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Tritrophic Interaction of Parasitoid *Lysiphlebus testaceipes* (Hymenoptera: Aphidiidae), Greenbug, *Schizaphis graminum* (Homoptera: Aphididae), and Greenbug-Resistant Sorghum Hybrids

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ABSTRACT Interactions of the parasitoid *Lysiphlebus testaceipes* (Cresson) and the greenbug, *Schizaphis graminum* (Rondani), on greenbug-resistant 'Cargill 607E' (antibiosis), 'Cargill 797' (primarily tolerance), and -susceptible 'Golden Harvest 510B' sorghum, *Sorghum bicolor* (L.) Moench, were tested using three levels of biotype I greenbug infestation. The parasitoid infestation rate was 0.5 female and 1.0 male *L. testaceipes* per plant. For all three greenbug infestation levels, the parasitoid brought the greenbug under control (i.e., prevented the greenbugs from killing the plants) on both resistant hybrids, but it did not prevent heavy leaf damage at the higher greenbug infestation rates. At the low greenbug infestation rate (50 greenbugs per resistant plant when parasitoids were introduced), greenbugs damaged 5 and 18% of the total leaf area on 'Cargill 797' and 'Cargill 607E', respectively, before greenbugs were eliminated. Leaf damage was higher for the intermediate infestation study (120 greenbugs per plant), 21% and 30% leaf area were damaged on the resistant sorghum hybrids 'Cargill 797' and 'Cargill 607E', respectively. At the high greenbug infestation rate (300 greenbugs per plant), heavy damage occurred: 61% on 'Cargill 607E' and 75% on 'Cargill 797'. The parasitoids did not control greenbugs on the susceptible sorghum hybrid 'Golden Harvest 510B'. *L. testaceipes* provided comparable control on both greenbug-resistant hybrids. This study supports previous studies indicating that *L. testaceipes* is effective in controlling greenbugs on sorghum with antibiosis resistance to greenbugs. Furthermore, new information is provided indicating that *L. testaceipes* is also effective in controlling greenbugs on a greenbug-tolerant hybrid.

KEY WORDS parasitoid, resistance, biological control, antibiosis and tolerant sorghum hybrids

THE PARASITOID *Lysiphlebus testaceipes* (Cresson) has been identified as one of the most important natural enemies of the greenbug, *Schizaphis graminum* (Rondani), in the United States (Hunter 1909, Webster and Phillips 1912, Wadley 1931, Sekhar 1957, Schlinger and Hall 1960, Knipling and Gilmore 1971, Hight et al. 1972, Starks and Wood 1974). *L. testaceipes* is often mentioned in association with greenbug outbreaks. During the greenbug outbreak of 1916, *L. testaceipes* was found in alate greenbugs during their flight northward from sorghum and cornfields (Kelly 1917). Sekhar (1957) reported the parasitoid was effective in controlling greenbugs during the outbreak on wheat in 1939. Jackson et al. (1970) reported *L. testaceipes* was the most abundant parasitoid of greenbugs in Oklahoma in 1969.

Emergence of new virulent greenbug biotypes led to a concerted effort to identify resistant germplasm and transfer the resistance to adapted cultivars (Olonju Dixon et al. 1990). In 1990, ≈40–50% of sorghum acreage was planted to biotype E-resistant sorghum hybrids (Porter et al. 1997). Generally, after deploying resistant hybrids, new greenbug biotypes have occurred. However, no clear cause-and-effect relationship between resistant sorghum hybrids and greenbug biotype development was determined (Porter et al. 1997). Biotype E, I, and K greenbugs virulent to resistant sorghum hybrids have occurred since biotype C was discovered on sorghum in 1968 (Porter et al. 1982; Harvey et al. 1991, 1997).

Greenbug populations in the northern United States sometimes reach high densities after massive migratory flights, probably from southern states (Kieckhefer et al. 1974, Kring and Kring 1990). Fernandes et al. (1998) reported 0.33–0.5 parasitoid per plant can effectively control initial greenbug populations of 20 greenbugs per plant. The parasitoids in some years and locations may be slow to develop and may not control greenbugs. In these situations, insecticides may be necessary to prevent economic losses to sorghum. However, insecticide-resistant greenbugs also have been described (Peters et al. 1975, Teetes et al. 1975, Mayo et al. 1987, Shotkoski et al. 1990, Sloderbeck et al. 1991).

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Plant resistance and biological control methods generally have been assumed to be compatible in modern integrated pest management (IPM) strategies (Horber 1972, Maxwell 1972, Bergman and Tingey 1979, Adkisson and Dyck 1980). Because information on plant resistance mechanisms is not available for many insects, it is not always possible to determine what constitutes compatibility (Duffey and Bloem 1986). The assumptions about compatibility of plant resistance and biological control are based on short-term effects. Long-term effects are often unknown; hence, compatibility with plant-resistance is both speculative and unclear (Duffey and Bloem 1986).

Some research has demonstrated compatibility and enhancement of plant resistance with biological control (Starks et al. 1972, 1974; Salto et al. 1983), whereas other research indicates negative relationships (Landis 1937, Campbell and Duffey 1979, Rice and Wilde 1989). Price et al. (1980) reported unaltered host plant toxins can be tolerated by herbivorous insects but may be toxic to their natural enemies. The ichneumonid *Hyposoter exiguae* (Viereck), a parasitoid of *Helicoverpa zea* (Boddie), was adversely affected by a tomato plant antibiosis compound, α-tomatine, resulting in significantly prolonged larval stages, reduced pupal eclosion, and smaller adult weight (Campbell and Duffey 1979). The development of soybean looper, *Pseudoplusia includens* (Walker), and its parasitoid *Copidosoma truncatellum* (Dalman) was affected by the resistant soybean genotype PI 227687. The parasitoid had a significantly longer pupal stage for individuals developing in *P. includens* fed on a resistant genotype compared with those fed on the susceptible cultivar (Orr and Boethel 1985). Some authors have reported a host preference in *L. testaceipes* to different hosts under different choice conditions. *Aphis gossypii* Glover was not parasitized by *L. testaceipes* when the aphid fed on Palay rubber plants. However, parasitoids attacked the pest when reared on cotton (Knight 1944). Sekhar (1960) reported that *L. testaceipes* preferred *A. gossypii* reared on squash over those reared on hibiscus, and *Myzus persicae* (Sulzer) reared on tobacco over those reared on radish.

L. testaceipes was more effective in controlling biotype C greenbugs on resistant cultivars of sorghum and barley than on susceptible cultivars. However, mummies from aphids reared on resistant barley were significantly smaller than those from susceptible barley (Starks et al. 1972). Salto et al. (1983) found no significant interaction between plant resistance and fecundity of the parasitoid, and they also reported that *L. testaceipes* did not show significant preference either to biotype C or E greenbugs.

The notion that plant resistance is compatible with biological control is appealing but is not well substantiated. Plants probably always influence the third trophic level, but there is lack of detailed information to understand what assists and impedes natural enemies in most systems (Price et al. 1980). Detailed information is needed to better determine whether the two sorghum greenbug pest management approaches, biological control and plant resistance, complement each other, or whether plant resistance has deleterious effects on natural enemies of the greenbugs. Thus, the objective of this study was to determine whether *L. testaceipes* in combination with sorghum hybrids containing antibiosis or tolerance to biotype I greenbugs provided more effective control of greenbugs compared with susceptible sorghum. Sorghum hybrids were selected for this study based on their differential levels of resistance or susceptibility to biotype I greenbugs. Sorghum hybrids included in the study were 'Golden Harvest 510B', biotype I susceptible; 'Cargill 797', biotype I tolerant; and 'Cargill 607E', biotype I antibiosis (Bowling and Wilde 1996, Girma et al. 1998, Nagaraj et al. 2002). Although the differences in the two resistant hybrids were not clear cut, earlier studies indicated that feeding tolerance was greater in 'Cargill 797' and antibiosis was readily apparent in 'Cargill 607E'. Resistance categories of these two hybrids were tested and they represented the best tolerance and antibiosis hybrids available when these studies were initiated (Dogramaci 1998).

Materials and Methods

Biotype I greenbugs used in this study were initially collected from a field near York, NE, in 1996 and identified as biotype I following a procedure similar to Bowling et al. (1994). Greenbugs used in each test were cultured on the same hybrid they were to be tested on for at least 1 wk before each study started.

The three sorghum hybrids were planted in Hummert poly-tainer pots Pc-4 (25.4 by 30.5 by 22.2 cm) and covered with plastic cages (25 cm in diameter by 94 cm). One week after plant emergence, sorghum seedlings were thinned to two plants per pot. The temperature in the greenhouse ranged from 25 to 30°C; temperature was recorded by a hydrothermograph. Photoperiod was 14:10 (L:D) h. When plants were ≈50 cm in height, they were infested with adult greenbugs collected from greenhouse-grown sorghum plants of the same size and cultivar used in the experiment. Greenbugs were first placed on a filter paper slipped around the stem of the plant. This procedure allowed greenbugs to move onto the plant from the filter paper and reduced the number that fell from the plant when greenbugs were placed directly on the leaves with a camel's hair-brush. Seven to 10 d after infesting the plant with greenbugs, two male and one female *L. testaceipes* were released into each parasitoid treatment cage.

Parasitoids were reared in the greenhouse under the same conditions as in the experiments. Mummies were collected from the rearing cages and placed in a Plexiglas (30 by 30 by 30.5 cm) emergence box. After 12 h, emerged parasitoids were collected, and one female and two males were placed in glass (4.5 by 1.45 cm) vials and left ≈2 h to mate. The vials were transferred into the experiment cages, and the parasitoids were released. Because the focus of this study was on greenbug-resistant sorghum, the ratio of greenbugs to female parasitoids was higher than used by Fernandes et al. (1998) to control greenbugs on susceptible sor-

Table 1. Low greenbug density: impact of *L. testaceipes* on the development of greenbugs on resistant/susceptible sorghum hybrids

Sorghum hybrid	Treatment	Days after greenbug infestation[a] (greenbugs per two plants)						
		7	10	16	19	22	31	38
'Cargill 607E'	Parasitoids	99.0c	192.5d	365.0c	750c	900.0b	250.0c	15.0b
'Cargill 607E'	No parasitoids	125.0bc	305.0c	1,195.0c	2,450c	7,450.0a	14,900.0a	6,050.0a
'Cargill 797'	Parasitoids	96.0c	250.0cd	465.0c	900c	950.0b	125.0c	0.0
Cargill 797	No parasitoids	93.0c	240.0cd	920.0c	2,400c	6,350.0a	11,350.0a	—[b]
'Golden Harvest 510B'	Parasitoids	272.5a	605.0b	3,275.0b	5,900b	5,000.0a	—	—
'Golden Harvest 510B'	No parasitoids	205.0ab	715.0a	5,150.0a	8,450a	—	—	—

Within columns, means followed with same letter do not differ significantly at $P = 0.05$ (Fisher's protected LSD test).
[a] Parasitoids were released on day 7 after greenbug infestation.
[b] —, indicates plants were dead.

ghum. After parasitoid infestation, the following data were collected at 3-d intervals until either plant death or greenbugs were brought under control: number of greenbugs (adults and nymphs) and parasitoid mummies per two plants, and average plant damage per cage (percentage of leaf area damaged). Because the emphasis of this study was to compare parasitoids on resistant and susceptible sorghum, extra replications were established in case the parasitoids did not become established in some cages. If the parasitoids did not become established (parasitoid mummies on the plants) in one or more pots in a replication, the entire replication was eliminated, and the remaining replications were included in the analyses.

The experiments were conducted under three different initial greenbug/female parasitoid ratios: low (100:1), intermediate (240:1), and high (600:1). The parasitoids were released into cages when average greenbug numbers on resistant plants reached the predetermined level of 50 (i.e., 100 per two plants), 120, or 300 per plant. In the first two experiments, all three hybrids were initially infested with 20 adult greenbugs per plant. Infesting with the same number of aphids resulted in different numbers of greenbugs on susceptible plants (higher) compared with the resistant plants 7–10 d later when the parasitoids were introduced. In the last experiment, the resistant hybrids were initially infested with higher numbers of greenbugs compared with the susceptible (i.e., 60, 60, and 20 greenbugs per plant, respectively) to have similar numbers of greenbugs on all hybrids when parasitoids were released.

Low Greenbug Population Study with Parasitoids versus No Parasitoids. For each hybrid, the parasitoids were released into half of the cages (two plants per cage) when greenbug numbers on the resistant sorghum hybrids reached 50 greenbugs per plant. The experiment consisted of a randomized complete block design (RCBD). Six treatments were included in the experiment (each hybrid with and without parasitoids), replicated two times, with each pot representing one replication. A block design was used because the temperature inside the greenhouse was not homogeneous, due to uneven cooling and heating in different parts of the greenhouse.

Intermediate Greenbug Population Study with Parasitoids in All Treatments. This test was similar to that described above except all plants were infested with parasitoids and an intermediate (120 greenbugs per resistant plant) number of greenbugs was present when the parasitoids were released. Because the results of the first experiment confirmed that greenbugs eventually kill all sorghum hybrids in the absence of parasitoids, nonparasitoid treatments were discontinued in subsequent studies. The experimental design was a randomized complete block with three treatments (hybrids), and five replications.

High Greenbug Population Study with Similar Greenbug Density at the Time of Parasitoid Infestation. This test was similar to that described above except for the initial greenbug infestation procedure. When the plants were ≈50 cm in height, the cultivars were infested with 60:60:20 mature greenbugs per plant on the antibiosis ('Cargill 607E'), tolerant ('Cargill 797'), and susceptible ('Golden Harvest 510B') sorghum hybrids, respectively. The greenbug numbers used were based on the results of the previous studies that indicated the susceptible sorghum hybrid would produce approximately three-fold more progeny in the 7–10-d period before introduction of parasitoids. If plants did not have an equal number of greenbugs 7 d after greenbug infestation and before the parasitoid release, extra greenbugs were removed by using a brush. Then, two male and one female *L. testaceipes* were released into each cage. After infestation, observations were made and data recorded as in the first experiments. Experimental design was identical to that in the second experiment, but included six replications

Statistical Analysis. All experiments were arranged as RCBDs. Treatment differences were analyzed using PROC GLM (SAS Institute 1997).

Means were separated using a protected Fisher's least significant difference (LSD) test ($P = 0.05$). After all plants of the susceptible sorghum hybrid were killed by greenbugs, the resistant sorghum hybrids were compared overall sampling dates using PROC TTEST (SAS Institute 1997).

Data in all studies were collected at ≈3-d intervals. To avoid long lists of data, only salient dates (population levels at ≈7–10-d intervals, plus peak populations, and peak damage) are included in the tables. Data from all collection dates are included in Dogramaci (1998).

Table 2. Low greenbug density: impact of *L. testaceipes* on damage caused by greenbugs on resistant/susceptible sorghum

Sorghum hybrid	Treatment	Days after greenbug infestation[a] [leaf damage (%)]					
		13	16	22	28	31	38
'Cargill 607E'	Parasitoids	0.0	0	2.5b	5.0b	2.5c	17.5b
'Cargill 607E'	No parasitoids	0.0	0	2.5b	15.0b	55.0b	97.0a
'Cargill 797'	Parasitoids	0.0	0	0.0	5.0b	5.0c	5.0b
'Cargill 797'	No parasitoids	0.0	0	5.0b	25.0b	65.0b	100.0a
'Golden Harvest 510B'	Parasitoids	5.0a	5.0a	82.5a	100.0a	100.0a	100.0a
'Golden Harvest 510B'	No parasitoids	7.5a	22.0a	100.0a	100.0a	100.0a	100.0a

Within columns, means followed with same letter do not differ significantly at $P = 0.05$ (Fisher's protected LSD test).
[a] Parasitoids were released on day 7 after greenbug infestation.

Results

Low Greenbug Population Study with Parasitoids versus No Parasitoids. The parasitoids were released 7 d after greenbug infestation. Three days after parasitoid release, greenbug numbers on 'Golden Harvest 510B' were two- to three-fold higher (significant; $F = 63$; df = 5, 5; $P = 0.0002$) than on 'Cargill 797' and 'Cargill 607E' (Table 1). When the same sorghum hybrids with and without parasitoids were compared, there were ≈15% more greenbugs on 'Golden Harvest 510B' without parasitoids, 50% more greenbugs on 'Cargill 607E', whereas greenbug numbers were similar on 'Cargill 797' (Table 1).

In the parasitoid treatments, greenbug numbers peaked by 19 d after introduction of greenbugs (12 d after parasitoid release) on 'Golden Harvest 510B' and 22 d on 'Cargill 607E' and 'Cargill 797'. Without parasitoids the greenbug populations were considerably higher and peaked by 19 d on 'Golden Harvest 510B' and 31 d on 'Cargill 797' and 'Cargill 607E' (Table 1). The decreasing greenbug population after day 19 on 'Golden Harvest 510B', with the parasitoids, was probably due more to the rapid decline in plant quality as a result of greenbug feeding than to the parasitoids. Without the parasitoids, greenbugs killed susceptible sorghum hybrids ≈2 wk earlier than resistant sorghum hybrids. Susceptible sorghum lasted slightly longer (1 wk) in the presence of the parasitoids, but eventually all plants were killed by greenbugs (Table 2).

On resistant plants, greenbugs caused very little damage before the parasitoids brought them under control. Total greenbug damage (percentage of total leaf area damaged) was slightly higher on 'Cargill 607E' (17.5%) than on 'Cargill 797' (5%), but both were considerably less than on 'Golden Harvest 510B' (100%) ($F = 54.66$; df = 2, 2; $P = 0.0004$) where all plants were killed by day 22. In the absence of parasitoids, greenbugs increased to very high numbers and eventually killed the resistant hybrids (Table 2). Greenbugs in the absence of parasitoids killed the susceptible hybrid 'Golden Harvest 510B' in ≈21 d after greenbug infestation. In the presence of parasitoids, the susceptible plants remained alive ≈6 d longer.

Intermediate Greenbug Population Study with Parasitoids in All Treatments. Although all plants were initially infested with 20 greenbugs per plant, greenbug numbers on 'Golden Harvest 510B' were significantly higher than on 'Cargill 607E' and 'Cargill 797' 6 d after greenbug infestation (Table 3; $F = 11.77$; df = 2, 8; $P = 0.004$). Greenbug populations continued to increase and peaked on 'Cargill 797' by 27 d and on 'Cargill 607E' by 31 d after greenbug introduction (Table 3), whereas greenbugs on 'Golden Harvest 510B' peaked by 19 d after infestation. Greenbug populations rapidly increased on 'Golden Harvest 510B' regardless of the parasitoids, whereas on the resistant hybrids, greenbugs decreased due to control exerted by the parasitoids (Table 3).

Six days after releasing the parasitoids, parasitoid mummies were significantly higher on 'Golden Harvest 510B' than on 'Cargill 797' and 'Cargill 607E' ($F = 8.23$; df = 2, 8; $P = 0.012$) (Table 4). However, there was no significant difference in the final number of first generation parasitoid mummies among hybrids on day 19 (9 d postintroduction of parasitoids; $F = 2.76$; df = 2, 8; $P = 0.12$). The parasitoid did not complete its second generation on the susceptible sorghum before the plants died as a result of heavy greenbug damage. Because plants died due to greenbug damage, no additional mummies were recorded on 'Golden Harvest 510B'. Parasitized greenbugs increased to 9,020 per two plants on 'Cargill 797' and by 8,500 on 'Cargill 607E' by the time all greenbugs were elimi-

Table 3. Intermediate greenbug density: greenbug numbers on resistant/susceptible sorghum hybrids

Sorghum hybrid	Days postgreenbug infestation[a] (greenbugs per two plants)						
	6	13	19	27	31	34	45
'Cargill 607E'	112.0b	500.0b	2,600.0b	6,920.0a	7,740a	5,430.0a	80.0a
'Cargill 797'	125.0b	518.0b	2,400.0b	5,800.0a	2,980a	1,650.0a	24.0a
'Golden Harvest 510B'	235.0a	1,700.0a	13,460a	—[b]	—	—	—

Within columns, means followed with same letter do not differ significantly at $P = 0.05$ Fisher protected LSD test.
[a] Parasitoids were released on day 10 after greenbug infestation.
[b] —, indicates plants were dead.

Table 4. Intermediate greenbug density: number of parasitoid mummies on resistant/susceptible sorghum hybrids

Sorghum hybrid	Days postgreenbug infestation[a] (parasitoid mummies per two plants)				
	16	19	27	34	45
'Cargill 607E'	21.4b	107.2a	1,094.0a	5,820.0a	8,500.0a
'Cargill 797'	25.2b	164.6a	1,652.0a	6,800.0a	9,020.0a
Golden Harvest 510B[b]	69.0a	219.6a	—[c]	—	—

Within columns, means followed with same letter do not differ significantly at $P = 0.05$ (Fisher's protected LSD test).
[a] Parasitoids were released on day 10 following greenbug infestation.
[b] No additional mummies were recorded after the first parasitoid generation because susceptible sorghum plants died due to greenbug damage.
[c] —, indicates plants were dead.

Table 5. Intermediate greenbug density: impact of *L. testaceipes* on greenbug damage to resistant/susceptible sorghum hybrids

Sorghum hybrid	Days postgreenbug infestation[a] [leaf damage (%)]				
	13	19	27	34	45
'Cargill 607E'	0.0b	0.0b	11.0b	20.0b	30.0b
'Cargill 797'	0.0b	0.0b	14.0b	18.0b	21.0b
'Golden Harvest 510B'	9.0a	52.0a	100.0a	100.0a	100.0a

Within columns, means followed with same letter do not differ significantly at $P = 0.05$ Fisher protected LSD test.
[a] Parasitoids were released on day 10 following greenbug infestation.

nated by the parasitoids (Table 4). After the susceptible sorghum hybrid was killed by greenbugs (22 d postgreenbug infestation), there was no significant difference in the cumulative number of mummies on the two resistant hybrids ($t = -1.14$, df = 58, $P = 0.2606$).

Damage by greenbugs became visible on the susceptible sorghum 14 d earlier than on resistant sorghum hybrids. Damage increased very quickly on 'Golden Harvest 510B' and reached 100% in 14 d after first damage was recorded, whereas damage was only 14 and 11% on 'Cargill 797'and 'Cargill 607E', respectively (Table 5). Damage on 'Cargill 607E' and 'Cargill 797' increased to 30 and 21%, respectively, by the time all greenbugs were eliminated by *L. testaceipes* (Table 5). Although slightly higher damage was detected on 'Cargill 607E' than on 'Cargill 797', the difference was not significant ($t = 0.71$, df = 43.6, $P = 0.4813$).

High Greenbug Population Study with Similar Greenbug Density at the Time of Parasitoid Infestation. Approximately equal numbers of greenbugs (≈300 per plant) were present on each hybrid at the time parasitoids were released 7 d after greenbug infestation. Greenbug populations reached 7,083 greenbugs per two plants on 'Cargill 607E' and 5,983 greenbugs on 'Cargill 797' when greenbugs killed 'Golden Harvest 501B' (day 20, Table 6). Greenbug populations started to decrease after day 13 on 'Golden Harvest 510B', by day 20 on 'Cargill 797', and by day 23 on 'Cargill 607E'. As in the previous experiments, decreasing greenbug populations on 'Golden Harvest 510B' were due primarily to poor plant quality as a result of heavy greenbug damage. Although, on most 'Cargill 607E' and 'Cargill 797' plants, greenbug populations decreased due to control by the parasitoid, on some plants the parasitoids did not provide timely control of greenbugs and heavy levels of damage were recorded. Resistant plants had moderately heavy levels of damage (27% Cargill 607E and 35% Cargill 797) when overall greenbug numbers began decreasing due to the parasitoids or poor host plant quality.

In the first parasitoid generation (days 15–23), the highest numbers of mummies counted were 46.2 on 'Golden Harvest 510B', 90.7 on 'Cargill 797', and 57.3 on 'Cargill 607E'. The second generation of parasitoids did not complete development on 'Golden Harvest 510B', because of heavy greenbug damage. A total of 5,950 mummies were recorded on 'Cargill 607E' and 2,485 on 'Cargill 797' by 53 d (Table 7). Although the total number of mummies were higher on 'Cargill 607E' compared with 'Cargill 797', the cumulative number of parasitoid mummies on the two resistant hybrids was not significantly different ($t = 1.62$, df = 10, $P = 0.14$).

Unlike the low and intermediate initial greenbug infestation levels, at the high greenbug density the parasitoids did not prevent heavy plant damage. The susceptible 'Golden Harvest 510B' plants were heavily damaged (Table 8) and died ≈20 d after greenbug infestation. On the same date, 'Cargill 607E' and 'Cargill 797' had 17.5 and 35% damage, respectively (Table 8). Average damage increased to 61% on 'Cargill 607E' and 75% on 'Cargill 797' by the time greenbugs were controlled by the parasitoids. Although, 'Cargill 797' had a higher level of damage than 'Cargill 607E' when the experiment was terminated,

Table 6. High greenbug density: greenbug numbers on resistant/susceptible hybrids

Sorghum hybrid	Days postgreenbug infestation[a] (greenbugs per two plants)						
	6	13	20	23	33	42	53
'Cargill 607E'	578.3a	3,083.3b	7,083.3a	8,450.0a	3,983.3a	1,166.7a	150.0a
'Cargill 797'	611.7a	3,591.7b	5,983.3a	4,183.0b	733.3b	23.3b	0.0a
'Golden Harvest 510B'	645.0a	5,158.3a	—[b]	—	—	—	—

Within columns, means followed with same letter do not differ significantly at $P = 0.05$ 'Fisher's protected LSD test).
[a] Parasitoids were released on day 7 following greenbug infestation.
[b] —, indicates plants were dead.

Table 7. High greenbug density: number of *L. testaceipes* mummies (parasitized greenbugs) on resistant/susceptible sorghum hybrids

Sorghum hybrid	Days postgreenbug infestation[a] (no. parasitoid mummies per two plants)							
	13	15	17	20	23	33	42	53
'Cargill 607E'	9.7a	30.3b	40.5a	57.3a	52.5a	4,208.0a	5,275.0a	5,950.0a
'Cargill 797'	22.5a	76.8a	90.7a	90.7a	90.7a	1,850.0a	2,517.0a	2,485.0a
'Golden Harvest 510B'	35.8a	46.2ab	46.2a	46.2a	—[b]	—	—	—

Within columns, means followed with same letter do not differ significantly at $P = 0.05$ (Fisher's protected LSD test).
[a] Parasitoids were released on day 7 after greenbug infestation.
[b] No additional mummies were recorded after the first parasitoid generation because susceptible sorghum plants were killed by greenbugs.

the difference was not significant ($t = -0.67$, df = 10, $P = 0.52$).

Discussion

Resistant sorghum hybrids in combination with *L. testaceipes* were highly effective in controlling greenbugs, but they did not prevent heavy damage at the high greenbug infestation level. In the absence of parasitoids, greenbugs killed both resistant and susceptible hybrids, but resistant hybrids lived longer.

Similar to the results reported by Fuentes-Granados et al. (2001) on greenbug-resistant wheat, the first parasitoid generation mummies and emergence of adult parasitoids were observed earlier on susceptible sorghum than on the resistant sorghum. However, early emergence of the parasitoids did not seem to help control greenbugs on susceptible plants. Resistant hybrids tolerated greenbugs over a longer period of the time, probably because of a combination of reduced reproductive rate and greater tolerance to greenbug feeding. On the resistant hybrids, greenbug populations declined due to the parasitoids after the second parasitoid generation.

Parasitoids provided good greenbug control and damage prevention on resistant hybrids 'Cargill 797' (5% leaf damage) and 'Cargill 607E' (18% leaf damage) when initial greenbug densities were low (≈50 greenbugs per resistant plant) at time of parasitoid establishment. In this study, greenbug numbers on the susceptible hybrid 'Golden Harvest 510B' were higher (100 greenbugs per plant) than on the resistant sorghum hybrids. At this density, the parasitoids slightly reduced greenbug numbers on the susceptible sorghum hybrid and plants lived slightly longer (6 d).

At the intermediate greenbug density level (≈120 greenbugs per resistant plant at the time the parasitoids were released), parasitoids also brought greenbugs under control on the resistant hybrids but slightly more leaf damage occurred ('Cargill 607E', 30%; and 'Cargill 797', 21%). As in the low infestation study, greenbugs killed the susceptible sorghum hybrid before the second parasitoid generation could be completed.

At the high greenbug population density (≈300 greenbugs per plant) at time of parasitoid establishment, parasitoids brought greenbugs under control on most of the resistant plants, but not before heavy damage occurred: 'Cargill 607E', 61% leaf damage; and 'Cargill 797', 75%.

Under low-to-intermediate greenbug levels, *L. testaceipes* provided greenbug control on the tolerant hybrid 'Cargill 797' that was at least equal to or slightly better (9–12% less leaf damage) than the antibiosis hybrid, 'Cargill 607E'. Parasitoids slightly slowed greenbug development and damage on the susceptible hybrid, but they did not prevent greenbugs from killing the plants.

Parasitoids in combination with sorghum hybrids possessing either antibiosis or tolerance resistance to greenbugs resulted in high levels of plant protection, especially at the low and intermediate infestation levels. Whether the level of protection provided would have maintained pest damage below the economic injury level (EIL) cannot be directly assessed from the data collected in these studies. However, some inferences are possible. Considering only greenbug number, the low infestation rate (an initial 100:1 ratio of greenbugs to female parasitoids) on resistant sorghum prevented greenbug numbers from reaching the resistant hybrid EIL of 2,500–3,000 greenbugs per plant proposed by Teetes (1982, 1994). At the intermediate infestation rate (240:1), parasitoids maintained greenbug levels below 3,000 per plant on the tolerant hybrid, but greenbugs on the antibiosis sorghum hybrid reached almost 4,000 per plant before the number of greenbugs started to decrease. Obviously, economic damage is influenced by a variety of factors not accounted for in this study, but the results of this study

Table 8. High greenbug density: impact of *L. testaceipes* on greenbug damage caused to resistant/susceptible sorghum hybrids

Sorghum hybrid	Days postgreenbug infestation[a] [leaf damage (%)]					
	13	20	23	33	42	53
'Cargill 607E'	1.7b	17.5b	27.5b	53.3b	55.8b	61.0b
'Cargill 797'	8.3b	35.0b	55.0b	78.3ab	76.1ab	75.0ab
'Golden Harvest' 510B	46.6a	100.0a	100.0a	100.0a	100.0a	100.0a

Within columns, means followed with same letter do not differ significantly at $P = < 0.05$ (Fisher's protected LSD test).
[a] Parasitoids were released on day 7 after greenbug infestation.

indicate the combined benefits of *L. testaceipes* and resistant sorghum, even at the high infestation rate.

Our studies on the tritrophic interactions of *L. testaceipes* and biotype I greenbugs on resistant and susceptible sorghum support earlier studies by Starks et al. (1972) indicating that the combination of biological control and antibiosis plant resistance seems to be compatible and that control of greenbugs is highest when the two tactics were used in combination. Additionally, this study adds new information indicating that tolerance was as effective as antibiosis in reducing greenbug damage under both low and intermediate greenbug levels. The parasitoids (0.5 per plant) effectively controlled greenbugs at low and intermediate initial levels of greenbugs (50–120 greenbugs per resistant plant) on resistant plants. The intermediate rate is approximately 6 times higher than the ratio of 0.5 parasitoid per 20 greenbugs per plant that controlled greenbugs on susceptible sorghum hybrids reported by Fernandes et al. (1998). This study confirms that a hybrid with primarily tolerance to greenbugs is also effective in reducing greenbug damage. These studies indicate that sorghum, with either tolerance or antibiosis resistance to greenbugs, may significantly increase the effect of parasitoids in controlling greenbug populations.

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