, suggested that laboratory tests involving caged plants and atypical environmental conditions may give atypical results.

In the greenhouse where these studies of greenbug resistance were conducted, there were atypical lighting and temperature conditions which could influence greenbug reactions to the plants. The cages may also affect plant and greenbug reactions and give atypical results.

CHAPTER V

SUMMARY AND CONCLUSIONS

Antibiosis and nonpreference mechanisms of greenbug resistance in "bloomless" sorghums were investigated using three near-isogenic bloom and bloomless pairs of grain sorghum. A susceptible and a resistant variety were also included in the greenhouse studies.

The antibiosis mechanism studied was the daily rate of reproduction of the greenbug. This study was conducted at three growth stages of the plant with each growth stage being a period of 20 days. Ten replications of each growth stage were conducted over four different seasons.

The nonpreference mechanism of resistance was studied using a paired experiment at three different ages of the plant. The eight sorghum entries were paired with each other to determine the degree of nonpreference between them. The experiment was replicated five times at each age of the plant. The three ages of the plants were 10 days, 40 days, and 60 days of age. Individual "t" tests were used to determine differences between the sorghum entries in each pair and a least squares analysis was used to rank the varieties according to their least squares means.

In the antibiosis study, the rate of reproduction of the greenbug was lower rather consistently on the bloomless sorghums than on their respective near-isogenic bloom sorghums. The differences between them, however, were not significant at the .05 level of probability. In season 4, the rate of reproduction of the greenbug was higher on the bloomless sorghums than on the bloom sorghums. However, the plants were severely damaged by spider mites. The higher rates in season 4 were consequently attributed to the damage incurred by the spider mites.

The differences between the rates of reproduction on the bloom and bloomless varieties seemed to increase as the age of the plant increased from one growth stage to another. But an increase in resistance, if any, could not be separated from the difference in environmental conditions from one growth stage to another.

In the nonpreference study, there was no indication of the presence of the nonpreference mechanism of greenbug resistance in the bloomless sorghums at 10 days of age. There was an indication of nonpreference in the bloomless sorghums when the plants were 40 days of age. The mean number of greenbugs on the bloomless sorghums were lower than those on the bloom sorghums. However, there were no significant differences between the number of greenbugs on the near-isogenic bloom and bloomless sorghums. Severe damage to the plants by the spider mite probably prohibited the detection of the nonpreference mechanism of resistance in the bloomless sorghums at 60 days of age.

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