Antibiosis Effect of Sorghum on the Convergent Lady Beetle (Coleoptera: Coccinellidae), a Third-Trophic Level Predator of the Greenbug (Homoptera: Aphididae)

MARLIN E. RICE[1] AND GERALD E. WILDE

Department of Entomology, Kansas State University,
Manhattan, Kansas 66506

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ABSTRACT The effects of a tri-trophic level (grain sorghum–greenbug–coccinellid) interaction were examined in the laboratory using greenhouse-grown plants. Two resistant sorghum, *Sorghum bicolor* (L.) Moench, hybrids, Dekalb DK-41Y and DK-59E, which exhibit antibiosis to greenbugs, *Schizaphis graminum* (Rondani), were tested along with a greenbug-susceptible hybrid, Horizon 101G. Single egg clusters from *Hippodamia convergens* Guerin females were randomly separated at hatching into two groups. Each group was fed greenbugs from either a resistant or susceptible grain sorghum hybrid. Plant antibiosis reduced larval–pupal survival and increased the amount of time from egg eclosion to pupation in coccinellids that fed on greenbugs from both of the resistant hybrids compared with the susceptible hybrid. Survival to adulthood was 82.9% in the 101G-susceptible treatment and 62.1% for larvae fed greenbugs from resistant DK-41Y. Survival was 91.6% in the susceptible 101G treatment and 86.5% in the resistant DK-59E treatment. Resistant sorghum hybrid DK-59E had a significant treatment-by-sex interaction effect on coccinellid adult weights, with females that consumed greenbugs from the resistant hybrid weighing less, whereas males weighed more when compared with the respective sexes feeding on greenbugs from the susceptible sorghum hybrid.

KEY WORDS Insecta, *Hippodamia convergens*, *Schizaphis graminum*, tri-trophic interactions

HOST-PLANT RESISTANCE and biological control strategies usually have been assumed to be generally or highly compatible in integrated pest management systems (Horber 1972, Maxwell 1972, Bergman & Tingey 1979, Adkisson & Dyck 1980, Kogan 1982). Because detailed information on a crop's mechanism(s) of resistance to a given insect species may be limited or lacking, it is not always possible to determine what comprises compatibility (Duffey & Bloem 1986). However, the assumption of compatibility remains untested in many areas. Long-term effects on biological control are unknown, therefore compatibility with host-plant resistance is both speculative and vague (Duffey & Bloem 1986). Problems also may arise if the pest species develops tolerance to the antibiotic while the natural enemy remains sensitive (Campbell & Duffey 1979). This concern becomes apparent when the desire is to use a plant chemical as a basis for resistance against a given herbivorous insect while at the same time not adversely affecting the insect's natural enemies (Duffey & Bloem 1986). Maxwell (1972) additionally cautioned for the need to determine whether host-plant resistance affects beneficial insects and their efficiency.

Research has been conducted demonstrating both compatibility and enhancement of host-plant resistance with biological control. The parasitic wasp, *Lysiphlebus testaceipes* (Cresson), more effectively reduced greenbug populations on resistant varieties of sorghum and oats than on less resistant varieties (Starks et al. 1972, Schuster & Starks 1975).

However, incompatibility (i.e., chemical antibiosis) also has been recorded by a number of researchers. Plant toxins, more or less unaltered from the plant, may render herbivorous insects toxic to their predators (Price et al. 1980). Nymphal mortality in the predaceous pentatomid, *Podisus maculiventris* Say, was only 33% when preying upon *Leptinotarsa decemlineata* (Say) larvae that had consumed tomato plants, but mortality increased to 89% when host larvae ate foliage of *Solanum carolinense* L. or *Solanum atropurpureum* Schrank (Landis 1937). The ichneumonid, *Hyposoter exiguae* (Viereck), which parasitizes *Heliothis zea* (Boddie), is toxified by a tomato plant antibiotic, alpha-tomatine, resulting in significantly prolonged larval duration, reduced pupal eclosion, and smaller adult weights (Campbell & Duffey 1979). Resistant soybean genotype PI 227687 similarly affected the development of the soybean looper, *Pseudoplusia includens* (Walker), and its parasitoid, *Copidosoma truncatellum* (Dalman). Parasitoid pupal duration was significantly longer for individuals developing in *P. includens* fed a resistant genotype than for those from larvae fed a susceptible cultivar (Orr & Boethel 1985).

[1] Current address: Department of Entomology, Iowa State University, Ames, Iowa 50011.

Table 1. Influence of antibiosis in sorghum on *H. convergens* days to pupation, adult weight, and survival to adult eclosion

Resistant hybrid[a]	Source of variation	df	*F* and *P* values for dependent variables[b] Days to pupation	Adult wt	% survival
Dekalb DK-41Y	Parent	13	18.28 ($P = 0.0001$)	14.60 ($P = 0.0001$)	2.35 ($P = 0.069$)
	Treatment	1	4.91 ($P = 0.040$)	NS	7.65 ($P = 0.016$)
	Sex	1	NS	51.06 ($P = 0.0001$)	—
	Treatment × sex	1	NS	NS	—
Dekalb DK-59E	Parent	19	20.48 ($P = 0.0001$)	7.58 ($P = 0.0001$)	7.07 ($P = 0.0001$)
	Treatment	1	4.18 ($P = 0.046$)	NS	3.30 ($P = 0.085$)
	Sex	1	NS	157.23 ($P = 0.0001$)	—
	Treatment × sex	1	NS	4.76 ($P = 0.034$)	—

[a] Susceptible sorghum hybrid Horizon 101G also was used in both experiments.
[b] NS, not significant by analysis of variance (SAS Institute 1982).

The greenbug, *Schizaphis graminum* (Rondani), has been a serious pest of sorghum, *Sorghum bicolor* (L.) Moench, in the United States since 1968 (Kindler et al. 1984), and pest management programs designed to combat the pest have integrated both host-plant resistance and biological control by natural enemies. Greenbug-resistant sorghum reduces greenbug densities through nonpreference and antibiosis and increases the economic injury level through tolerance. Antibiosis also increases the length of greenbug developmental stages but reduces progeny produced per female, adult longevity, and duration of reproductive period (Young & Teetes 1977). In addition to host-plant resistance, greenbug densities can be significantly reduced by endemic coccinellids such as *Coleomegilla maculata lengi* Timberlake and *Hippodamia convergens* Guerin (Rice & Wilde 1988).

Information is lacking on the effects of host-plant resistance on biological control organisms inhabiting sorghum. There is a need to determine if the two pest management approaches complement each other, or if host-plant resistance has detrimental effects on the natural enemies. The objective of this experiment was to determine if antibiosis in grain sorghum could be transferred through greenbugs to a third-trophic level predator, the coccinellid *H. convergens*.

Materials and Methods

First Trophic Level. Greenbug-resistant sorghum hybrids Dekalb DK-41Y, Dekalb DK-59E, and greenbug-susceptible sorghum hybrid Horizon 101G were grown in a greenhouse under natural photoperiods during the spring and summer. Single plants were grown in 3.8-liter plastic pots containing commercial potting soil. All hybrids were situated in metal trays on benches and were uniformly watered and fertilized with N/P/K (20:20:20) as needed.

Dekalb DK-41Y and Dekalb DK-59E exhibit some degree of nonpreference or antibiosis or both to greenbugs (Youngman et al. 1987), and this antibiosis is adversely expressed by smaller and fewer progeny being produced on the resistant plants compared with greenbugs on the susceptible Horizon 101G (unpublished data).

Second Trophic Level. Biotype-E greenbug colonies were established on the sorghum hybrids before growth stage 3 (growing point differentiation, approximately eight-leaf stage, Vanderlip [1979]). Greenbugs that were later fed to coccinellid larvae were not removed from any sorghum hybrid until the plants were at least in the 10-leaf stage and a greenbug colony had been on the plant for a minimum of 2 wk.

Third Trophic Level. Field-collected *H. convergens* females were brought into the laboratory and allowed to oviposit on the inside of a plastic cylinder which enclosed a greenbug colony on a greenbug-susceptible sorghum plant. After a female *H. convergens* laid an egg cluster, it was partitioned from other clusters by a sticky Styrofoam tape (2.54 by 2.54 by 0.3 cm) (Converters, Philadelphia) with a mesh-covered center hole (1.6 cm diameter). The tape enclosure prevented cannibalism by adult *H. convergens* and sibling dispersal after eclosion. After hatching, the larval coccinellids usually remained on the chorions for up to a day after hatching while their exoskeletons fully sclerotized (Hodek 1973). When larvae became actively mobile and dispersed from the egg cluster, each was transferred with a camel hair brush to a separate plastic Petri dish (10 by 1.5 cm). Sibling larvae from single clusters then were randomly divided into two treatments. Each treatment consisted of offering greenbugs reared on one of the greenbug-resistant (Dekalb DK-41Y or Dekalb DK-59E) or greenbug-susceptible (Horizon 101G) sorghum hybrids to the coccinellid larvae. Immediately after placing a larva in a Petri dish, greenbugs from the appropriate resistant or susceptible sorghum hybrid were placed in front of the larva so that feeding stimuli could be elicited. If a larva did not feed immediately on a greenbug or appeared lethargic, it was eliminated from the experiment. Larvae were supplied with an abun-

Table 2. Influence of antibiosis in sorghum on *H. convergens* developmental time to pupation, adult weight, and percentage survival to adult eclosion

Sorghum hybrid	Egg clusters (n)	Larvae (n)	Developmental time to pupation-days $\bar{x} \pm$ SE	Adult wt (mg) $\bar{x} \pm$ SE	% survivorship $\bar{x} \pm$ SE
Dekalb DK-41Y	14	104	6.74 ± 0.16**	19.50 ± 0.90	62.07 ± 8.40**
Horizon 101G	14	100	6.67 ± 0.11	18.98 ± 0.74	82.86 ± 4.91
Dekalb DK-59E	20	144	6.23 ± 0.08**	18.82 ± 0.41	86.50 ± 5.11*
Horizon 101G	20	141	6.15 ± 0.08	18.81 ± 0.46	91.60 ± 3.72

*, $P < 0.10$; **, $P < 0.05$; significantly different from coccinellids fed greenbugs reared on Horizon 101G by analysis of variance (SAS Institute 1982).

dance of greenbugs and were inspected two or three times a day to ensure that a surplus of food was always available. After a larva pupated, the remaining greenbugs, dead and alive, were removed from the Petri dish with a brush and compressed air. Sibling coccinellids from both treatments were kept in the same growth chamber at 32°C, 75–85% RH, and a photoperiod of 16:8 (L:D).

Data Collection and Analysis. Each coccinellid was monitored for death before adult eclosion, or days to pupation and adult weight. Death was characterized as cessation of feeding, contraction of abdominal segments, absence of movement and dehydration in larvae, or a failure in pupae to eclose to adults. Days to pupation were determined by examining larvae every 6 h, beginning with the prepupal stage (Hodek 1973) and until pupation occurred. When a pupa split its larval exuvia and emerged, the quarter-day in which the ecdysis occurred was recorded. The number of days to pupation, in 6-h increments, could then be determined based upon the date and quarter-day when the larvae initially hatched from the egg cluster. Live weights of adults were taken within 36 h after eclosion on a Mettler AC 100 scale and recorded in milligrams.

Data were blocked by egg cluster and analyzed using analysis of variance procedures (SAS GLM, SAS Institute 1982) with means judged significantly different at $\alpha < 0.10$. Sexes were combined within each egg cluster–treatment to determine total percentage survivorship.

Results and Discussion

Hippodamia convergens larvae from 34 egg clusters were tested in the antibiosis experiment. Fourteen egg clusters (204 larvae) were given greenbugs from resistant Dekalb DK-41Y and susceptible Horizon 101G, and 20 egg clusters (285 larvae) were fed greenbugs from resistant Dekalb DK-59E and susceptible Horizon 101G grain sorghum hybrids. Sources of variation and F values for dependent variables from the analysis of variance are given in Table 1.

Days to Pupation. Developmental time from egg eclosion to pupation was significantly increased in coccinellid larvae when they ate greenbugs from both of the greenbug-resistant hybrids (Table 1), although the mean difference between the resistant and susceptible hybrid effects was small (Table 2). The parent of each egg cluster also had a significant effect on the days to pupation of the progeny. Whether these differences were because of genetic disparities among the parents, physiological differences such as age of the female, or nutritional deficiencies of the females' food sources, was not determined. Larval sex had no significant effect on days to pupation.

Adult Weight. Consumption of greenbugs from the resistant hybrid DK-41Y did not significantly reduce adult coccinellid weights compared with those individuals that ate greenbugs from the susceptible hybrid. However, there was a significant treatment-by-sex interaction for coccinellids that consumed greenbugs from resistant hybrid DK-59E (Table 3). An antibiosis effect was expressed in the size of the adult females, which weighed an average 0.62 mg less than the susceptible group females (Table 3). But males actually averaged 0.60 mg more than males that ate greenbugs from the susceptible hybrid. Sex was also a significant factor in affecting adult weight. This is expected because female coccinellids are normally larger than conspecific males (Hodek 1973). The parent of each egg cluster was also a significant source of variation in adult weight of the progeny.

Percentage of Survival. Percentage of survival was significantly affected by sorghum antibiosis in larvae that had eaten greenbugs which fed and reproduced offspring on the resistant sorghum hybrids. Percentage of survival for coccinellid larvae that fed on greenbugs from the resistant DK-41Y hybrid was 20.79% less than for larvae that consumed greenbugs from the susceptible hybrid (Table 2). A similar, but less dramatic, effect occurred in the larvae that ate greenbugs from the resistant DK-59E. A 5.1% decrease in survivorship resulted compared with sibling larvae that received greenbugs from the susceptible hybrid (Table 2). In ad-

Table 3. Adult *H. convergens* weights for significant treatment by sex interaction

Sorghum hybrid[a]	Sex	Adult wt (mg) $\bar{x} \pm$ SE
R	♀	20.35 ± 0.29
R	♂	17.40 ± 0.27
S	♀	20.97 ± 0.29
S	♂	16.80 ± 0.28

[a] R, resistant hybrid DK-59E; S, susceptible hybrid Horizon 101G.

dition to an antibiosis effect, the parent of each egg cluster was a significant source of variation in percentage of survival.

Analysis of grain sorghum-greenbug-coccinellid interactions in the laboratory indicates varying effects on the predator depending on the grain sorghum hybrid. Greenbugs reared on resistant hybrids were found to have a diversity of negative, positive, or neutral effects on the predators. Dekalb DK-59E and Dekalb DK-41Y, which exhibit antibiosis to greenbugs, decreased the percentage of survival in larvae and pupae and increased the length of larval development time of the coccinellids. Hagen & van den Bosch (1968) noted a similar situation in an aphid species that varied in its nutritional value to coccinellids, being toxic to coccinellids at one time of year (spring) but quite innocuous during another (summer). The long-term impact of increased time to pupation for larvae eating greenbugs from resistant DK-59E or DK-41Y than larvae feeding on greenbugs from a susceptible sorghum hybrid is unknown. From an ecological perspective, the difference in days to pupation between groups of predators consuming prey from either a resistant or susceptible sorghum plant may be trivial in field situations. However, this difference, coupled with the reduced survivorship, could have an important adverse effect from a biological control standpoint by greatly reducing the intrinsic rate of increase of the predator in field situations. Although neither resistant hybrid adversely affected coccinellid adult weight, fecundity may not be affected on an individual basis but would be diminished across the population because of reduced survivorship.

The statement that host-plant resistance is compatible with biological control is too broad a generalization. Laboratory experiments with two different resistant grain sorghum hybrids showed that different physiological responses can be exhibited within a third-trophic level predator. An understanding of the effects of plant products upon predator fitness is essential in determining compatibility of host-plant resistance exhibiting antibiosis and biological control in suppressing insect pests.

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