THREE TROPHIC LEVEL INTERACTIONS: CEREALS-GREENBUGS-NATURAL ENEMIES

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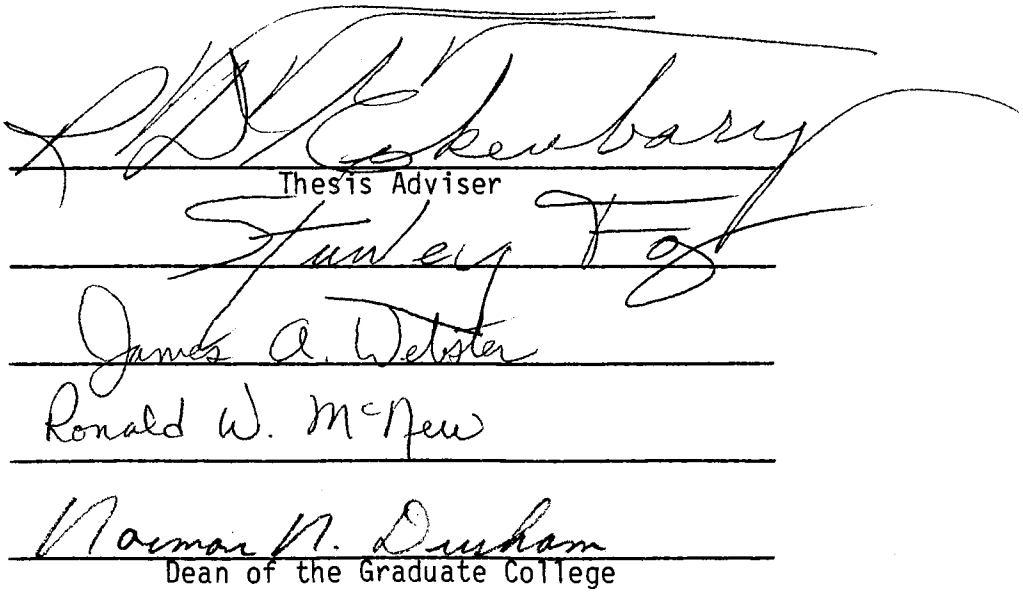

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CHAPTER I

OLFACTOMETER EXPERIMENTS

Introduction

Olfaction, the mechanism of perception of chemicals present in a gaseous state in relatively low concentrations, is important in many aspects of the life of insects. Smell can assist insects in finding food, ovipositional sites or a mate, and it is clear that there are specific chemoreceptor cells in the insect body, providing a mechanism by which certain odors can be distinguished.

Many insect parasitoids appear to be directed to their host through a series of physical and chemical cues. These cues elicit a series of responses by the female parasitoid that serves to restrict the area searched, and thus the species of host located.

The plant where the host feeds is one of the most important environmental factors that may affect host selection in different ways. There are several reports of hosts that are readily attached when occurring on one food plant but not on another (Vincon, 1976). For example, Aphidius smithi Sharma and Subba Rao (Hymenoptera: Aphidiidae), a parasitoid of the pea aphid, Acyrthosiphon pisum Harris (Homoptera: Aphididae), will also attack the green peach aphid, Myzus persicae Sulzer (Homoptera: Aphididae) when this aphid is reared on

broad bean, but not when it is reared on tobacco (Fox, et al., 1967), due to chemical constituents of the plant.

Plant chemicals seem to play an important role at every level of the host selection process. Plant volatiles can be shown to be important cues in host habitat location for a number of hymenopteran parasitoids (Arthur, 1962; Camors and Payne, 1971; and Nishida, 1956).

Through domestication and breeding, man has altered the natural ecosystem, creating a usually unbalanced crop pathosystem, under deterministic control imposed by man. In this concept, the recent introduction of genes for resistance to pests has added another factor of imbalance in the system, with some known influences on the crop pests, but, in most cases, with unknown influences on the third trophic level composed of predators and parasitoids.

The chemical cues involved in the host habitat and host location phases of a parasitoid may be derived from the host's food, the host, or a combination of food and host factors. These cues elicit a series of responses which restrict the searching process until the appropriate host is located. Any change in the plant odors, due to genetic manipulation, could alter this delicate system, thus changing the approaching sequences of the parasitoid to its prey.

Olfactometers are relatively simple devices that create clearly distinct, contiguous odor fields that can be easily entered, left and re-entered by walking or flying insects, providing information about the insect response to odors. Several species of Hymenoptera have been tested with olfactometers, and were attracted to odors from the food plant of their most common host (Arthur, 1962; Camors and Payne, 1973; and Nishida, 1956).

The present investigation was performed with an olfactometer with four distinct odor fields where parasitoids could move around freely. The objectives were to determine if the parasitoid, Lysiphlebus testaciepes (Cresson) (Hymenoptera: Braconidae) is able to differentiate between greenbug resistant and susceptible sorghum cultivars, and how they respond to the host insect, Schizaphis graminum (Rondani) (Homoptera: Aphididae), and its host plant.

Review of Literature

Olfactometers

Since the olfaction of both predators and parasitoids are important factors in prey location, olfactometers appear to be ideal devices to monitor their responses to different olfactory stimuli.

Olfactometers are widely used to clarify some causes of animal behavior (Dawley, 1986; and Dong and Chant, 1986). The designs are quite variable, ranging from very simple to highly sophisticated. Among the former is the cage used by Colburn and Asquith (1970), which consists of a plastic square box (2x2x1.5 in.) with four lateral tubes where the material to be tested is placed. A small desk fan maintains the air current.

The most widely used models are those with a Y shape, where each branch receives an odor. Both odors come together in the central base where the insects have a choice. One of the first to apply this model was McIndoo (1926), who examined the response of potato beetles, Leptinotarsa decemlineata (Say) (Coleoptera: Chrysomelidae) to the presence or absence of living potato plants. Several studies were

performed with insects using this type of olfactometer with various modifications.

Read et al. (1970) used a Y-shaped model constructed entirely from detachable glass sections for easy cleaning and sterilization. They determined the host selection of the aphid parasitoid Diaeretiella rapae (McIntosh) (Hymenoptera: Braconidae). Other authors (van der Meer et al., 1979) introduced a baffle into the structure at the junction of the two branches to prevent premature mixing of the air streams, thus giving the coconut beetle, Oryctes rhinoceros L. Coleoptera: Scarabeidae), a clear choice between the host smells that had been tested. Condit and Cate (1982) described the choices of a braconid parasitoid among several of its hosts with and without the plants. They introduced several changes to the formerly used Y models, basically in the air flow system. They added an air flow meter, an air drying chamber, and, finally, the odor source chamber, before each branch. All of these changes helped to increase the air quality entering the olfactometer. Brewer et al. (1983) determined the olfactory behavior of the alfalfa seed chalcid, Bruchophagus roddi (Gussakovsky) (Hymenoptera: Eurytomidae), with different alfalfa clones. They added a humidifier flask to the basic Y design. Howell and Goodhue (1965) tested the attractants and repellents against cockroaches. The cockroaches were placed in a glass cylinder with a double entrance for odors on one side and the aspirator pump on the other. The authors claimed simplicity and efficiency in this model.

Another type, with an H shape (Kudon and Berisford, 1981), was used to test the response of parasitoids of the bark beetle, Dendroctonus frontailis Zimmermann (Coleoptera: Scolytidae), to various

beetle and host tree odors. The main advantage of this olfactometer seemed to be the low air currents used, which created better conditions for studying insect behavior, since air turbulence was reduced. Lecompte and Thibout (1986) used a one odor source olfactometer, and checked the behavior of a Lepidopteran pupae parasitoid with and without the odor. A special design, developed by Wilson and Bean (1959) permitted the use of three odor sources in combinations of two, with the third one as blank, using valves to open and close the air flow. Todd et al. (1977) developed a low-flow-rate air delivery system for use with olfactometers. The most important features were the presence of two outer chambers which receive the air flow and provide for the mixing of gases; and an inner chamber, where the insects were released. Another type was developed for working with adult moths, to measure the oviposition response of Ostrinia nubilalis (Hubner) (Lepidoptera: Pyralidae) to different host plants (Schurr and Holdaway, 1970). For this work, a large cage was used with one side receiving the odor choices and with its surface roughened to receive the eggs.

During a study concerning the olfactory sense in aphid parasitoids, Bouchard and Cloutier (1984) described the olfactory response of Aphidius nigripes Ashmead (Hymenoptera: Aphidiidae) to their hosts and hosts' food plants, using different combinations. The parasitoids did not respond to the plants, but the females were strongly attracted to odors of their preferred host. A similar study with Aphidius uzbekistanicus Luzhesky (Hymenoptera: Aphidiidae) and Aphidius ervi Haliday (Hymenoptera: Aphidiidae), both parasitoids of cereal aphids,

was performed and again only the females responded to aphids, but both sexes were attracted to plant odors (Powell and Zhi-li, 1983).

The response of L. testaceipes to one of its natural insect hosts, S. graminum, to a non-host insect, Heliothis zea (Boddie) (Lepidoptera: Noctuidae), to a greenbug host plant and to a non-host plant, the peanut cactus (Camaecereus silvestrii Speg.) was studied (Schuster and Starks, 1984). Only the females were able to locate the host and the plant's odors. Going further, the same authors (1985) determined that L. testaceipes responded positively to the resistant oat "CI 1580" and not to the susceptible "Chilicco". They found no differences between resistant and susceptible rye (Secale cereale L.), barley (Hordeum vulgare L.), sorghum (Sorghum bicolor Moench), and wheat (Triticum aestivum L.).

Certain shortcomings are inherent in most olfactometers (Visser, 1976; and Finch, 1980). Most designs provide limited space in which the test organisms, especially flying insects, can behave normally. The air flow is difficult to regulate and hence the odor gradient is limited. Long-range orientation of insects cannot be detected in these types of apparatus.

In an attempt to overcome most of the described shortcomings, a new type of olfactometer was designed by Vet et al. (1983) to measure behavioral olfactory responses of hymenopteran parasitoids. It was better than the traditional Y shaped olfactometer because it has four odor sources and the insect can test and reject or accept each one of them, providing more complex preference test situations. The air flow in this model is constantly regulated with flowmeters and is clearly defined for each odor tested, thus providing a more precise and

objective measurement of insect responses to odor. The design by Vet et al. (1983) was chosen and constructed to conduct the present study.

Experimental Insects and Plants

The greenbug, S. Graminum, was first found in Italy in 1847 and in the United States in 1882 (Webster and Phillips, 1912). The first outbreak of the pest was reported in 1901 in northern Texas (Kelly, 1917). Since then, the greenbug has always been detectable in the field, sometimes causing severe damage to small grain and sorghum crops.

The first record of greenbug biotypes was in 1958 when the resistant wheat "Dickinson Selection 28 A" was damaged by the new strain, called biotype B (Wood, 1961). Other biotypes were reported and designated as C, D, E, F, G, and H (Puterka et al., 1988). Biotype E, used in the experiment reported here, was found in Bushland, Texas, when "Amigo" wheat and its derivatives (A, B, and C resistant cultivars) failed to survive an attack from the new greenbug (Porter et al., 1982).

The sorghum entries used in the tests were biotype E susceptible "Pioneer 8300" (Kerns et al., 1987) and resistant "Capbam". The main component of resistance of Capbam is tolerance, since it had low damage ratings when compared with several susceptible cultivars (Johnson et al., 1981; Porter et al., 1982; and Starks et al., 1983).

L. testaceipes, one of the most important natural enemies of the greenbug in the United States is indigenous to North America. Since the early greenbug attacks, this parasitoid has been an important factor in the pest population regulation (Kelly, 1917). It is cur-

rently the most abundant parasitoid of S. graminum in the United States (Jackson, 1970).

Materials and Methods

Olfactometer

The airflow olfactometer described by Vet et al. (1983) was constructed of Plexiglass TM. The floor was 5 mm thick and 260 mm square. The center consists of a four-arm star-shaped test chamber, constructed of four crescent (90 arc, radius 135 mm) sides 5 mm thick, glued to the floor with methylene chloride (Figure 1). The roof of the exposure chamber was made of the same material as the floor, and attached to the assembled chamber with 3 mm screws and bolts. Air leaks were prevented by using foam rubber weather stripping. Each arm of the chamber was connected to a set of three 50 ml glass flasks by 5 mm (inside diameter) Tygon (TM) tubing and arranged sequentially so that all air flowed through each of the flasks. The closest flask to the chamber served as a trap for catching the insects reaching it through that arm. The odor source was placed in the middle flask and the outer flask contained distilled water through which the incoming air was passed to create a high, uniform humidity. A flow meter was connected to each set of flasks to regulate the air flow.

The air flow was obtained with a vacuum compressor by pumping air out of the chamber through a 1 cm diameter hole in the center of the floor, thus creating four distinct moving air fields in the chamber. The air flow rate was ca. 300 ml/min through each arm. With the

Figure 1. Top view of the olfactometer exposure chamber

extractor tube disconnected, this hole was also used to introduce test insects into the chamber.

To avoid disturbances by the observer, the chamber was enclosed inside a 28 x 28 cm cardboard box with white interior walls and observation holes on top. The light source, fixed to the box roof, was a GE cool white, 22 watt, 8-inch, circular fluorescent tube.

To observe the performance of the olfactometer, smoke formed from a mixture of NH_4OH and HCl in one of the central flasks was drawn through the apparatus over a black background. Within seconds, the borderlines of each field in the chamber became uniform and clear.

Tests

The aphids and parasitoids used in the experiment were obtained from non-caged pots from greenhouse cultures maintained on "Pioneer 8300" sorghum. Parasitoid mummies were collected and the newly emerged females (4 to 6 hours old) were used to check their orientation to different odor sources.

The parasitoids were tested individually. The odors were set in the chamber by running the pump with 1200 ml/min overall flow rate (300 ml/min/arm) during ca. one minute. Then the extractor tube was disconnected, the parasitoid was put inside the tube which was reconnected in the center hole of the chamber floor, and the air flow restarted. In most of the trials, the parasitoid showed positive anemotaxis. If, after five minutes, the insect did not walk up into the chamber, it was replaced with a new one.

Inside the connection tube the insect was exposed to a mixture of the four odors. Once it reached the floor of the chamber, it started

walking in the central zone of odor mixing. Thus, the parasitoid had the opportunity to select the odor field. When the parasitoid crossed one of the lines marking the entrance into the narrowing of the odor field, the time was recorded with a stopwatch and ten minutes were given to the insect in the olfactometer. During this period, the times in each field were recorded. If the parasitoid made a "final choice" (went into a catching flask), all the remaining time to complete the ten minutes was given to this odor field.

Three different odor situations were tested, with 20 replications (parasitoids) for each situation:

	Odor Field in Arena			
Test No.	1	2	3	4
1	S	B	R	B
2	G	B	S	B
3	B	B	B	G-S
4	B	B	B	G-S

G = Greenbugs
S = Susceptible sorghum "Pioneer 8300"
R = Resistant sorghum "Capbam"
B = Blank

In tests 2, 3, and 4, ca. 200 greenbugs of mixed ages were put in the flask, and four young plants (2-3 leaves) were used, thus providing greenbugs and half crushed plants inside the flask. The plants used were uninfested. When G and S were together (field 4 in tests 3 and 4), the plants were damaged by the same aphids. The whole system,

including flasks and chamber, was washed with water and 70% ethanol every five replications. Therefore, the odor source, greenbugs, and plants were renewed with the same frequency.

The time spent in each field was calculated as percentage of the total time spent in the four fields without counting the time that the parasitoids were in the central area. The mean percentages of time were compared by paired t-test.

Since tests 3 and 4 had the same odor sources in the same fields, a one-way analysis of variance was performed to check the difference between the same fields in the two tests. No difference was found; therefore, the two tests were combined in one analysis, with 40 replicates.

Results

Test one. In this test, field number one had greenbug susceptible sorghum "Pioneer 8300" as odor source and field number three had sorghum resistant "Capbam" as odor source. No significant differences were found among the four odor fields (Table I), which demonstrates that L. testaceipes females were not able to distinguish between greenbug susceptible and resistant plants, or between the two odor fields and the two blank fields without odor.

Test Two. In this test the odor sources were greenbugs in field one and undamaged greenbug susceptible sorghum plants in field three. The female parasitoids were attracted to the odor of both fields, compared with the blanks, but they did not distinguish between sorghum and greenbug odors (Table II).

TABLE I

RESPONSE OF FEMALE L. TESTACEIPES TO THE ODOR OF GREENBUG RESISTANT AND SUSCEPTIBLE SORGHUM PLANTS (MEAN PERCENTAGES OF TIME IN EACH FIELD ±S.E.)

Odor Field in Arena[1]	Mean Percentage of Time[2]
1--SS	31.0 ±6.1 a
2--SR	29.3 ±7.0 a
3--Blank	26.1 ±7.1 a
4--Blank	13.6 ±5.1 a

[1]SS: Sorghum Susceptible. SR: Sorghum resistant. The numbers before the odor source identifies the field in the olfactometer arena.

[2]Values followed by the same letter are not significantly different (t-test, $P < .05$).

TABLE II

RESPONSE OF FEMALE L. TESTACEIPES TO THE ODOR OF GREENBUG SUSCEPTIBLE SORGHUM PLANTS AND GREENBUGS (MEAN PERCENTAGES OF TIME IN EACH FIELD ±S.E.)

Odor Field in Arena[1]	Mean Percentage of Time[2]
1--Greenbugs	42.4 ±8.7 a
3--SS	35.4 ±8.5 a
2--Blank	14.0 ±5.8 b
4--Blank	8.2 ±3.6 b

[1]SS: Sorghum Susceptible.
The numbers before the odor source identifies the field in the olfactometer arena.

[2]Values followed by the same letter are not significantly different (t-test, $P < .05$).

Test three. Tests three and four were combined for the analysis, thus having 40 replicates. The choices given to the female parasitoids were one odor source (greenbugs plus greenbug damaged sorghum susceptible plants), and three blanks (Table III). The females were strongly attracted to the greenbug and sorghum plant odor, where they spent a mean of ca. 50% of all the time that they were exposed to the four fields. This was significantly different from the time spent in the blanks, which was ca. 15, 20, and 15% for fields 1,2, and 3, respectively. No differences were found among the blanks.

TABLE III

RESPONSE OF FEMALE L. TESTACEIPES TO THE COMBINED ODORS OF GREENBUGS AND GREENBUG SUSCEPTIBLE SORGHUM PLANTS (MEAN PERCENTAGES OF TIME IN EACH FIELD ±S.E.)

Odor Field in Arena[1]	Mean Percentage of Time[2]
4--GB+SS	49.8 ±6.0 a
2--Blank	20.5 ±4.6 b
1--Blank	15.0 ±3.4 b
3--Blank	14.7 ±3.8 b

[1]GB+SS: Greenbugs plus sorghum susceptible.
The numbers before the odor source identifies the field in the olfactometer arena.

[2]Values followed by the same letter within a column are not significantly different (t-test, $P < .05$).

Discussion

Since the parasitoids occupy the third trophic level, they have to locate not only an appropriate habitat, but also a suitable host within the habitat. Due to this fact, they might be able to detect a wider range of chemicals than insects in the second trophic level.

This versatility in parasitoid behavior is supported by the nature of their sensory system. Chapman (1982) reported that the olfactory sensillae of Hymenopteran parasitoids are of a general nature (few sensillae with many neurons), which makes the parasitoids versatile in their response spectrum, but intensive searchers when they localize something attractive. Both characteristics are favorable for their lifestyle.

Lysiphlebus testaceipes follows this pattern. In the four tests performed, the female parasitoids located the host and the host's plants, although with different degrees of success. In Test 1, when SR and SS plants were offered as separate odor sources, the parasitoids failed to distinguish between them and between plant odors and blanks. These results are not as those obtained by Schuster and Starks (1974), when female parasitoids were able to distinguish between SS "BOK-8" and a blank and to results obtained by the same authors (1975), where female parasitoids demonstrated a preference for SS "BOK-8" and SR "IS-809" in olfactometer tests. It should be pointed out that the olfactometer used in both studies was of the common Y shape, and the sorghum cultivars were different from the ones used in our study.

When greenbugs were added as an odor source (Tests 2, 3, and 4), the parasitoid behavior changed: females responded positively to both

the aphids and to the sorghum plants, either in different fields or to both sources combined, as a common odor source. Schuster and Starks (1984) found a similar response when they checked the parasitoid host-finding behavior of greenbug versus an odorless control. The greenbug odor was more attractive to the females, and no difference was found when greenbugs and sorghum were compared as odor sources, as in Test 2.

Using a Y-shaped olfactometer, studies by Powell and Zhi-li (1983), involving A. uzbekistanicus and A. ervi, found that adult females were attracted to their host and host's plants, which is similar to the response found with L. testaceipes.

The results from Tests 2, and 3 and 4 combined suggest that the presence of greenbugs plus host plants stimulates the searching behavior of the adult female parasitoids. Components from both odor sources combined were necessary to create a positive attraction.

Two points should be emphasized. First, the repellence and attractance of an odor source will depend largely on the airborne molecular concentration of chemicals that trigger the responses. Under experimental conditions, this concentration can be altered most easily by changing the quantity of the source material or by altering the flow rate of air moving through the apparatus. In the present study and other studies made with Hymenopteran parasitoids of cereal aphids, only one odor concentration and one air flow rate were used. Thus, more work should be done in this area.

Second, the olfactometer is a simple system, with almost pure odor sources, when compared with the more complex odors of agricultural and natural ecosystems. These ecosystems have a large variety

of chemicals as odor sources, which might serve to increase the total input that a parasitoid receives and thus increase or decrease the probability of response from the insect.

Summary and Conclusions

Four tests were performed with an olfactometer to determine if female adult parasitoids L. testaceipes were able to use olfaction to differentiate among greenbugs, S. graminum, and their host plants, greenbug resistant, and susceptible sorghum plants. The olfactometer designed by Vet et al. (1983) was built and used in this work because it has four odor sources and the insect can test and reject or accept each one of the odor sources offered.

In Test one, no difference was found in the attractiveness of "Capbam" resistant sorghum, "Pioneer 8300" susceptible sorghum, and the two blanks. In Test two, the parasitoids responded positively to greenbugs and sorghum susceptible plant odors located in different fields. In Tests three and four, the female parasitoids showed marked attraction to the odor released by the greenbugs plus sorghum susceptible plants located in the same odor field.

These results suggest that adult female parasitoids do not react to plant odor alone. The odor of greenbugs plus plants is necessary to trigger the host searching behavior.

CHAPTER II

THREE TROPHIC LEVEL INTERACTIONS OF A PARASITOID

Introduction

Despite recent advances (Boethel and Eikenbary, 1986), the interactions between plant resistance and arthropod parasitoids remain poorly known. Host plant resistance and biological control are generally considered compatible pest management strategies and the use of these two methods of pest control can introduce unrelated stress factors into the food web composed of the plant (first trophic level), herbivorous insects (second trophic level) and natural enemies (third trophic level).

Nutritional substances offered by a host plant can indirectly affect parasitoid fitness in several ways. Prey feeding on resistant plants can experience reduced growth rates, greater developmental time and mortality, or decreased fecundity. With this alteration of physiological processes, prey quality as a food source for the parasitoids may decrease, having dramatic consequences on the life history of the parasitoids. Natural enemies can also be exposed to toxic chemicals sequestered by prey from resistant plants, either as larvae feeding internally or as adults through feeding on hemolymph exuded from feeding punctures. A third kind of influence attributable to the resistant plant can be its disruption of normal behavior patterns of

the prey. A parasitoid's searching pattern depends, among other things, on the type of distribution of its prey, either within the plant or among plants. This distribution is normally fairly constant for each species. The disruption of normal prey distribution patterns through agricultural use of unsuitable plants can lead to increasing difficulties for the parasitoid in making actual contact with the prey.

The present study was conducted to determine if in the system composed of barley (Hordeum vulgare L.) and sorghum, their pest the greenbug (S. graminum), and the parasitoid L. testaceipes, the introduction of plant resistance can alter the normal developmental patterns of members of the third trophic level.

Review of Literature

Host Plants, Greenbugs and Parasitoids

The barley cultivars used were biotype E greenbug susceptible "Wintermalt" (Webster and Starks, 1984) and resistant "Post". Post barley has a high level of antibiosis, with fewer nymphs/female born when compared with susceptible genotypes (Starks et al., 1983; and Webster and Starks, 1984). In the same tests, this cultivar showed a medium level of tolerance and a low level of antixenosis.

The sorghum entries used in the test were biotype E susceptible "Pioneer 8300" (Kerns, 1989) and resistant "Capbam". The main component of resistance of "Capbam" is tolerance, since it had low damage ratings when compared with several susceptible cultivars (Johnson et al., 1981; Porter et al., 1982; and Starks et al., 1983).

The first description of the greenbug was made by C. Rondani, who found it on grasses in Italy in 1847 (Hunter, 1909). In the United States, it was found in 1882 (Webster and Phillips, 1912). The first outbreak of the pest was reported in 1901 in northern Texas (Kelly, 1917). Since then, the greenbug has been present each year where small grains or sorghum are grown, sometimes causing severe damage to these crops.

The first record of different greenbug biotypes was made in 1958, when the resistant wheat Dickinson Selection 28 A was damaged by the new strain, called biotype B (Wood, 1961). Other biotypes were reported, called C, D, E, F, G, and H (Puterka et al., 1988). Biotype E, used in this experiment, was found in Bushland, Texas, when "Amigo" wheat and its derivatives (A, B, and C resistant cultivars) failed to survive an attack from the new greenbug (Porter et al., 1982).

L. testaceipes, one of the most important natural enemies of the greenbug, is an indigenous species to North America. Since the early greenbug attacks, this parasitoid has been an important factor in pest population regulation (Kelly, 1917). It is still the most abundant parasitoid of S. graminum in the United States (Jackson et al., 1970).

Host Plant Influence on Parasitoids

Greenbug resistant cultivars and biological control may complement each other in reducing greenbug populations (Starks et al., 1972). This was also suggested by Salto et al. (1983), who found no differences in parasitism between susceptible "Nora" and resistant "CI 4888" oat, Avena sativa L., lines. But aphids feeding in the field on resistant plants are small; therefore, the parasitoids will also be

smaller. The parasitoids also spend more time searching for their prey, since generally on resistant plants the greenbugs are less abundant. These two factors could lead to a reduction in the fecundity of the aphid's parasitoids and could create long-term problems in any integrated pest management program utilizing biological control and host plant resistance (Kuo, 1986).

The size and sex ratio of Aphelinus asychis Howard (Hymenoptera: Encyrtidae) was strongly influenced by the diet of its host, M. persicae (Zohdy, 1976). Working with A. smithi, Mackauer (1983) concluded that parasitoids chose larger aphids over smaller ones of the same species. Some species of Aphidius exhibited a strong ovipositional preference for certain aphids in laboratory studies, corresponding to the host aphid on which they were found in the field (Pungerl, 1984). This suggests an adaptation to the host present in the field. The weight and fertility of Aphidius sonchi Marshal (Hymenoptera: Aphidiidae) were affected by host size in a study performed by Shu-sheng (1985).

Working with other species, McCutcheon and Turnipseed (1981) found that the green cloverworm, Plathypena scabra (F.) (Lepidoptera: Noctuidae) attracted lower populations of its parasitoid, Apanteles marginiventris (Cresson) (Hymenoptera: Braconidae) when it was fed the resistant soybean "ED 73-371" when compared with the susceptible "Bragg".

Materials and Methods

The experiments were conducted under controlled conditions, in a Model E 54 B Percival growth chamber. The interior dimensions were 95

cm (width) by 61 cm (height and depth). Light was provided by eight high-output cool white (daylight) 45 watt fluorescent tubes. The temperature was set at 24 ±1 °C during the 13-hour photophase and at 20 ±1 °C during the scotophase. Relative humidity was not controlled and ranged between 60% and 70%.

Experimental Insects and Plants

Biotype E (Identification by Gary Puterka, based on Puterka et al., 1988) greenbugs were collected on sorghum in the field near Stillwater, Oklahoma, and kept in greenhouse cultures on greenbug susceptible "Wintermalt" barley during the fall and winter months, and on greenbug susceptible "Pioneer 8300" sorghum during the spring and summer months in the year before the beginning of the experiments. During the same year, a special culture was set up on greenbug resistant "Post" barley, in caged 15 cm diameter pots, in a growth chamber under the previously described conditions. These conditions were required to maintain a successful culture on "Post", due to the strong antibiosis of this cultivar.

The parasitoids used in the experiments were L. testaceipes (Identification by the author, based on Johnson et al., 1979). They were collected as mummies from the field in May, 1987, two months before beginning the test. With newly emerged adults, a culture was started in the growth chamber on greenbugs reared on susceptible barley and sorghum plants, under the previously described conditions.

Cultivars used in this study were greenbug resistant "Post" barley (BR) and "Capbam" sorghum (SR), and greenbug susceptible "Wintermalt" barley (BS) and "Pioneer 8300" sorghum (SS). Two seeds were

planted in 7.6 cm diameter plastic pots in a greenhouse mixture of 3 parts soil, 3 parts sand, and 1 part peat moss.

Tests

The three variables in this study were plant species (barley and sorghum), plant cultivars ("Wintermalt", "Post", "Pioneer 8300", and "Capbam"), and five parasitoid generations for each cultivar. This made a 2 by 2 by 5 factorial test in a completely randomized design, with ten replications for each plant-cultivar-generation combination.

Each replication consisted of one pot with two ca. 6 cm high plants, covered with plastic cages having cloth-covered ventilation holes. There were 50 to 70 greenbugs of any age present at the beginning of each generation. The greenbugs placed on "Post" barley and "Capbam" sorghum came from their respective cultures. The greenbugs placed on susceptible plants came from the general culture.

For the first parasitoid generation, a male/female pair of newly emerged adult L. testaceipes were released into each cage. For the following generations (second through fifth), the adults released in each cage were from the preceding generation and from the same cultivar.

The Observations

Each male and female parasitoid remained in the cage until natural death, which occurred within ca. 36 hours of emergence. All mummies were collected daily from each pot and put individually in No. 1 gelatin capsules (Ely Lilly Company). A maximum of five mummies/pot/

day were collected and identified by writing pot identification, mummy number, and date directly on the gelatin capsules.

The data collected were as follows: success or failure of each parasitoid pair to produce mummies; fecundity obtained from the total number of mummies produced/mating pair; and days to first mummy formation. The following data were obtained only from identified mummies (5/pot/day): percentage of adult emergence; sex ratio; days from mummy formation to emergence; maximum width of mummy abdomen before and after adult emergence; maximum head capsule width of emerged parasitoid adults; and femur length of either of the third pair of legs. Measurements of mummy and adult parasitoid body parts were made using an ocular micrometer.

All observations were subjected to analysis of variance and the means were compared by t-test. Correlation analyses were made between body measurements and between body measurements and emergence time (mummy collection day to adult emergence). Sex ratio and adult emergence success were analyzed by z-test. The rate of mummy collection was analyzed by Chi-square test for heterogeneity between resistant and susceptible plants, within each plant species studied. The description and discussion of the results were based on those means which were significantly different.

Results

Total number of mummies. The number of aphids parasitized per mating pair of parasitoids decreased from the first generation (A) to the following four, namely B, C, D, and E. At generation A, the parasitoids were able to parasitize more than 21 aphids per pot. The fol-

lowing generations had between 14 and 16 mummies per pot, which were significantly less than generation A (Table IV).

TABLE IV

MUMMIES PRODUCED PER PARASITOID COUPLE PER GENERATION (MEANS ±S.E.)

Generation	Number of Mummies
A	21.7 ±1.6 a
B	15.5 ±1.4 b
C	14.7 ±1.5 b
D	16.1 ±1.4 b
E	15.0 ±1.4 b

Values followed by the same letters are not significantly different (t-test, $P < 0.05$).

The number of progeny produced also depended on the variety upon which the aphids were reared. An average of only 6.8 mummies were collected from resistant "Post" barley, which was significantly different from the mummies collected from the other three varieties: susceptible "Wintermalt" barley, and resistant "Capbam" and susceptible "Pioneer 8300" sorghums (Table V).

TABLE V

MUMMIES COLLECTED/MATING PAIR FROM THE FOUR CULTIVARS (MEANS ±S.E.)

Cultivars[1]	Mummies Collected
BR	6.8 ±1.5 a
BS	20.0 ±1.3 b
SR	19.3 ±1.3 b
SS	20.3 ±1.3 b

[1]BR: Barley-resistant cultivar Post.
BS: Barley-susceptible cultivar Wintermalt.
SR: Sorghum-resistant cultivar Capbam.
SS: Sorghum-susceptible cultivar Pioneer 8300.

Values followed by the same letter are not significantly different (t-test, $P < 0.05$).

Parasitization success. The parasitization success value was obtained by counting the number and calculating the percentage of parasitoid couples that produced mummies. No difference was observed among the generations. The lowest parasitization success (67.9%) was recorded on resistant barley. This value was significantly lower than the other three varieties, which did not differ (Table VI).

TABLE VI

PARASITIZATION SUCCESS, IN PERCENTAGES OF COUPLES PRODUCING MUMMIES (MEANS ±S.E.)

Cultivar	Parasitization Success
BR	67.9 ±5.3 a
BS	87.3 ±5.2 b
SR	94.0 ±5.1 b
SS	91.3 ±5.2 b

Values followed by the same letters are not significantly different (t-test, $P < 0.05$).

Parasitoid larval developmental time. Parasitoid developmental time, from egg to mature larva, was determined by tabulating the period from the day that the adult parasitoids were released into the cage with the greenbugs until the day of first mummy collection.

Although the average time to first mummy formation on susceptible plants was 6.65 days, and was 7.05 days on resistant plants, the difference was significant in generation B only. When the generations were considered in either resistant or susceptible plants, they showed significant differences but without any clear tendency (Table VII).

When plant species were compared, the larval development period lasted longer on barley than on sorghum in generations A and E. No clear tendency was observed among the generations within each species of plant, combining both resistant and susceptible, although some differences were significant (Table VIII).

TABLE VII

DAYS TO FIRST MUMMY FORMATION ON RESISTANT AND SUSCEPTIBLE PLANTS (MEANS ±S.E.)

Generation	Kind of Plant					
	Resistant	1	2	Susceptible	1	2
A	6.88 ±0.21	a	y	6.36 ±0.17	a	xy
B	7.69 ±0.17	a	z	6.06 ±0.17	b	y
C	6.91 ±0.19	a	y	6.99 ±0.16	a	z
D	6.69 ±0.17	a	y	7.00 ±0.16	a	z
E	7.11 ±0.17	a	y	6.83 ±0.16	a	xz
$\bar{X}$	7.05 ±0.08	a		6.65 ±0.08	b	

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

TABLE VIII

DAYS TO FIRST MUMMY FORMATION ON BARLEY AND SORGHUM (MEANS ±S.E.)

Generation	Plant Species					
	Barley	1	2	Sorghum	1	2
A	6.96 ±0.22	a	y	6.27 ±0.18	b	y
B	6.85 ±0.18	a	y	6.90 ±0.16	a	z
C	6.74 ±0.20	a	y	7.16 ±0.16	a	z
D	6.80 ±0.17	a	y	6.89 ±0.16	a	z
E	7.56 ±0.18	a	z	6.39 ±0.16	b	y

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

Mummy formation interval. Mummy collection interval was the period, in days, elapsed from the first to the last mummy collection day, from each pot.

In both resistant barley and sorghum, this interval was longer than on the same susceptible plant species. The largest difference was between "Capbam" resistant sorghum, which had an interval of 5.13 days; and "Pioneer 8300" susceptible sorghum, which had a mummy formation period of 3.52 days (Table IX).

TABLE IX

MUMMY FORMATION INTERVAL, IN DAYS, ON RESISTANT AND SUSCEPTIBLE BARLEY AND SORGHUM (MEANS ±S.E.)

	Kind of Plant	
Plant Species	Resistant	Susceptible
Barley	3.51 ±0.24 a	2.77 ±0.20 b
Sorghum	5.13 ±0.19 a	3.52 ±0.20 b

Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

The difference in mummy formation interval between resistant and susceptible plants also depended on the generation considered. The collection was more lengthy on resistant plants in generations A, D, and E (Table X).

TABLE X

MUMMY FORMATION INTERVAL, IN DAYS, ON RESISTANT AND SUSCEPTIBLE PLANTS, ALONG THE FIVE GENERATIONS (MEANS ±S.E.)

Generation	Kind of Plant				
	Resistant	1	2	Susceptible	1 2
A	4.38 ±0.39	a	xyz	3.29 ±0.31	b x
B	3.80 ±0.31	a	xy	3.13 ±0.32	a x
C	3.53 ±0.36	a	x	3.09 ±0.30	a x
D	4.57 ±0.32	a	xz	3.33 ±0.30	b x
E	5.31 ±0.31	a	z	2.89 ±0.30	b x
$\bar{X}$	4.32 ±0.15	a		3.14 ±0.14	b

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

No difference was found among generations on susceptible plants, and the variation observed on resistant plants was without any tendency.

Rate of mummy collection. The mummies collected per day were rated as percentages from the total of mummies collected from each mating pair, and these percentages were analyzed by the Chi-square test for heterogeneity between resistant and susceptible plants, within each species studied.

Mummy formation was intensive during the first two days on susceptible barley, with 87.4% of the total collected. Then it declined rapidly. On resistant barley, the first two days had 61% of the total, with a gradual decline during the rest of the collection days (Table XI).

TABLE XI

PERCENTAGES OF MUMMIES COLLECTED DURING THE MUMMY FORMATION PERIOD ON BARLEY

Day of Collection	Kind of Plant	
	Resistant	Susceptible
First	31.1	43.5
Second	30.1	43.9
Third	21.4	10.8
Fourth	13.3	1.7
Fifth	3.1	0.1
Sixth	1.0	0.0

Chi-square = 107.7. P = 0.0001.

A similar pattern was found in sorghum. In the first two days, 75.7% of the mummies were collected from susceptible sorghum, declining during the next three days. On resistant sorghum, only 45.3% of the mummies were collected during the first two days of mummy formation (Table XII).

TABLE XII

PERCENTAGES OF MUMMIES COLLECTED DURING THE MUMMY FORMATION PERIOD ON SORGHUM

Day of Collection	Kind of Plant	
	Resistant	Susceptible
First	18.9	36.6
Second	26.4	39.1
Third	24.8	17.8
Fourth	15.9	5.9
Fifth	10.5	0.6
Sixth	2.6	0.0
Seventh	1.1	0.0

Chi-square = 226.0. P = 0.0001.

Maximum mummy width. The maximum mummy width was taken across the abdomen before and after adult emergence, as a measure of general mummy size. Tables XIII and XIV show the mummy measurements on barley before and after adult emergence, respectively.

TABLE XIII

MAXIMUM MUMMY WIDTH, IN MM, BEFORE ADULT EMERGENCE ON BARLEY (MEANS ±S.E.)

Generation	Kind of Plant: Resistant	1 2	Susceptible	1 2
A	.723 ±.023	a x	.960 ±.018	b v
B	.717 ±.019	a x	.847 ±.016	b x
C	.769 ±.023	a x	.895 ±.016	b y
D	.732 ±.019	a x	.771 ±.016	a z
E	.733 ±.019	a x	.839 ±.015	b x
$\bar{X}$	.735 ±.009	a	.862 ±.007	b

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

TABLE XIV

MAXIMUM MUMMY WIDTH, IN MM, AFTER ADULT EMERGENCE ON BARLEY (MEANS ±S.E.)

Generation	Kind of Plant: Resistant	1 2	Susceptible	1 2
A	.773 ±.024	a z	.696 ±.018	b x
B	.783 ±.019	a z	.853 ±.017	b y
C	.773 ±.024	a z	.887 ±.017	b y
D	.757 ±.019	a z	.762 ±.016	a z
E	.767 ±.019	a z	.843 ±.016	b y
$\bar{X}$	.771 ±.010	a	.863 ±.007	b

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

On resistant barley, no difference was found among the generations before and after the emergence of adults. On susceptible barley, the mummy width was strongly reduced after generation A, which averaged ca. 0.96 mm before and after emergence. The other four generations ranged from 0.77 to 0.89 mm.

In all generations, the mummies were larger on susceptible barley than on resistant barley both before and after adult emergence. In generation D, for both before and after emergence, this difference was not significant.

Tables XV and XVI show the mummy measurememts on sorghum before and after adult emergence, respectively. On resistant sorghum, the mummies of the first generation were larger than the mummies of the other four generations. The maximum abdomen width before and after emergence of adults was ca. 0.78 mm in the first generation, declining to ca. 0.72 mm in the other four generations.

On susceptible sorghum, the mummies were larger than on resistant sorghum in all generations. The same pattern of decline in mummy size seen on barley was observed among the generations, but not as clearly as on resistant sorghum or on susceptible barley, since no significant difference was found among generations A, B, and E.

Femur length. The femur length of the adult parasitoids was taken on either of the third pair of legs, as a measure of general body size.

The femur length of adult parasitoids coming from "Post" resistant barley was similar among the five generations studied (Table XVII). The only exception was generation C, which had larger adults

TABLE XV

MAXIMUM MUMMY WIDTH, IN MM, BEFORE ADULT EMERGENCE ON SORGHUM (MEANS ±S.E.)

Generation	Kind of Plant				
	Resistant	1	2	Susceptible	1 2
A	.780 ±.015	a	y	.904 ±.018	b y
B	.716 ±.014	a	z	.860 ±.016	b y
C	.712 ±.016	a	z	.810 ±.015	b z
D	.717 ±.016	a	z	.810 ±.016	b z
E	.717 ±.016	a	z	.838 ±.016	b yz
$\bar{X}$	.728 ±.007	a		.843 ±.007	b

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

TABLE XVI

MAXIMUM MUMMY WIDTH, IN MM, AFTER ADULT EMERGENCE ON SORGHUM (MEANS ±S.E.)

Generation	Kind of Plant				
	Resistant	1	2	Susceptible	1 2
A	.776 ±.016	a	y	.896 ±.018	b x
B	.720 ±.015	a	z	.860 ±.017	b xy
C	.725 ±.016	a	z	.793 ±.015	b z
D	.723 ±.016	a	z	.798 ±.016	b z
E	.725 ±.016	a	z	.844 ±.016	b y
$\bar{X}$	.733 ±.007	a		.838 ±.007	b

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

than the other four. On susceptible barley, the femur length decreased from generation A through each successive generation. The average femur length on resistant barley was 0.241 mm, which was significantly smaller than on susceptible barley, with a length of 0.276 mm.

TABLE XVII

ADULT PARASITOIDS FEMUR LENGTH ON BARLEY (MM) (MEANS ±S.E.)

Generation	Kind of Plant				
	Resistant	1	2	Susceptible	1 2
A	.231 ±.008	a	y	.315 ±.006	b y
B	.238 ±.007	a	y	.285 ±.006	b x
C	.265 ±.008	a	x	.271 ±.006	a xy
D	.228 ±.007	a	y	.261 ±.005	b y
E	.242 ±.007	a	y	.245 ±.005	a z
$\bar{X}$	.241 ±.003	a		.276 ±.003	b

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

Femur length on both resistant and susceptible sorghum decreased from generation A through the other four generations (Table XVIII). On resistant plants, femurs of generation A had a length of 0.267 mm.

Those of the other four generations had a length from 0.236 to 0.223 mm, without significant differences among them. On susceptible plants, femurs of generation A had a length of 0.308 mm, B had 0.290 mm, and C, D, and E ranged from 0.247 to 0.251 mm, without significant differences among the last three generations. The average length on resistant sorghum was 0.236 mm, significantly smaller than on susceptible sorghum, which was 0.272 mm.

TABLE XVIII

ADULT PARASITOID FEMUR LENGTH ON SORGHUM (MM) (MEANS ±S.E.)

Generation	Kind of Plant				
	Resistant	1	2	Susceptible	1 2
A	.267 ±.005	a	y	.308 ±.006	a x
B	.236 ±.005	a	z	.290 ±.006	b y
C	.223 ±.005	a	z	.251 ±.006	b z
D	.225 ±.005	a	z	.262 ±.005	b z
E	.229 ±.005	a	z	.247 ±.005	b z
$\bar{X}$	.236 ±.002	a		.272 ±.005	b

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

Head capsule width. Head capsule width of adult parasitoids was taken from the dorsal view of the head capsule as another comparison of general body size.

On barley, the head capsule was larger on susceptible plants, with significant differences in generations A and B (Table XIX). Analysis of the five generations on resistant plants did not show any clear tendency, with the largest head capsule, 0.359 mm, at generation C; and the smallest, 0.331 mm, at generation B.

TABLE XIX

ADULT PARASITOID HEAD CAPSULE WIDTH ON BARLEY (MM) (MEANS ±S.E.)

Generation	Kind of Plant				
	Resistant	1	2	Susceptible	1 2
A	.336 ±.008	a	yz	.418 ±.006	b x
B	.331 ±.007	a	z	.375 ±.006	b y
C	.359 ±.008	a	y	.374 ±.006	a yz
D	.350 ±.007	a	y	.351 ±.006	a z
E	.345 ±.007	a	yz	.361 ±.006	a yz
$\bar{X}$	.344 ±.003	a		.376 ±.003	b

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

On susceptible barley, a reduction of the head size was observed among the generations, since generation A had the largest, with 0.418 mm, which was significantly different from the other four generations. They ranged from 0.375 mm (generation B) to 0.351 mm (generation D).

On sorghum, the head capsule was larger on susceptible plants than on resistant plants in all five generations studied (Table XX). The former had an average of 0.369 mm, which was significantly different from resistant plants, with 0.329 mm.

TABLE XX

ADULT PARASITOID HEAD CAPSULE WIDTH ON SORGHUM (MM) (MEANS ±S.E.)

Generation	Kind of Plant				
	Resistant	1	2	Susceptible	1 2
A	.348 ±.006	a	x	.391 ±.006	b y
B	.314 ±.005	a	z	.369 ±.006	b xy
C	.325 ±.006	a	yz	.349 ±.005	b z
D	.324 ±.006	a	yz	.358 ±.006	b yz
E	.332 ±.006	a	y	.377 ±.006	b yx
$\bar{X}$	.329 ±.003	a		.369 ±.003	b

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

Within resistant sorghum plants, generation A had the largest head width, with 0.348 mm. The other four generations ranged from 0.332 to 0.314 mm. On susceptible sorghum, no tendency was observed among the generations, with the largest registered in generations A and E, and the smallest in generation C.

Mummy developmental time. This time was taken from the mummy collection day to the adult parasitoid emergence day. Only generation C had significant differences between resistant barley, where the mummies developed for 4.45 days; and susceptible barley, where they lasted 3.65 days (Table XXI).

Within each kind of plant, no tendency in mummy developmental time was observed among the generations. On susceptible barley, there was a tendency for the developmental time to increase, lasting 3.65 days in generation A, and 4.29 and 4.22 days in generations D and E, respectively (Table XXI).

On sorghum, only the last generation showed significant differences between resistant and susceptible plants, where the mummies developed in 4.49 days, compared to 3.72 days, respectively. No clear tendency was observed among the generations in either kind of plants (Table XXII).

Relationships between adult parasitoid and mummy sizes. The head capsule width and femur length of the adult parasitoids were positively correlated with the abdominal width of the mummies, before and after adult emergence (Table XXIII). The correlation coefficients (r) indicated that the adult size depended on the mummy size, since a larger mummy produced a larger adult.

TABLE XXI

MUMMY DEVELOPMENTAL TIME, IN DAYS,
ON BARLEY (MM) (MEANS ±S.E.)

Generation	Kind of Plant			Susceptible		
	Resistant	1	2		1	2
A	4.33 ±.193	a	z	3.65 ±.146	a	z
B	4.38 ±.158	a	z	4.00 ±.137	a	yz
C	4.45 ±.193	a	z	3.65 ±.137	b	z
D	4.28 ±.158	a	z	4.29 ±.129	a	y
E	4.28 ±.158	a	z	4.22 ±.129	a	y
$\bar{X}$	4.35 ±.077	a		3.96 ±.061	b	

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

TABLE XXII

MUMMY DEVELOPMENTAL TIME, IN DAYS,
ON SORGHUM (MM) (MEANS ±S.E.)

Generation	Kind of Plant			Susceptible		
	Resistant	1	2		1	2
A	4.14 ±.129	a	z	3.99 ±.146	a	y
B	4.26 ±.123	a	z	3.96 ±.137	a	yz
C	4.15 ±.129	a	z	4.12 ±.123	a	yz
D	4.31 ±.129	a	z	4.13 ±.129	a	y
E	4.49 ±.129	a	z	3.72 ±.129	b	z
$\bar{X}$	4.26 ±.057	a		3.98 ±.059	b	

[1]Values followed by the same letters within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letters within a column are not significantly different (t-test, $P < 0.05$).

TABLE XXIII

CORRELATION COEFFICIENTS (r) BETWEEN MUMMY AND ADULT PARASITOID SIZE MEASUREMENTS ($P < 0.05$)

Mummy Abdomen Width	Adult Body Parts	
	Head Width	Femur Length
Before Emer.	0.65	0.57
After Emer.	0.78	0.56

Femur length and head width of the adults were also positively correlated ($r = 0.54$, $P < 0.05$), which indicated a positive relationship in size of the two body parts studied.

Relationships between mummy developmental time and mummy size. A negative relationship was found between mummy developmental time and mummy width, both before and after adult emergence. This relationship indicated that the larger mummies required less time than the smaller ones to complete development. The linear regression equations are shown in Table XXIV. Both slopes and intercepts were highly significant (t-test, $P < 0.001$). No difference was found between the slopes for resistant and susceptible barley or sorghum.

Relationship between mummy developmental time and adult parasitoid size. Head capsule width and femur length of the adult parasitoids were negatively related to mummy developmental time, which indicated that larger individuals took less time to emerge from the

TABLE XXIV

RELATIONSHIP BETWEEN MUMMY WIDTH (x), IN MM, AND MUMMY DEVELOPMENTAL TIME (y), IN DAYS

Kind of Plant*	Linear Regression of y on x (Equation)
Before Adult Emergence	
BR	$y = 7.69 - 4.38\ x$
BS	$y = 5.87 - 2.22\ x$
SR	$y = 6.25 - 2.66\ x$
SS	$y = 5.45 - 1.75\ x$
After Adult Emergence	
BR	$y = 7.91 - 4.64\ x$
BS	$y = 6.01 - 2.39\ x$
SR	$y = 6.20 - 2.60\ x$
SS	$y = 5.45 - 1.75\ x$

*BR: Barley resistant.
BS: Barley susceptible.
SR: Sorghum resistant.
SS: Sorghum susceptible.

mummy. The linear regression equations of head capsule width and femur length on mummy developmental time are shown in Tables XXV and XXVI, where x is either adult body part and y was time spent as a mummy. In all cases but one, slopes and intercepts were significantly different from zero (t-test, $P < 0.05$). The only nonsignificant slope was for femur length in susceptible sorghum. No difference was found when the slopes of susceptible and resistant plants were compared within plant species.

Adult emergence success and sex ratio. The mean percentage emergence of the adults from the mummies and the sex ratio were studied using the individual mummies kept in gelatine capsules.

In resistant barley, 37.4% of the adults failed to emerge from the mummy, which was significantly more than those that did not emerge in susceptible barley, 17.8% (Table XXVII). Among the emerged adults, no difference was observed between female and male percentages. The sex ratio was biased toward males in both resistant and susceptible barley (Table XXVII).

On resistant sorghum, 22.8% of the adult parasitoids did not emerge from the mummies, which was significantly more than the 12.8% of emergence failure observed on susceptible sorghum (Table XXVIII). From the emerged adults, more females emerged (40.5%) from susceptible sorghum than from resistant sorghum (28.7%). More males emerged from resistant sorghum (71.3%) than from susceptible sorghum (59.9%). The sex ratio was biased toward males in both resistant and susceptible sorghum (Table XXVIII).

TABLE XXV

RELATIONSHIP BETWEEN ADULT PARASITOID HEAD WIDTH (x), IN MM, AND MUMMY DEVELOPMENTAL TIME (y), IN DAYS

Kind of Plant*	Linear Regression of y on x (Equation)
BR	$y = 7.26 - 8.57\ x$
BS	$y = 5.47 - 4.07\ x$
SR	$y = 5.86 - 4.75\ x$
SS	$y = 5.19 - 3.23\ x$

*BR: Barley resistant.
BS: Barley susceptible.
SR: Sorghum resistant.
SS: Sorghum susceptible.

TABLE XXVI

RELATIONSHIP BETWEEN ADULT PARASITOID FEMUR LENGTH (x), IN MM, AND MUMMY DEVELOPMENTAL TIME (y), IN DAYS

Kind of Plant*	Linear Regression of y on x (Equation)
BR	$y = 5.99 - 7.05\ x$
BS	$y = 5.14 - 4.37\ x$
SR	$y = 5.14 - 3.57\ x$
SS	$y = 3.55 + 1.58\ x$

*BR: Barley resistant.
BS: Barley susceptible.
SR: Sorghum resistant.
SS: Sorghum susceptible.

TABLE XXVII

ADULT PARASITOIDS EMERGENCE SUCCESS AND SEX RATIO ON BARLEY*

Sex		Kind of Plant: Resistant	Kind of Plant: Susceptible
Female	(n)	43	99
	(%)	37.71 a	32.89 a
Male	(n)	71	202
	(%)	62.28 a	67.11 a
Non-	(n)	68	65
emer.	(%)	37.36 a	17.76 b

*Values followed by the same letters within a row are not significantly different (z-test, $P < 0.05$).

Nonemergence percentages are from total number of mummies and male and female percentages are from emerged adults.

TABLE XXVIII

ADULT PARASITOIDS EMERGENCE SUCCESS AND SEX RATIO ON SORGHUM*

Sex		Kind of Plant: Resistant	Kind of Plant: Susceptible
Female	(n)	148	159
	(%)	28.68 a	40.05 b
Male	(n)	368	238
	(%)	71.32 a	59.94 b
Non-	(n)	152	58
emer.	(%)	22.75 a	12.75 b

*Values followed by the same letters within a row are not significantly different (z-test, $P < 0.05$).

Nonemergence percentages are from total number of mummies and male and female percentages are from emerged adults.

Discussion

The data and results of the analyses present a complicated picture of the influence of host plant resistance (first trophic level) on the greenbug parasitoid L. testaceipes (third trophic level).

Although the study of five generations was important to clarify some of the aspects of the host plant influence, the only life-history pattern that changed through time was the total number of mummies produced per mating pair parasitoids. The reduction in progeny observed in the progression from generation A to the other four generations, regardless of the host plants, may be due to the environmental conditions within the growth chamber used in the study (Table IV). Starks et al. (1972), working with L. testaceipes and S. graminum as host, produced from 15 to 27 mummies/mating pair on different plants from those used in this experiment and under greenhouse conditions. Sekhar (1957) reported a range from ca. 40 to 100 offspring produced per mating pair of L. testaceipes, using Aphis gossypii Glov., M. Persicae and Macrosiphum rosae (L.) as hosts. Salto et al. (1983) did not find any difference when two oat varieties, one resistant and one susceptible, were used to study the parasitoid's reaction to the greenbugs reared on those plants. The number of mummies collected from each mating pair ranged from 15 to 17 and the environmental conditions were similar to those described for the present experiments. The barley cultivar "Post" seems drastically to affect this biological parameter, since the parasitoids reared on this cultivar were able to produce an average of only six mummies, much less than the number produced on the other three cultivars and in previously reported studies. Thus, impor-

tant factors that control L. testaceipes fecundity are environmental conditions, host species, and host food source.

The potential reproductive success of the female adult parasitoids was greatly affected by the host plant. On "Post" resistant barley, only 68% of the mating pairs produced offspring of variable size, versus ca. 90% parasitization success observed on the other three varieties. Several reasons could lead to this lack of parasitization success on "Post" barley, among them a lack of preference by the adult females to lay eggs in greenbugs reared on this variety, failure of the parasitoid egg to hatch inside the greenbug, parasitoid mortality during the immature stages, and failure of the parasitoid larva to mummify the aphid. All these reasons could be related to the strong antibiosis of "Post" barley (Starks et al., 1983; and Webster and Starks, 1984).

The analysis of mummy abdominal width (mummy size) and adult head capsule width and femur length (adult size) strongly suggests that the size of an adult parasitoid is largely determined by the size of the host, when the parasitoid larva is in its destructive feeding phase (Shu-sheng, 1985; and Ruth et al., 1974). Although the size of the greenbugs was not taken in this study, mummies and adult parasitoids were smaller on both resistant barley and sorghum than on susceptible barley and sorghum. This agrees with Starks et al. (1972), who found fewer and smaller mummies on resistant plants compared with susceptible plants, suggesting the smaller greenbugs as being the main reason for the size reduction. This size reduction can greatly affect the overall fitness of the parasitoid, since it can lead to other problems, such as failure of the adults to emerge from the mummy

(Tables XXVII and XXVIII) and less vigor during the short adult life-span. Smaller adults, coming from smaller mummies, took more time as pupae, leading to longer life cycles of the insect. This negative effect of the small body size may be produced by a longer time needed by the adult parasitoid to emerge from the mummy, producing failure to emerge (Tables XXVII and XXVIII).

On "Post", 37% of the adults did not emerge from the mummies. This percentage is high compared with the nonemergence on susceptible "Wintermalt" barley, which was 18%. A similar pattern was observed between resistant and susceptible sorghum, although with lower failures to emerge. Salto et al. (1983) found between 18 and 23%, and Hight et al. (1972) found between 5 and 13% of the nonemerging adults, both authors working with L. testaceipes and S. graminum, but using other host plants. The reduction of the normal emergence percentage observed on "Post" barley might also be explained by the differences found in the mummy size before and after adult emergence. No difference was found between these measurements on "Wintermalt" nor on either sorghum cultivar. However, on "Post", the empty mummy skin was larger than the full mummy, perhaps suggesting extra effort required for the mature adult to leave the case, which could lead to a deformation or enlargement of the mummy, or to a failure to emerge.

Mummies developing on resistant plants were smaller and took more time to develop than on susceptible plants. Salto et al. (1983), working in similar conditions but with other cultivars, found no difference between resistant and susceptible oats. A large variation in this period was found by Hight et al. (1972), who reported a range from 3.3 to 4.7 days, working at different temperatures. But the

mummy formation rate was very different when comparing that of "Post" with "Wintermalt" barleys and between "Capbam" with "Pioneer 8300" sorghums. The formation of mummies was intensive in the first two days on the susceptible plants (Tables XI and XII), since ca. 80% of all mummies were found on those two days. On the other hand, only 62 and 45% of all mummies were collected on resistant barley and sorghum, respectively, during the first two days of mummy formation. Considering the reduction in mummy size, the lengthening of the stage, and the delay in mummy formation, the detrimental effect that the resistant plants used in this study can produce in this particular developing stage of the parasitoid is clear.

Other biological parameters studied, like the number of days required to complete the parasitoid larval period, and the adult sex ratio, registered sigificant differences among plant species, resistant and susceptible varieties, and in some cases, among the generations. But these variations were not large enough to be considered as determining factors in the normal life history patterns of the parasitoids.

In summary, there was considerable variation in development time, size, and fecundity among the parasitoids reared on greenbugs feeding on resistant and susceptible plants. This indicated that the suitability of a host may also vary with the quality of the food received by the host itself.

Summary and Conclusions

The effect of a greenbug resistant barley (primarily antibiosis)

and a greenbug resistant sorghum (primarily tolerance) on the third trophic level, the aphid parasitoid L. testaceipes, was tested.

Development of immature stages, mummy and adult size, and fecundity of the parasitoid were studied during five generations, under laboratory conditions. The first trophic level of the system was composed of susceptible "Wintermalt" and resistant "Post" barleys and of susceptible "Pioneer 8300" and resistant "Capbam" sorghums; the second trophic level was composed of the biotype E greenbug, S. graminum.

Fecundity, efficiency to parasitize, and adult emergence of the parasitoids were greatly reduced by the influence of resistant barley. Reduced body size and increased development time was the effect of both resistant barley and sorghum.

The use of host plant resistance can greatly affect the long-term fitness of the parasitoids, as was demonstrated mainly by "Post" barley in the three trophic level systems. Its strong antibiosis can influence important life-history and reproductive traits of the third trophic level.

CHAPTER III

THREE TROPHIC LEVEL INTERACTIONS OF A PREDATOR

Introduction and Review of Literature

Within the coccinellid predator complex, Hippodamia convergens Guerin-Meneville (Coleoptera: Coccinellidae) is one of the most important species native to North America. It is easily found in sorghum and small grain fields, feeding readily on the aphid complex found there, including S. graminum. Although parasitoids have been indicated as the major regulating factor of greenbug populations (Teetes, 1976; Wiseman and Morrison, 1981; and Kring et al., 1985), other studies have demonstrated that greenbug regulation is also obtained in the field due to the action of predators like H. convergens (Kring, 1985). Furthermore, the high visibility and large numbers of mummified greenbugs apparently contribute to overestimating the regulatory impact of parasitoids while underestimating the action of predators.

Predators of the family Coccinellidae are not very selective in the prey they feed upon. The final outcome of an encounter of the predator and a potential prey depends more on the size and defensive capabilities of the prey than on its intrinsic quality (Salto et al., 1986). This lack of selectivity was demonstrated in extreme situations, when larvae and adults of Adalia bipunctata (L.) (Coleoptera:

Coccinellidae) and Coccinella 7-punctata (L.) (Coleoptera: Coccinellidae) seemed unable to detect and avoid feeding on unsuitable or toxic aphids like Megoura viciae (Homoptera: Aphididae), even when given the choice of suitable aphids. Apparent preferences were not always expressed for the most suitable food (Blackman, 1967). Hodek (1956, 1957, 1960) reported 100% mortality in larval stages and young adults of C. 7-punctata when feeding on Aphis sambuci L. (Homoptera: Aphididae). This author concluded that a glucoside, sambunigrin, which is present in the host plant, is transferred to the body of the aphid and in turn eaten by the predator where it is transformed by enzymes to cyanic acid and other toxic compounds.

In some cereals the presence of the hydroxamic acid 2,4-dihydroxy -7-methoxy-1,4-benzoxazin-3-one (DIMBOA) resulted in antibiotic and antifeedant effects against various cereal aphids. One of the most sensitive aphids is S. graminum (Zuniga et al., 1983; Argandona et al., 1980, 1981, 1983; and Long et al., 1977). DIMBOA is sequestered in aphids feeding on DIMBOA-containing wheat plants (Niemeyer, unpublished), suggesting that this hydroxamic acid, which is an inhibitor of various insect enzymatic complexes, can be easily transferred to the third trophic level, including coccinellids, with unknown results.

The influence of physical factors involved in host plant resistance on the behavior and development of predators has been extensively studied in host plants other than cereals. Way and Murdie (1965) showed that cultivars of brussel sprouts with glossy leaves were more attractive to predators than those with waxy foliage. Movement of all instars of H. convergens was adversely affected by the sticky exudate of leaf trichomes of tobacco cultivars (Belcher and

Thurson, 1982). The younger the instar, the greater was the inhibition of movement. Carter et al. (1984) summarized these findings, concluding that plant structure is an important factor in determining the quality of a habitat for coccinellids.

Since little is known about the effect of cereals having greenbug resistance on predators, an experiment was conducted to evaluate the effects on development and adult weight of H. convergens fed during four generations on greenbugs nourished on resistant and susceptible cereals.

Materials and Methods

The test was conducted under controlled conditions, in a model E 54 B Percival growth chamber. The interior dimensions were 95 cm (width) by 61 cm (height and depth). The light was provided by eight high output cool white (daylight) 45 watt fluorescent tubes. The temperature was set at 24 ±1 C during the 13-hour photophase and at 20 ±1 C during the 11-hour scotophase. The relative humidity was not controlled and ranged between 60 and 70%.

Experimental Insects and Plants

Biotype E (Identification by Gary Puterka, based on Puterka et al., 1988) greenbugs were collected from sorghum in the field and kept in greenhouse cultures on greenbug susceptible "Wintermalt" barley during fall and winter months, and on susceptible "Pioneer 8300" sorghum during spring and summer months, in the year before the beginning of the experiment. During the same year, a special culture was set up on resistant "Post" barley, in caged 15 cm diameter plastic pots, in a

growth chamber under the previously described conditions. These conditions were required to maintain a successful culture on "Post", due to the strong antibiosis of this cultivar.

The first generation of the test was started from eggs deposited by H. convergens adults collected from the field. The identification of these adults was made by the author, based on Gordon (1985).

The cultivars used in this study were greenbug resistant "Post" barley (BR) and "Capbam" sorghum (SR), and greenbug susceptible "Wintermalt" barley (BS) and "Pioneer 8300" sorghum (SS). Two seeds were planted in 7.6 diameter plastic pots, in a medium of 3 parts soil, 3 parts sand, and 1 part peat moss.

Tests

The three variables studied were plant species, plant cultivars, and four predator generations in each cultivar. This resulted in a 2 by 2 by 4 factorial arrangement of the experiment in a completely randomized design, with ten replications for each plant-cultivar-generation combination.

Each replication consisted of a 7.6 diameter plastic pot, with two ca. 8 cm high plants covered with plastic cages having cloth-covered ventilation holes. To begin the first generation, one newly emerged larva of H. convergens was put in each pot. Enough greenbugs were added daily to permit normal development of the larva (Michels and Bateman, 1986). The source of the greenbugs was always from the corresponding plant cultivar. The larvae used in the second, third, and fourth generations originated from eggs laid by adults coming from the preceding generation, within the same plant cultivar. The adults

were fed with the same kind of greenbugs received by their larvae. To avoid inbreeding, a parallel culture was kept under the same described conditions, to have adults for mating with the ones coming from the experimental pots.

The Observations

Developmental time (in hours) was established for each preimaginal stage (egg, larva, and pupa) as well as the total developmental time. A prepupal stage was analyzed also, beginning when the fourth instar larva became immobile and ending when the larval skin was shed and the pupa was visible. Upon emergence the weight of adults was taken.

Analyses of the resulting data consisted of analysis of variance, with means being compared by t-test. Correlation studies were made between developmental time for each stage and body weight. The description and discussion of the results were based on those means which were significantly different.

Results

Egg stage duration. The time in hours for development of the eggs was studied in generations B, C, and D. The data for generation A was not recorded because the eggs were collected from the field; the day of oviposition was unknown.

On resistant barley the eggs required less time (94 hours) than on susceptible barley (122 hours) to develop (Table XXIX). This difference was significant in generations B and D. A clear tendency was observed on resistant barley to increase the duration among the gener-

ations, since it lasted 74 hours on generation B, 96 hours on generation C, and 112 hours on generation D.

TABLE XXIX

EGG STAGE DURATION, IN HOURS, ON BARLEY
(MEANS ±S.E.)

Generation	Kind of Plant				
	Resistant	1	2	Susceptible	1 2
B	74 ±5	a	x	139 ±5	b z
C	96 ±5	a	y	98 ±5	a y
D	112 ±5	a	z	131 ±5	b z
$\bar{X}$	94 ±3	a		122 ±3	b

[1]Values followed by the same letter within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letter within a column are not significantly different (t-test, $P < 0.05$).

On sorghum significant differences were found between resistant and susceptible plants or among the generations, on resistant plants. A strong reduction of time was observed on susceptible plants, where the eggs took 167 hours to hatch in generation B, and 74 and 77 on generations C and D, respectively (Table XXX).

TABLE XXX

EGG STAGE DURATION, IN HOURS, ON SORGHUM
(MEANS ±S.E.)

Generation	Kind of Plant				
	Resistant	1	2	Susceptible	1 2
B	110 ±5	a	z	167 ±5	b z
C	98 ±5	a	z	74 ±5	b y
D	106 ±5	a	z	77 ±5	b y

[1]Values followed by the same letter within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letter within a column are not significantly different (t-test, $P < 0.05$).

Larval stage duration. The larval developmental time in hours was established from the time of egg hatch to the beginning of prepupa, the immobile stage before actual pupation.

On resistant and susceptible barley and on susceptible sorghum, a tendency was observed for the larval stage duration to increase among the generations (Table XXXI). No difference was observed on resistant sorghum.

When both plant species were compared, this period was longer on barley, with a pooled mean of 327 hours, than on sorghum, with a pooled mean of 307 hours. The difference was statistically different.

TABLE XXXI

LARVAL STAGE DURATION, IN HOURS
(MEANS ±S.E.)

Generation	Resistant	1	2	Susceptible	1	2
			Barley			
A	308 ±7	a	y	307 ±7	a	x
B	293 ±7	a	y	279 ±7	a	y
C	337 ±7	a	z	353 ±7	a	y
D	358 ±7	a	z	381 ±7	a	z
$\bar{X}$	324 ±4	a		330 ±3	a	
$\bar{X}$[3]			327 ±3 a			
			Sorghum			
A	301 ±7	a	z	317 ±7	a	y
B	294 ±7	a	z	250 ±8	b	x
C	316 ±8	a	z	300 ±7	a	y
D	309 ±7	a	z	369 ±7	b	z
$\bar{X}$	305 ±3	a		309 ±3	a	
$\bar{X}$[3]			307 ±3 b			

[1]Values followed by the same letter within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letter within a column are not significantly different (t-test, $P < 0.05$).

[3]Pooled means for barley and sorghum, respectively, with letters comparing them.

Prepupal stage duration. The prepupa is the immobile stage preceding pupal ecdysis. This period lasted 36 hours on sorghum and 31 hours on barley, which was significantly different (Table XXXII). No difference was found among the generations and between resistant and susceptible plants.

TABLE XXXII

PRE-PUPAL STAGE DURATION, IN HOURS
(MEANS ±S.E.)

Plant Species	Kind of Plant		$\bar{X}^1$
	Resistant	Susceptible	
Barley	30.2 ±2.0	32.6 ±1.9	31.4 ±1.4 a
Sorghum	33.0 ±1.9	39.6 ±1.9	36.3 ±1.4 b
$\bar{X}^2$	31.6 ±1.4 a	36.1 ±1.3 b	

[1]Values followed by the same letter within a column are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letter within a row are not significantly different (t-test, $P < 0.05$).

Pupal stage duration. This period was that between the ecdysis of the last larval epidermis (end of prepupal stage) and adult emergence from the pupa.

The rate of development for the pupal stage increased from 140 hours in generation A to 155 hours in generation D (Table XXXIII).

This tendency was significant on barley, but was not on sorghum where the extreme measurements were less than those on barley. When plant species were compared in each generation, the only significant difference was found in generation B, where the pupal stage lasted 138 hours on sorghum and 126 hours on barley. No difference was found between resistant and susceptible plants.

TABLE XXXIII

PUPAL STAGE DURATION, IN HOURS
(MEANS ±S.E.)

Generation	Plant Species: Barley	1 2	Sorghum	1 2	$\bar{X}$	2
A	138 ±4	a y	142 ±4	a yz	140 ±2	y
B	126 ±4	a x	138 ±4	b y	132 ±2	x
C	145 ±4	a y	151 ±4	a z	148 ±2	z
D	160 ±4	a z	150 ±4	a z	155 ±4	z

[1]Values followed by the same letter within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letter within a column are not significantly different (t-test, $P < 0.05$).

Total developmental time. The total developmental time was the period between oviposition and adult emergence in generations B, C, and D, since no information was available from generation A egg stage duration.

A clear tendency of increase in total developmental time was observed from generation B to generation D, in both barley and sorghum. In generation B, the insects took 551 hours to complete the egg-larva-pupa period on barley and 592 hours on sorghum, which was a significant difference (Table XXXIV). In generation D, the predators took 621 hours to develop on barley and 670 hours on sorghum, which was a significant difference.

TABLE XXXIV

TOTAL DEVELOPMENTAL TIME IN GENERATIONS B, C, AND D, IN HOURS (MEANS ±S.E.)

Generation	Plant Species								
	Barley	1	2	Sorghum	1	2	$\bar{X}$		2
B	551 ±8	a	y	592 ±8	b	y	571 ±6		x
C	607 ±9	a	z	592 ±8	a	y	599 ±6		y
D	621 ±9	a	z	670 ±8	b	z	646 ±6		z

[1]Values followed by the same letter within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letter within a column are not significantly different (t-test, $P < 0.05$).

When the data from the three generations were pooled, the predators required 597 hours on resistant barley and 635 hours on susceptible barley, which was significantly different (Table XXXV). No difference was found between resistant and susceptible sorghum.

TABLE XXXV

TOTAL DEVELOPMENTAL TIME ON BARLEY AND SORGHUM, IN HOURS (MEANS ±S.E.)

Plant Species	Kind of Plant: Resistant [1] [2]	Susceptible [1] [2]	$\bar{X}$ [2]
Barley	597 ±7 a z	635 ±7 b y	616 ±5 y
Sorghum	590 ±7 a z	601 ±7 a z	595 ±5 z
$\bar{X}$	593 ±5a	618 ±5 b	

[1]Values followed by the same letter within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letter within a column are not significantly different (t-test, $P < 0.05$).

Adult emergence weight. The difference in the mean weight of the adult predators at emergence was significant on barley between generation A, with 17.3 mg; and the three following generations, with a weight of 13.3, 13.6, and 14.4 mg, respectively (Table XXXVI). No decline was observed among the generations on sorghum, where the variation was between 17.2 (generation B) and 17.8 mg (generation C).

No difference in weight was found among the adults from resistant or susceptible plants, within the same plant species. On barley, these values were 14.4 and 14.9 mg on resistant and susceptible plants, respectively. On sorghum, the mean weight was 17.4 mg on both resistant and susceptible plants.

TABLE XXXVI

ADULT EMERGENCE WEIGHT, IN MG
(MEANS ±S.E.)

Generation	Plant Species: Barley	1 2	Sorghum	1 2	$\bar{X}$	2
A	17.3 ±.5	a y	17.3 ±.6	a z	17.3 ±.4	y
B	13.3 ±.5	a z	17.2 ±.6	b z	15.3 ±.4	z
C	13.6 ±.5	a z	17.8 ±.6	b z	15.7 ±.4	z
D	14.4 ±.6	a z	17.4 ±.5	b z	15.9 ±.4	z
$\bar{X}$	14.7 ±.3	a	17.4 ±.3	b		

[1]Values followed by the same letter within a row are not significantly different (t-test, $P < 0.05$).

[2]Values followed by the same letter within a column are not significantly different (t-test, $P < 0.05$).

TABLE XXXVII

CORRELATION COEFFICIENTS (r)
FOR DEVELOPMENTAL TIME
AND ADULT WEIGHT

Time Period	r	P
Egg	0.059	0.56
Larva	-0.105	0.30
Pre-Pupa	0.059	0.56
Pupa	-0.017	0.87
Total Time	-0.038	0.71

Correlation analysis. In this analysis all values were pooled to see if the independent variables egg stage duration, larval stage duration, prepupal stage duration, pupal stage duration, and total developmental time were related to the dependent variable adult emergence weight. Total developmental time was obtained by adding times of each stage.

None of the correlation coefficients were significant, indicating that adult weight did not depend on the length of time spent as egg, larva, prepupa, pupa, or total developmental time (Table XXXVII).

Discussion

The results indicate that H. convergens was not greatly affected in its development and initial adult weight by the introduction of "Post" greenbug resistant barley and "Capbam" greenbug resistant sorghum in the three trophic system composed of cereals, greenbugs, and predators.

The comparison of the rate of development observed in this study with other studies made with greenbugs and other aphid species denotes a coincidence in the time spent as egg, larva, and pupa by H. convergens. Butler (1972) studied the predator at different temperatures. Feeding on S. graminum at 25 C, egg, larval, prepupal, and pupal stages lasted 72, 365, 31, and 120 hours, respectively, with a total of 588 hours. Obrycky and Tauber (1982), using pea aphids, Acyrthosiphon pisum (Harris), as hosts, reported 98, 350, and 149 hours for the egg, larval, and pupal stages, respectively, with a total of 597 hours, working at 21.1 C. Finally, Karnes and Manglitz (1985) introduced pea aphid host plant resistance to the system composed of al-

falfa, Medicago sativa L., the pea aphid, and H. convergens. These authors did not find any developmental rate difference due to the use of "Barker", a pea aphid resistant cultivar, with reported antixenosis and antibiosis properties against the aphids. The overall means observed in our studies were 106, 317, 33, and 143 hours for egg, larval, prepupal, and pupal developmental stages, respectively. These values are similar to the ones mentioned.

The adult weight reduction observed among the generations and the longer developmental period required by the predators on both resistant and susceptible barley cultivars, suggests that a combination of factors, including the plant species and environmental conditions in the growth chamber, produced smaller adults in a longer time.

Summary and Conclusions

Preimaginal development and initial adult weight of the predator H. convergens were studied during four generations feeding on greenbugs reared on resistant cultivars "Post" barley and "Capbam" sorghum, and susceptible cultivars "Wintermalt" barley and "Pioneer 8300" sorghum. The test was conducted under controlled conditions, at 24 and 20 C during the light and dark periods, respectively.

The introduction of host plant resistant plants in the three trophic system affected the developmental stages and the adult weight of the predator, but without altering drastically these biological parameters.

A significant decrease in the initial adult weight was observed among the generations on barley. The total developmental time was significantly longer on barley than on sorghum.

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