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Categories of Resistance, Antibiosis and Tolerance, to Biotype I Greenbug (*Schizaphis graminum* (Rondani) Homoptera: Aphididae) in Four Sorghum (*Sorghum bicolor* (L.) Moench. Poales:Gramineae) Hybrids

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ABSTRACT: Resistance categories (antibiosis and tolerance) of four sorghum (*Sorghum bicolor* (L.) Moench) hybrids to biotype I greenbug, *Schizaphis graminum* (Rondani), were determined in environmental growth chamber and field studies. Greenbug weight and fecundity were lower on 'Cargill 607E' compared with 'Cargill 797'. Percentage of leaf damage area was significantly less on two resistant hybrids (Cargill 607E and Cargill 797) after a 14-d greenbug feeding period compared to two susceptible hybrids ('Golden Harvest 510B' and Garst 5715). In growth chamber studies on sorghum seedlings, 'Cargill 607E' and 'Cargill 797' reduced greenbug weight significantly compared with 'Golden Harvest 510B' and 'Garst 5715'. Greenbug weight was 2.9 mg/25 greenbugs on 'Cargill 607E', 3.1 mg/25 greenbugs on 'Cargill 797', 3.9 mg/25 greenbugs on 'Golden Harvest 510B', and 4.8 mg/25 greenbugs on 'Garst 5715'. On field grown sorghum plants, 'Cargill 797' did not reduce greenbug growth compared with 'Golden Harvest 510B'. 'Cargill 607E' had a negative impact on weight of greenbugs. Greenbug weight was 7.9 mg/25 greenbugs on 'Cargill 607E', 9.2 mg/25 greenbugs on 'Cargill 797', and 10.0 mg/25 greenbugs on 'Golden Harvest 510B'. 'Cargill 607E' and 'Cargill 797' were resistant to biotype I greenbugs compared with susceptible 'Golden Harvest 510B' and 'Garst 5715'. Antibiosis was confirmed as the primary category of resistance in 'Cargill 607E.' 'Cargill 797' was primarily tolerant but may have some level of antibiosis, because smaller greenbugs developed in some of the studies.

KEY WORDS: plant resistance, aphid feeding, biotype, greenbug weight, antibiosis and tolerance in sorghum hybrids

Sorghum, *Sorghum bicolor* (L.) Moench (Poales:Gramineae) was first reported as a host plant of greenbug, *Schizaphis graminum* (Rondani) (Homoptera: Aphididae) by Passerini in 1863 (Webster and Phillips, 1912). However, greenbugs in the United States were not considered a serious sorghum pest until 1968, when biotype C was discovered (Harvey and Hackerott, 1969; Starks and Wood, 1974). Biotype A and B are not considered to be serious pests of sorghum in the United States, although it was reported that biotype B could be virulent to sorghum (Harvey and Hackerott, 1969).

Resistance (i.e., tolerance, antibiosis, and antixenosis) is the relative amount of heritable qualities of a plant that reduces the degree of damage done by pests (Painter, 1951). Tolerance is a genetic trait of a plant that enables the plant to tolerate higher pest populations before damage occurs compared with a susceptible cultivar while antibiosis is a heritable quality possessed by a plant that adversely affects the life history or biology of the insect (Panda and Khush, 1995). Panda and

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Khush (1995) reported the appearance of new pest biotypes when antibiosis is the major component of resistance. Host plants that possess different categories of resistance are considered more beneficial than the effect of individual categories of resistance that may increase selection pressure (Smith, 1989).

Since the appearance of biotype C, development of greenbug resistant sorghum has been a high priority (Bennett *et al.*, 1990). Deployment of resistant cultivars has been the most effective pest management practice for reducing serious damage to sorghum (Starks *et al.*, 1983; Bramel-Cox *et al.*, 1986; Kofoid *et al.*, 1991; Andrews *et al.*, 1993). Appearance of new greenbug biotypes capable of damaging previously resistance hybrids is a continuing problem with respect to incorporation of greenbug resistance into sorghum management practices (Bramel-Cox *et al.*, 1986).

Sorghum hybrids having biotype C-resistant germplasm were developed for the U.S. southern plains. A widely used biotype C-resistant source SA7536-1 had comparatively high levels of all three-resistance categories: antibiosis, antixenosis, and tolerance (Schuster and Starks, 1973). Use of biotype C-resistant hybrids gradually increased to approximately 50–60% of the U.S. southern plains sorghum acreage until 1979, when biotype E greenbugs were discovered (Porter *et al.*, 1997).

Capbam (known as ‘Sarvasi’), PI220248 and PI264453 were found resistant to biotype E greenbugs after the identification of this biotype in 1979 (Johnson *et al.*, 1981; Porter *et al.*, 1982). In 1990, most of the biotype E-resistant hybrids were found to be susceptible to a newly discovered biotype, biotype I (Harvey *et al.*, 1991). Biotype E resistant hybrid PI 266965 and *Sorghum halepense* (L.) Pers. were resistant to biotype I. A commercial biotype E-resistant hybrid, ‘Cargill 607E’, was reported resistant to biotype I greenbug (Kofoid *et al.*, 1991; Andrews *et al.*, 1993). Grain-type Russian sorghum accessions, PI 550607 and PI550610 had the highest level of resistance to biotype I (Andrews *et al.*, 1993). Greenbugs collected in Haskell County, KS, in 1992, were found to be virulent to Biotype I resistance sorghum line PI 550610. This isolate was designated as biotype K (Harvey *et al.*, 1997).

Antibiosis and antixenosis were found to be the primary categories of resistance in ‘Cargill 607E’, PI 550607 and PI 550610 (Bowling and Wilde, 1996). Based on leaf damage response to greenbug feeding, tolerance was identified as a category of resistance in ‘Cargill 797’ (Girma *et al.*, 1998). Until 1997, ‘Cargill 607E’ was the only biotype I-resistant hybrid available to farmers, and it was limited to southwestern Kansas because it is not well adapted to other regions (Porter *et al.*, 1997). ‘Cargill 607E’ has been commercially available to farmers in the southern plains since 1990.

From an integrated pest management perspective, determination of the categories governing resistance in sorghum should be an important part of any plant resistance program. Interaction of pest numbers and damage are very different on tolerant versus antibiosis greenbug resistant sorghums (Dixon *et al.*, 1990; Teetes *et al.*, 1975). Various general threshold adjustments are incorporated for greenbug resistant versus susceptible sorghum management recommendations (Sloderbeck *et al.*, 2004; Teetes, 1996; Wright *et al.*, 1994). Incorporation of categories of resistance could improve these management recommendations. Also, the impact of predators and parasitoids on greenbugs may differ on antibiotic and tolerant plants. Although several studies have indicated plant resistance and biological control are compatible (Starks *et al.*, 1972; Salto *et al.*, 1983), antibiosis has been reported to have a negative impact on some greenbug predators and parasitoids (Rice and Wilde, 1989; Starks *et*

al., 1972). Resistance categories of 'Cargill 607E' have been investigated and was determined as antibiosis to biotype I greenbugs (Bowling and Wilde, 1996) However in the later studies 'Cargill 607E' and 'Cargill 797' were reported as tolerant when either chlorophyll loss or photosynthetic rate changes were tested (Reese *et al.*, 1994; Girma *et al.*, 1998; Nagaraj *et al.*, 2002). No in-depth studies directly comparing both Cargill hybrids, 607E and 797, have been conducted. Therefore, the objectives of this study were to compare the relative resistance, and the categories of resistance of two biotype I-resistant sorghum hybrids, 'Cargill 607E' and 'Cargill 797'. Additionally, because resistance is a relative rating, this study also included two biotype I susceptible hybrids that showed differential levels of susceptibility in preliminary studies.

Materials and Methods

Sorghum hybrids were selected for this study based on their differential levels of resistance/susceptibility: biotype I susceptible 'Golden Harvest 510B' and 'Garst 5715'; biotype I tolerant 'Cargill 797' (Girma *et al.*, 1998); and biotype I antibiosis 'Cargill 607E' (Bowling and Wilde, 1996).

The biotype I greenbugs used in this study were initially collected from a field near York, Nebraska in 1996, and identified as biotype I following procedures similar to those of Bowling *et al.* (1994). Greenbugs were reared and maintained on biotype I susceptible sorghum hybrid 'Golden Harvest 510B' in a greenhouse. However, greenbugs used in each test were cultured on the same hybrid they were to be tested on for at least one week before each study started.

Relative levels of greenbug resistance and categories of resistance were determined by comparison of greenbug fecundity, sorghum damage and greenbug weight (Bowling and Wilde, 1996). Greenbugs collected from resistant plants with the highest level of antibiosis were expected to be smaller or have reduced fecundity compared to tolerant lines.

Fecundity. To determine greenbug fecundity under controlled environmental conditions, for each sorghum line three seeds of a sorghum hybrid were planted in 7 separate 'SC-10 Super cell' Single Cell Containers (4 diameter × 21 cm depth) (Stuewe & Sons, Inc., Corvallis, OR). There were seven replications. The containers were placed in a plastic holding rack in an environmental growth chamber. Seedlings were thinned to one plant per container after emergence. One-wk-old seedlings were infested with one adult biotype I greenbug and covered with a ventilated polyethylene cage (4.5 by 30.8 cm) and placed in a growth chamber with a photoperiod of 14:10 (L: D) at $25.5 \pm 2^\circ\text{C}$. The next day, the adult and all nymphs but one were removed from each plant. When the remaining nymph matured and started reproducing, greenbug fecundity, as measured by the production of nymphs, was recorded and nymphs were removed from the plant daily.

Greenbug weight. To determine greenbug weight, the four sorghum hybrids were cultured as described for the fecundity test. Five adult biotype I greenbugs, pre-conditioned for 1 wk on the same hybrid, were placed on one-wk-old seedlings and covered with a ventilated polyethylene cage (4.5 by 30.8 cm) and placed in a growth chamber with a photoperiod of 14:10 (L: D) at $25.5 \pm 2^\circ\text{C}$. Because of different growth rates on antibiosis versus tolerant and susceptible lines, aphid weights were

not determined based on a specific number of days after infestation. Before plant quality decreased (less than 10% leaf area damaged), five adults (selected the largest aphids) were collected from each plant. A total of 25 greenbugs was collected from five plants per hybrid per replication and weighed. Greenbugs were stored in a freezer until their weight was recorded.

In another study, 10 greenbugs (pre-conditioned for 1 wk on the same hybrid) were infested on one-wk-old seedlings. To obtain approximately similar age aphids, twenty-four hours after infestation all greenbugs, except nymphs produced during the 24 hr period, were removed from each seedling. The remaining greenbug nymphs were checked daily and on the first day of reproduction all adult greenbugs (largest) were collected from each plant and 25 greenbugs per replication were weighed. There were 8 replications for each hybrid. Nymphs were left on the plants in order to repeat the study on second-generation greenbugs on the same host. Ten adult greenbugs were collected from each plant. A total of 30 greenbugs per replication per treatment were weighed.

A field study was also conducted to determine if plant resistance traits were expressed similarly under laboratory and field conditions. Greenbug adults were collected from replicated caged, field grown sorghum (Cargill 607E, Cargill 797, and Golden Harvest 510B) in 1997 (greenbug life stage was not determined) and 1998 (only adult greenbugs were weighed). The sorghum field was located at the University of Nebraska Agricultural Research and Development Center, near Mead, NE. In 1997, four samples (replications) of greenbugs were taken from each hybrid when plants reached pre-boot stage. A portion of each greenbug sample was transferred to a glass vial and weighed. These greenbugs were counted and the average weight per 25 greenbugs was determined.

Plant Damage and Greenbug Number. This test was conducted to determine the relationship between sorghum plant damage and greenbug numbers. The four sorghum hybrids were grown in the greenhouse as described in the fecundity test. Five adult biotype I greenbugs were infested on a one-wk-old seedling and each plant was covered with a ventilated polyethylene cage (4.5 by 30.8 cm). The plants were placed in a growth chamber with a photoperiod of 14:10 (L: D) at $25.5 \pm 2^\circ\text{C}$. The number of greenbugs (adults and nymphs) and damage was recorded daily until plants died. Cumulative insect-days (Ruppel, 1983) before plant death was used an index of total aphid exposure to compare antibiosis, tolerant, and susceptible hybrids. There were 10 replications for each hybrid. Sorghum damage due to greenbug was assessed by estimating the percentage leaf area damaged.

Statistical Analysis. All experiments were arranged as randomized complete block designs (RCBD). Treatment differences were analyzed using PROC GLM (SAS Institute, 1997). Means were separated using a protected Fisher least-significant difference (LSD) test.

Results

Greenbug Fecundity. There were no significant differences in the greenbug pre-reproductive period among the four hybrids ($F=1.25$; d.f.=3, 18; $P=0.3223$). There were highly significant differences in greenbug reproduction among hybrids ($F=8.16$; d.f.=3, 18; $P=0.0012$). Higher greenbug reproduction was recorded on 'Garst 5715' compared with the other three hybrids, and the lowest on 'Cargill 607E' (Table 1).

Table 1. Greenbug fecundity on resistant and susceptible sorghum hybrids in no-choice tests.

Sorghum hybrids	Greenbug fecundity (nymphs/♀)	
	Total progeny ¹ (N=7)	Progeny/aphid/day (N=7)
Cargill 607E	29.9c	1.2
Cargill 797	41.3b	1.7
Golden Harvest 510B	46.1b	1.8
Garst 5715	59.0a	2.4

¹ Means in a column followed by same letter are not significantly different, Fisher protected LSD, ($P=0.05$).

Greenbug reproduction was higher on 'Garst 5715' from the first day of reproduction through 16 days. Seventy-five percent of the nymphs were produced in 13 days on 'Garst 5715' and 'Cargill 607E', in 14 days on 'Cargill 797' and in 15 days on 'Golden Harvest 510B'. The reproduction study was terminated after 25 days because most greenbugs ceased reproducing for three consecutive days. The reproduction studies showed that 'Cargill 607E' significantly reduced greenbug fecundity when compared to the other hybrids.

Greenbug weight. In the environmental chamber greenbug weight studies, highly significant differences were detected among hybrids, for the first generation ($F=8.46$; d.f.=3, 21 $P=0.0007$) and second generation ($F=25.14$; d.f.=3, 21; $P=0.0001$) studies (Table 2). Greenbugs reared on 'Garst 5715' were heavier than greenbugs reared on 'Cargill 607E' or 'Cargill 797' (Table 2). Greenbugs on 'Cargill 607E' were lighter than those collected from all other hybrids. Results were similar for the second generation study except greenbugs from the two Cargill hybrids were similar in size.

In the 1997 field study, combined weight of greenbug adults and nymphs reared on 'Cargill 607E', 'Cargill 797' and 'Golden Harvest 510B' were not significantly different ($F=2.81$; d.f.=2, 6; $P=0.1378$). In the 1998 study when only adults were weighed, greenbugs collected from 'Cargill 797' and 'Golden Harvest 510B' were significantly ($F=11.86$, d.f.=2; 6; $P=0.0082$) heavier than greenbugs collected from 'Cargill 607E' (Table 3).

Plant Damage and Greenbug Numbers. Significant difference in plant damage on resistant versus susceptible hybrids was detected ($F=30.17$; d.f.=3, 27; $P=0.0001$). Plant damage was visible on all hybrids by the 4th day after greenbug infestation.

Table 2. Weight of adult greenbugs reared on resistant and susceptible sorghum hybrids.

Sorghum hybrids	Greenbug weight ¹	
	Environmental chamber study	
	First generation (mg/25 greenbugs) (N=8)	Second generation (mg/30 greenbugs) (N=8)
Cargill 607E	3.68c	2.80b
Cargill 797	4.76b	3.15b
Golden Harvest 510B	5.43ab	5.31a
Garst 5715	6.17a	5.02a

¹ Means in a column followed by same letter are not significantly different, Fisher protected LSD, ($P=0.05$).

Table 3. Weight of greenbugs grown on resistant and susceptible sorghum hybrids.

Sorghum hybrids	Adult Greenbug Weight (mg/25 greenbugs) ¹		
	Environ. chamber study Adult+Nymph (N=4)	Field study (1997) Adult+Nymph (N=4)	Field study(1998) Adult (N=4)
Cargill 607E	2.88c	3.98a	7.95b
Cargill 797	3.13c	4.03a	9.20a
Golden Harvest 510B	3.93b	4.98a	10.00a
Garst 5715 ²	4.78a	-----	-----

¹ Means in a column followed by same letter are not significantly different, Fisher protected LSD, ($P=0.05$).

² Garst 5715 was not included in the field study.

Fourteen days after greenbug introduction, the two susceptible hybrids, 'Golden Harvest 510B' (87%) and 'Garst 5715' (99%) were more heavily damaged than either resistant hybrid, 'Cargill 607E' (41%) and 'Cargill 797' (51%), (Table 4). When cumulative greenbug pressure (cumulative insect-days) over the course of the study is considered, 'Cargill 797' had 30% more insect-days than 'Cargill 607E,' but comparable insect-days to the two susceptible hybrids, 'Golden Harvest 510B' and 'Garst 5715' (Table 5). However, 'Cargill 797' had 36–48% less damage than the two susceptible hybrids, but the damage level was similar to the other resistant hybrid, 'Garst 607E' (Table 5).

Table 4. Greenbug damage on resistant/susceptible sorghum seedlings.

Sorghum hybrids	Greenbug damage (% leaf area damaged)			
	Days after greenbug infestation			
	4 (N=10)	8 (N=10)	11 (N=10)	14 (N=10)
Cargill 607E	3.0b	7.0c	31.0b	41.0b
Cargill 797	3.0b	12.0bc	38.0b	51.0b
Golden Harvest 510B	3.0ab	18.0ab	58.0a	87.0a
Garst 5715	7.0a	20.0a	71.0a	99.2a

¹ Means in a column followed by same letter are not significantly different, Fisher protected LSD, ($P=0.05$).

Table 5. Relationship between cumulative insect-days and damage to resistant / susceptible sorghum seedling.

Sorghum hybrid	Insect-days ¹ (N=10)	Plant damage (%) (N=10)	Plant damage/Insect-day (N=10)
Cargill 607E	695.4b	41.0b	0.055b
Cargill 797	1005.4a	51.0b	0.049b
Golden Harvest 510B	899.5ab	87.2a	0.098a
Garst 5715	1068.0a	99.2a	0.099a

¹ Numbers in a column followed by same letter are not significantly different, Fisher protected LSD, ($P=0.05$).

Discussion

'Cargill 607E' and 'Cargill 797' were resistant to greenbugs (36–58% less damage) compared to the susceptible hybrids, 'Golden Harvest 510B' and 'Garst 5715'. In all studies, greenbugs on 'Cargill 607E' were less fecund and smaller compared to the two susceptible hybrids, as would be expected from a hybrid with antibiosis characteristics. These data support Bowling and Wilde's (1996) conclusion that antibiosis is the primary category of resistance in 'Cargill 607E'. With respect to 'Cargill 797', because of the higher number of aphids (Table 1), cumulative insect-days (Table 5), slightly larger aphids, and no difference in damage compared to 'Cargill 607E', the data indicate a significant level of tolerance. However, in some studies, particularly compared to 'Garst 5715,' greenbug reproduction and weight were also impacted, indicating that some level of antibiosis is also present. Girma *et al.* (1998) and Nagaraj *et al.* (2002) reported both 'Cargill 607E' and 'Cargill 797' tolerant when chlorophyll and proportional plant weight loss were compared. These results indicate antibiosis may not be detected when cumulative insect-days, intrinsic rate of increase, and adult greenbug weight are not included in resistance screening studies. These results indicate that greenbug weight is also very important in determining levels of antibiosis. Only adult greenbugs should be used for weight determination. Proportionally, there would be fewer nymphs on antibiosis than tolerant hosts when individuals are selected at random. Because of high rates of reproduction on a tolerant host, weight differences between antibiosis and tolerant hosts may diminish when a combination of adults and nymphs are included.

With respect to the susceptible hybrids, greenbugs and damage on 'Garst 5715' were different from the resistant hybrids for all parameters measured, except cumulative insect-days for 'Cargill 797'. The latter difference would be consistent with the classification of 'Cargill 797' as tolerant. Although the damage data supports classification of 'Golden Harvest 510B' as susceptible, the fecundity data and some of the greenbug weight data suggest at least some level of host impact on greenbugs when compared to the other susceptible hybrid, 'Garst 5715'. Although differential levels of susceptibility were observed in some of the tests, the ultimate indicator of resistance, plant damage, was almost identical for the two susceptible hybrids.

The category of resistance is an important factor that needs to be considered in the development of improved pest management decision thresholds. In these studies, cumulative insect-days were not good predictors of final damage across the various categories of resistance. Cumulative insect-days were similar for the tolerant (Cargill 797) and susceptible hybrids, but damage was 36–48% less for the tolerant hybrid. Because tolerant hybrids support relatively large populations of greenbugs before damage occurs, management decision thresholds must be adjusted upward to effectively manage greenbugs. Clearly, plant resistance can be best incorporated into an IPM program when categories of resistance have been elucidated. Knowledge gained from this research will improve our ability to incorporate plant resistance into sustainable greenbug management programs.

Antibiosis has been the primary category of resistance incorporated into greenbug resistant sorghums. These data support previous studies and assertions that tolerance holds strong potential to expand our arsenal of greenbug management strategies. Incorporation of greenbug tolerant hybrids, as well as hybrids with antibiosis traits, should be better than relying primarily on antibiosis (Smith, 1989).

For example, tolerance may be more compatible with biological control than antibiosis due to the continued resource for natural enemies, and possible reduced sequestration of allelochemicals that could affect third trophic level organisms. High levels of antibiosis resistance cause high aphid mortality that may increase the selection pressure for new virulent aphid biotypes while tolerance can minimize aphid damage and sustain aphid populations that are important for reducing selection pressure (Flinn *et al.*, 2001). In addition, determining categories of resistance is crucial in molecular marker studies identifying genes linked to present and future aphid resistance host plant development programs.

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