

COMPONENTS OF SORGHUM RESISTANCE TO THE BIOTYPE C  
GREENBUG, SCHIZAPHIS GRAMINUM (RONDANI), AND HOST  
AND PLANT RESPONSE OF A NATIVE PARASITE,  
LYSIPHLEBUS TESTACEIPES (CRESSON)

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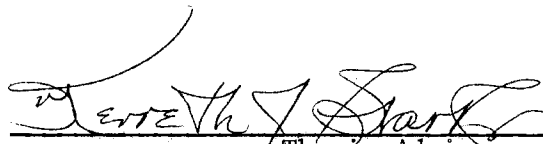
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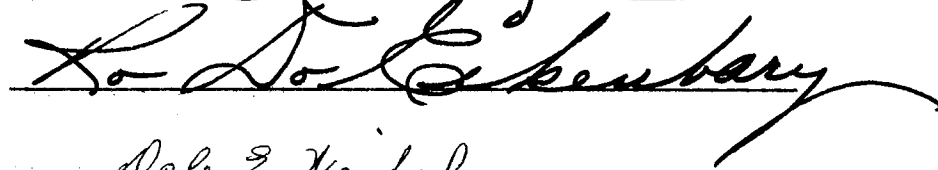
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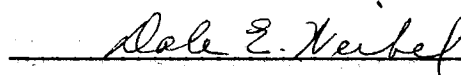
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## PREFACE

With the increasing awareness of possible pesticide hazard and pollution, attention has turned toward complementary and substitutive measures in the implementation of pest management programs. Host plant resistance and biological control have been successful in the past and have an important role in the present and future. Interactions between host plant resistance and biological control agents have been little studied and could have pronounced affects on applications to pest management.

I wish to convey a special note of appreciation to Dr. Kenneth J. Starks, Professor of Entomology and Investigations Leader, Entomology Research Division, United States Department of Agriculture, who offered much direction and encouragement as my major adviser.

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## INTRODUCTION

The greenbug, Schizaphis graminum (Rondani), has long been a serious pest of small grains. It has been responsible for considerable economic damage in 12 to 15 outbreaks in Oklahoma since its appearance (Rogers et al. 1972). The most recent outbreak in 1968 on sorghum was the result of the development of a new biotype (Harvey and Hackerott 1969a).

Insecticides previously used for greenbug control are effective but injurious to beneficial insects (Ward et al. 1970). In addition they increase production costs and present hazards both to applicators and to the environment. As a result, attention has been directed toward the utilization of host plant resistance and biological agents in controlling the pest.

The purpose of this study was twofold. First, resistant sorghum entries found through mass screening were more closely scrutinized to identify and relatively quantify the components of resistance (nonpreference, antibiosis and tolerance). It is hoped a further knowledge of these components might better enable entomologists and plant breeders to produce a sorghum variety which would retard development of further biotypes. Characterization of components is also the first step in determining the causes of resistance. Second, the attractancy of sorghum entries, other small grains and greenbugs to a native parasite, Lysiphlebus testaceipes (Cresson) was investigated.

## REVIEW OF LITERATURE

### The Greenbug

History and Importance - The greenbug was noted in abundance in 1847 in Italy but was not described until 1852 by Rondani (Webster and Phillips 1912). Originally named as Aphis graminum, it was later transferred to the genus Toxoptera in 1902 by Pergande and to Schizaphis in 1931 by Börner (Palmer 1952). The aphid quickly became cosmopolitan being recorded from North and South America, Europe, Africa and Asia (Pfadt 1962).

The greenbug was first reported in the United States in 1882, probably from Virginia (Webster and Phillips 1912). Since then it has progressed westward becoming distributed from Canada to the Gulf States and from the Atlantic to the Pacific (Davidson and Peairs 1966). Most destruction occurs from Texas north to Canada and eastward north of the Ohio River. From 1890 to 1968, 12 to 15 major greenbug outbreaks causing serious economic losses have been recorded (Rogers et al. 1972). An estimated 50 million bushels of grain is lost during severe outbreaks (Dahms et al. 1955).

Life History - The greenbug reproduces parthenogenetically throughout the year in the South (Davidson and Peairs 1966). Farther north adults may be present at all times but periods of dormancy may occur. Still farther north shiny black eggs may be laid in the autumn. The eggs are pale green when oviposited but later darken, ultimately turning black (Mayo 1972). Although many authors report that greenbug eggs hatch in

the spring, recent authors have been unable to accomplish this (Daniels 1956, Mayo 1972). However, it was shown that some embryonic development occurred.

Newborn nymphs undergo four instars and may or may not develop wings. After the last molt parthenogenetic reproduction begins and numerous generations are completed. As winter approaches winged males and females are produced and may mate. Only apterate females have been found oviparous (Mayo 1972).

Greenbug Biotypes - Wood (1961b) reported a greenbug biotype capable of destroying a previously resistant selection from Dickinson 28A wheat. The "original" or "field" strain was distinguished from the new "green-house" strain by the designations A and B, respectively. By 1965 biotype B predominated in the field (Wood and Starks 1972). Singh and Wood (1963) found that biotype A produced fewer young on Dickinson Sel 28A at optimum temperatures than did biotype B. Biotype A survival and reproduction were reduced at higher temperatures while biotype B fecundity was similar to that of biotype A on susceptible Ward barley at all temperatures. The biotypes were found further separable by the use of an artificial diet (Cress and Chada 1971). Prior to the discovery of biotype B, others had been suggested (Dahms 1948, Orlob 1961) but never became ascendant in the field.

Biotypes A and B are primarily pests of oats, wheat and barley but also attack other gramineous plants such as corn, rice, sorghum and forage grasses (Pfadt 1962). Hayes (1922) reported that the greenbug did considerable damage to sorghum in western Kansas in 1916 but was checked by a heavy rain. Greenbugs were also reported damaging to sorghum in Africa (Matthee 1962) and Rumania (Barbulescu 1964). Daniels and Jackson

(1968) noted that greenbugs collected on wheat in the field reproduced more on sorghum than on wheat at temperatures ranging from 70 to 80°F. Greenbugs collected on grain sorghum in August, 1967, were reared in the greenhouse on wheat and later transferred to grain sorghum and then back to wheat (Daniels 1969). Small colonies of the paler green aphids were noted on sorghum in 1966 while in 1967 the colonies were larger. The first widespread attack of the greenbug on sorghum in the United States occurred during the summer of 1968 (Anonymous 1968). Several million acres of grain and forage sorghum were attacked in all stages of growth in nearly all sorghum growing areas of the western U. S.

Harvey and Hackerott (1969a) designated the sorghum greenbug biotype C and separated it from biotype B on its ability to attack and damage previously resistant Piper sudangrass. Significant differences between biotypes were also noted in all entries in preference tests involving Piper sudangrass, Combine Kafir-60 sorghum, Pierre rye, Bison wheat and Reno barley. In a later study significant differences in injury between biotypes occurred on Bison wheat, Reno barley and Caribou Selection rye (Harvey and Hackerott 1969b). A cultivar of broomcorn, Deer, was shown highly nonpreferred over RS610 sorghum by biotype B but only moderately nonpreferred by biotype C (Starks et al. 1972b). This relationship was also true on the basis of nymph production and plant damage ratings.

Wood (1971) compared all three biotypes on resistant and susceptible sorghum species. In general biotype C did better on the resistant varieties while A did not survive except limitedly on SA 7536-1 and KS-30. Fecundity and longevity of biotype A was very low even on the susceptible check. Biotype B did slightly better than A on resistant and susceptible species. Wood and Starks (1972) found that except for resistant barley,

biotype C reproduced more than either A or B at optimum and extreme temperatures.

Wood et al. (1969a) gave additional differential characters of the biotypes. Feeding of biotypes A and C is in the phloem of the leaf vascular bundle while that of B is in the parenchyma of the leaf. Morphologically and ecologically A and B are indistinguishable but differ from C which is:

... much lighter in color; the cornicles are yellowish-green with no blackening (1/3 of distal end black in A and B), tips not expanded, and wrinkles present throughout their length (wrinkles present on basal portions only for biotypes A and B); lateral abdominal tubercles are present on more abdominal segments than I and VII, as is the case for biotypes A and B; it has more sensoria on the third antennal segment and reproduction rates on nearly mature sorghum plants are about 5 times greater than for biotypes A and B on similar plants; about 10% are males, and eggs are deposited inside cages, whereas, no males have been observed in colonies of biotypes A and B; and development takes place in the field at temperatures as high as 110°F, whereas biotypes A and B leave small grain plants when temperatures reach 80-85°F.

#### Host Plant Resistance to the Greenbug

Wheat Resistance to Biotype A - Wadley (1931) first suggested varietal wheat differences by noting that less than 50 percent of the nymphs survived on *Mindum durum*, although the second generation killed the plants, while less than 10 percent survived on Vernal emmer. Wheat strains shown most resistant during a widespread outbreak of the greenbug in 1942 were selections largely from the cross of Marquillo and Oro (Atkins and Dahms 1945). Others having less resistance included Denton, Early Blackhull, Wichita, Blackhull, Blackhull crosses and several Chinese and Russian strains. Dahms et al. (1955) found no wheat varieties with a high degree of resistance although some durums were more tolerant than existing adapted varieties. Of 2,000 wheat strains tested, 4 percent

appeared to have resistance approaching that of Dickinson Sel 28A while most were no better than the susceptible Pawnee (Painter and Peters 1956). Ortman and Painter (1960) compared three susceptible wheat varieties (Bison, Pawnee and Ponca) to a resistant variety (Dickinson Sel 28A) by four measurements: dry root weight, final greenbug count, dry leaf weight, and leaf length gain. All varieties experienced significant root weight loss with Dickinson losing the least except for Bison which, on a percent basis, averaged a smaller loss. Final greenbug count depended upon variety and infestation level. Dickinson Sel 28A had a lower maximum percent leaf weight reduction and leaf length gain reduction than the others. This last measurement was the most variable and judged the least reliable. Roots of five commercial wheat varieties sustained a greater percent damage than aerial portions (Daniels 1965). While supporting a greater greenbug population, Tascosa showed less leaf damage than the other entries. No entries of 320 oriental-derived wheats were found with sufficient tolerance to protect the crop (Chada et al. 1961). However, 11 resistant strains were separated from 111 entries which had previously been shown resistant elsewhere. Of 8,000 wheat lines, five Triticum vulgare and 14 T. durum with high degrees of tolerance were located (Wood 1961a). A resistant line ( $F_7$ -Ponca X Dickinson Sel 28A) had lower greenbug numbers in the field than did susceptible Ponca and produced significantly more grain (Harvey and Wilson 1962). Similar results were noted by Wood and Curtis (1967) who attributed reduced yields of Ponca largely to reduced tillering and reduced seed weight. The progeny of crosses between greenbug resistant and hessian fly resistant wheat were intermediate in their response to these insects (Abdel-Malek et al. 1966). However, the number of progeny produced by greenbugs on the  $F_1$ 's was nearly equal

to those on resistant parents.

In a study of three crosses of susceptible wheats to resistant Dickinson Sel 28A, the proportion of surviving plants suggested a single factor for the inheritance of resistance (Painter and Peters 1956). Daniels and Porter (1958) determined the single gene pair to be recessive. The single recessive gene pair designated *gbgb* was found to control resistance in both resistant strains, Dickinson Sel 28A and C.I. 9058, when crossed with each other and with susceptible varieties Ponca, Concho and Crockett (Curtis et al. 1960). Porter and Daniels (1963) likewise found no dominance factor for resistance in Dickinson Sel 28A but suggested a complex mode of inheritance influenced by the environment. Chada et al. (1961) found resistance of C.I. 11059 apparently governed by two genes indicating some dominance, while, contrary to other workers, Dickinson Sel 28A appeared governed by a single dominant gene. The possibility of modifying genes was suggested in certain genetic backgrounds.

Barley Resistance to Biotype A - Large numbers of barley varieties, mostly oriental varieties or oriental derivatives, showed a high degree of resistance (Atkins and Dahms 1945). Segregates among bulk hybrids indicated resistance could be transferred. Dahms et al. (1955) found a high degree of resistance in many barley varieties all of which came from China, Korea and Japan except for Dicktoo and Kearney. Omugi and Kearney showed the most resistance of 2,609 barley varieties tested (Daniels et al. 1956). Two barley varieties, Ward and Tenkow, suffered yield reductions even under light infestations (Dahms and Wood 1957). Tolerance was found in Smooth Awn 86, Esaw, Sunrise, Malwet, Nipa, Omugi and Sonbaku (Chada et al. 1961). Of 1,230 winter and intermediate-winter barleys, 160, largely of oriental origin, were found more resistant than Omugi.



Thirty-six of 6,174 spring barleys were found equal or superior to Omugi. Will barley (C.I. 11652) showed tolerance and some nonpreference while sustaining only a 0.4 bu decrease in yield under infestation (Jackson et al. 1964). This variety resulted from a cross between greenbug susceptible Rogers (C.I. 9174) and resistant Kearney (C.I. 7580).

Inheritance of barley resistance to the greenbug was found governed by two or more dominant genes (Dahms et al. 1955). Gardenhire and Chada (1961) and Chada et al. (1961) found resistance associated with the same or closely linked dominant genes. A single dominant gene was indicated to control greenbug resistance in Omugi and in a selection from a cross of Cordova and Omugi (Gardenhire 1965). The gene for resistance was not found associated with the genes conditioning green-seedling, powdery mildew and leaf rust resistance, and orange lemma. Smith et al. (1962), probably working with biotype A, suggested a single common dominant gene for resistance. Genes for resistance to greenbug in barley were apparently not those governing resistance to the corn leaf aphid, Rhopalosiphum maidis (Fitch) (Hormchung and Wood 1963). Omugi was susceptible to corn leaf aphid while greenbug susceptible Rogers and Davie were resistant. Selections of crosses of Rogers and Kearney were resistant to both species.

Oat Resistance to Biotype A - Atkins and Dahms (1945) found no oat varieties with high resistance although there were differences. Dahms et al. (1955) also found no high resistance but showed that Andrew and Cherokee varieties were 40 percent more tolerant than highly susceptible Wintok. Dahms and Wood (1957) later demonstrated that Andrew was slightly injured by a short infestation but suffered a reduced yield by an extended infestation. Wintok exhibited a large yield reduction under a

brief, light infestation. Cimarron was more attractive to greenbugs but was able to recover if control was performed before the plants were killed. Of 4,998 varieties, 683 exhibited a moderate resistance equal or better than that of Andrew (Chada et al. 1961). Seventy-seven were at least 10 percent more resistant.

Resistance of Russian 77 appeared conditioned by a single gene pair (Gardenhire 1964).

Causes of Resistance to Biotype A - Walton (1944) found a strong correlation between injury by greenbugs and plant vigor in field infestations, the lower the injury the higher the plant vigor. No correlation was found between amounts of mechanical tissue and resistance in wheat and barley (Chatters and Schlehuber 1951). Leaves of resistant barleys were thicker, but the importance of this character needs to be determined by investigating the length of the greenbug stylet. Although there were more stomatal openings in resistant barleys piercing habits of the greenbug made little use of them. Gardenhire and Chada (1961) did not find the resistance gene in barley associated with genes conditioning kernel row number, rough awns, hood, black pericarp or covered seed. Maxwell and Painter (1962a,b,c) in a series of papers found that tolerance of Dickinson Sel 28A wheat and Dicktoo barley was related to plant auxins present in the plants, greenbugs and honeydew.

Resistance to Biotype B - Although the biotype with which Apablaza and Robinson (1967a,b,c) worked was not given, it could have been biotype B since this biotype predominated in the field by 1965. The greenbug killed or severely damaged (reduced number of heads, average weight of kernels and weight of 1,000 kernels) seedlings of barley, wheat and oats even when introduced at advanced stages of development (Apablaza and

Robinson 1967a).. When the greenbug was transferred from barley, wheat or oats to barley or oats, there were no significant differences in average progeny produced in six days (Apablaza and Robinson 1967b). However, when transferred from barley or oats to wheat, significant reductions occurred. The greenbug also showed no varietal barley or species preference for barley, wheat or oats (Apablaza and Robinson 1967c).

Wood (1961b) in reporting the appearance of biotype B noted Omugi barley was resistant. Biotype B showed nonpreference for Will barley, P.I. 186270 oats, AR-4 (Insave F.A.) rye and RS610 sorghum with Will barley being the least preferred and AR-4 rye the least damaged (Wood et al. 1969a). In general, nonpreference was proportional to a low damage rating. Harvey and Hackerott (1969a) found Piper sudangrass resistant to biotype B. They later demonstrated resistance in C.I. 9058/7\*Bison wheat, Dicktoo barley, and Caribou Selection and Insave F.A. ryes (Harvey and Hackerott 1969b). Resistance in Will barley was shown greater at temperature extremes (Wood and Starks 1972). A cultivar of broomcorn, Deer, was highly nonpreferred over RS610 sorghum (Starks et al. 1972b).

Twenty rye varieties obtained from 12 states and Canada had 0-48 percent seedlings survive a four week infestation (Livers and Harvey 1969). Because rye is cross-pollinated, intra-varietal variation was noted with at least one plant surviving in all but three entries. Resistance equaling that of Caribou was successfully transferred to wheat. Inheritance in Caribou appeared regulated by a single dominant gene.

Todd et al. (1971) bioassayed compounds which are constituents of barley leaves against biotype B. Compounds which reduced the number and longevity of progeny had ortho-hydroxyl groups and included catechol, tannic acid, quercetin, chlorogenic acid and protocatechuic acid.

Cis-caffeic acid greatly reduced and halted reproduction whereas trans-caffeic acid (at a lesser concentration) reduced weight gain but did not affect reproduction. Compounds which were less toxic but reduced progeny survival were either benzoic or cinnamic acid derivatives having a para-hydroxyl group. Survival of less than 20% was produced by vanillic, sinapic, syringic, gentisic or ferulic acids.

Sorghum Resistance to Biotype C - Of 263 sorghum varieties and hybrids screened, only SA 7536-1 (Shallu Grain) was found highly tolerant to biotype C (Wood et al. 1969b). This entry also showed nonpreference and antibiosis. Dickson and Laird (1969) found no adapted sorghum varieties resistant. Of nearly every major group of the genus Sorghum, only S. virgatum entries showed a high degree of resistance (Hackerott et al. 1969). Although tolerance appeared to be the major resistance component, antibiosis and/or nonpreference were also suggested. Seven resistant entries were separated from 1498 received from the USDA Regional Plant Introduction Station at Experiment, Georgia (Wood 1971). Six of these entries plus resistant and susceptible checks were partly classified as to nonpreference and antibiosis. All showed a high degree of nonpreference relative to the susceptible. Fecundity and longevity did not vary appreciably but antibiosis was demonstrated by comparing aphid weights. Greenbugs reduced the yield of susceptible CK-60 but not tolerant KS30 (Hackerott and Harvey 1971). Yield appeared reduced more than grain quality. Wood and Starks (1972) showed that as temperature increased, sorghum resistance increased.

Crosses of susceptible and resistant sorghums indicated resistance was governed by dominant genes at more than one locus (Hackerott et al. 1969). Weibel et al. (1972) suggested that resistance was probably

regulated by a single incompletely dominant gene.

Resistance of Other Grains to Biotype C - Will barley, P.I. 186270 oats and AR-4 rye were nonpreferred by biotype C and AR-4 was the least damaged (Wood et al. 1969a). Of five oat varieties only one indicated some antibiosis to the greenbug (Dickson and Laird 1969). There were no differences among the tested wheat or barley varieties although greenbugs reproduced more on barley. Rice, corn and bermudagrass were highly resistant while watergrass, annual ryegrass and perennial ryegrass were immune. Harvey and Hackerott (1969b) found Dicktoo barley and Insave F.A. rye resistant. Of three millet species tested (pearl, foxtail and proso) all were found more resistant to biotype C than sorghum on the basis of fecundity and plant injury (Hackerott and Harvey 1970). Pearl millet was preferred over either proso or foxtail millets. Resistance of Will barley increased at temperature extremes (Wood and Starks 1972).

Gas chromatographic comparisons between isogenic greenbug resistant and susceptible barley strains, suggested benzyl alcohol as a resistance factor (Juneja et al. 1972). This was further indicated in bioassays in which 100 ppm benzyl alcohol imparted a phenotypic resistance in the isogenic susceptible barley strain.

A parasite, Lysiphlebus testaceipes (Cresson), and resistant sorghum and barley varieties were shown to have a combined effect in reducing plant damage and biotype C reproduction (Starks et al. 1972a).

#### Components of Host Plant Resistance

The components or mechanisms of resistance are complex, often inter-related, and are concerned primarily with effects rather than causes (Maxwell et al. 1972). As usually presented, they include nonpreference, antibiosis and tolerance. According to Maxwell et al. (1972) plants are

nonpreferred for oviposition, shelter or food, primarily because of the lack of or presence of chemical or physical factors; plants with antibiosis may affect the biology of the insect adversely; tolerant plants may survive under levels of infestation that would kill or severely injure susceptible plants.

Lysiphlebus testaceipes (Cresson)

History and Importance - The Braconid Lysiphlebus testaceipes is a native aphid endoparasite recorded on 32 hosts in eight genera (Schlinger and Hall 1960). It was first described as Trioxys testaceipes by Cresson in 1879 and since then has had no less than 18 specific names, given mostly on the basis of host and host plant.

This endoparasite is an important factor in checking greenbug populations but often not until damage has occurred (Metcalf et al. 1962). In Oklahoma and the High Plains of Texas L. testaceipes was found to be the most abundant parasite of the biotype C greenbug (Jackson et al. 1970, and Walker et al. 1973).

Biology and Life Cycle - Female L. testaceipes begin ovipositing within a few hours following emergence and continue from three days to a week with or without males present (Webster and Phillips 1912). Males predominate from unmated females but a very few females are also presumably produced. All aphid instars are attacked although the second and third are preferred. While aphid maturation following parasitization in early instars does not occur, later instars produce an average 4.0 nymphs/greenbug (Hight et al. 1972). Parasite emergence is not affected by age of aphid at parasitization. Although alate greenbugs are attacked, apterates are preferred and only one parasite develops per aphid (Webster and Phillips 1912). Development from egg to adult requires 7 to 24 days

(averaging 11.1 under warm conditions) depending upon temperature. Prior to pupation the larval parasite molds the greenbug exoskeleton into a globose, tan form. This mummy is attached to the plant surface by silking through a slit in the ventral surface (Kelly 1909).

#### Response of Entomophagous Insects to Host or Food Habitat

Besides importation, augmentation and conservation of parasites and predators in biological control programs, basic biological studies have been conducted. Included among these have been investigations of the host selection, and conversely, host restriction process. Salt (1935) summarized the sequence of host parasitization as host finding, host selection and host suitability. Later authors expanded this sequence to include an additional initial step of host habitat finding (Doutt 1959 and Sary 1964). It is probable that the same chain of events is true of predators.

Predator Response to Host Habitat - The importance of the relationship between host habitat and entomophagous insects is not clear. Many parasites and predators have been shown responsive to host habitat and others have not. Muir (1931) showed that under artificial conditions Cyrtoschinus mundulus (Bred.) will live and breed upon maize feeding on eggs of the corn leafhopper. However, in the field corn leafhopper eggs occurring on sugar cane and maize side by side will be eaten predominantly on the sugar cane. Few or no C. mundulus can be found on the maize while they are abundant on the sugar cane. Also, on sugar cane C. mundulus will feed on other homopterous eggs. It can be found on other plants but is never as plentiful as it is on sugar cane.

Chandler (1966) demonstrated that young female Syrphus balteatus Deg. do not lay eggs upon plants uninfested with aphids. Aging, however,

produces a gradual loss of restraint and, eventually, a loss of discrimination, thus promoting oviposition in the absence of an effective aphid stimulus.

Two beetle predators of Ips confusus (Lec.), Enoclerus lecontei (Wolc.) and Temnochila virescens chlorodia (Mann.), were attracted to some mono-terpenes, particularly alpha- and beta-pinene, while a parasite Tomicobia tibialis Ashm. was attracted only to materials associated with I. confusus males (Rice 1969). T. v. chlorodia was also strongly responsive to n-heptane while E. lecontei was not. Pitman and Vite (1971), however, found E. lecontei strongly reactive to conifer terpenes including alpha- and beta-pinene, myrcene and camphene while T. v. chlorodia was not.

Field olfactometer tests indicated that pine terpenes alone were not attractive to Medetera bistriata Parent, a predator of bark beetles (Williamson 1971). However, alpha-pinene in increased proportion in combination with bark beetle pheromones frontalin and verbenone elicited an increased response. Pre-ovipositional response was noted from 52 of 64 females of Medetera aldrichii Wh. in  $16.3 \pm 1.07$  seconds after predator introduction into containers with filter paper spotted with D-alpha-pinene (Fitzgerald and Nagel 1972). Thirty-one of the responding females oviposited in folds of the containers one or more times.

Parasite Response to Food Habitat - Parasites may be attracted to certain plants or habitats for mating, oviposition or food. Regardless of the reason, if the host is not present in the preferred habitat, then parasitization may not occur. Hence, attraction to certain plants or habitats for food purposes may be an important link in the host selection sequence. Adult parasites often require certain flowers as a source of



food in order to survive in large numbers (Wolcott 1942). Ichneumonid parasites generally must feed on nectar to complete egg development (Schneider-Orelli 1945). It appears that the flower, and hence, nectar needs are fulfilled largely by umbelliferae (Clausen et al. 1933, Gyorfi 1945 a,b, Kopvillem 1960, Leius 1960, van Emden 1962). Utilization of these plants may complement biological control. When small plots of umbelliferae were planted near fields of cabbage in the ratio 1:400, up to 94 percent of cabbage cutworm were parasitized (Kopvillem 1960). More parasites were trapped near or above flowering edgegrowth of wheat and cabbage than over the crops and this difference decreased as the flowers declined (van Emden 1962). Introduction of potted umbelliferae into uncultivated land appeared to increase parasite numbers. Orchards were classified as rich, average or poor on the basis of relative abundance of nectar producing flowers present in the undergrowth (Leius 1967). The ratio between rich, average and poor in parasitism of tent caterpillar pupae was 18:5:1, of tent caterpillar eggs, 4:2:1, and of codling moth and lesser apple-worms, 5:3:1.

Other foods found attractive for a Braconid, Microbracon hebeter (Say), included honey, karo, molasses and syrupy fruits (Grosch 1950). Flower odors, aromatic materials and fresh syrups made with simple sugars were unattractive, while acetic acid, acidic fluids and sour fruits were repellent.

If the food habitat does not coincide with the host habitat, a dual habitat response might occur. Pimpla ruficollis Grav., a pine shoot moth parasite, emerges and feeds on the flowers of certain umbelliferae and probably other plants (Thorpe and Caudle 1938). Tests during this period showed the parasites were repelled by odor of oil of Pinus sylvestris L.

After three or four weeks of flower feeding, the parasites return to the pine trees for oviposition. Tests during this stage showed the females attractive to the pine oil odor. This type of relationship might be considered intermediate between those parasites seeking food and those seeking ovipositional sites.

Parasite Response to Host Habitat - Limitation of a parasite to a given habitat spatially narrows the hosts which may be attacked. When these restrictions in host habitat finding are artificially eliminated, unnatural hosts may be utilized. A Bracon sp. attacks indifferently species of Apion and Bruchus whose only point in common is that they live on leguminous plants (Picard and Rabaud 1914). It is also thought the parasites deposit their eggs on particular plants which are frequented by the host but on which the host is not necessarily present. Thus the meeting of a possible host is left to chance. An ichneumonid, Scombus pterophori Ash., parasitizes representatives of several orders apparently only because they all frequent the stems of certain weeds while a chalcid, Acerophagus notativentris Gir., may attack several mealybug species but is restricted to the grape-feeding Pseudococcus maritimus (Ehr.) (Flanders 1962). A chalcid parasite of lepidopterous leaf miners was reared from sawfly eggs (Cushman 1926). Apparently the sawfly eggs were not parasitized because they were a favorite host but because they happened to be in the location of the favorite host. Zwolfer and Kraus (1957) artificially placed unparasitized fir budworms (Choristoneura murinana HB.) in oak leaf rolls in trees side by side with firs infested with the same insect. Thirteen adults of Apechthis rufata Gmel. were reared from 153 pupae from the oak while none were reared from 5,000 fir budworms from the nearby fir trees. A. rufata was also reared from both

oak tortricids present in the area.

Parasites may show preferences for hosts on different plants. Four fir tree species were infested with sawflies and placed in cages into which Tachinid parasites were released (Monteith 1955). The order of tree preference was Scots pine, red pine, jack pine and spruce. Smith (1957) released two species of hymenopterous parasites in a plastic greenhouse containing California red scale infested yucca and sago palm plants. Of 236 parasite pupae on scale from yucca, the ratio of Aphytis chrysomphali (Mercet) to A. lingnamensis Comp. was 1:3.1 while of 410 pupae on scale from sago palm the ratio was 1:81.0. Both parasites were released in small cages containing potato tubers and grapefruit infested with the scale. Progeny were obtained only from scales on the grapefruit.

Olfactory response to the host habitat or its constituents has been investigated for some parasites. Laing (1937) found that two parasites of flies, Alysia manducator Panz. and Mormoniella vitripennis Walk. were attracted to meat smell. M. vitripennis, being a parasite of pupae, responded more to old meat. Contrary to this finding Edwards (1954) showed that M. vitripennis responded to liver on which Calliphora larvae had fed but not to liver decomposed by bacteria. Thorpe and Jones (1937) indicated a slight attractiveness (58.5 percent) of oatmeal to Nemeritis canescens (Grav.), a parasite of Ephestia kuhniella (Zell.). Rhyssa persuasoria L. was more attracted to Siricid frass, and to a lesser extent, sawdust from infested timber than to sawdust from clean logs, Siricid larvae, fungal symbionts and larvae and frass of a Melandryid beetle (Spradbery 1970). However, response to fungal symbionts increased with age but then declined rapidly.

Sight and maybe chemoreception were thought to be important in the

attraction of female Eurytoma curta Walk. to knapweed flowers (Varley 1941). However, the presence of its host, Euribia jaceana Hering could not be determined without probing with the ovipositor.

Host Habitat Response of Lysiphlebus testaceipes - The Palay rubber plant was heavily attacked by the cotton aphid (Aphis gossypii Glov.) (Knight 1944). At no time were these aphids found to be parasitized by L. testaceipes on Palay rubber plants although they were attacked on cotton. The parasite was also active on the corn leaf aphid on corn, millet and undetermined grasses.

Sekhar (1960) showed that L. testaceipes preferred the cotton aphid on squash to the aphid on hibiscus when given a choice, while response was similar on both plant species when not given a choice. The parasite also preferred the green peach aphid (Myzus persicae Sulz.) on tobacco rather than on radish when given a choice, while response was again similar to both plant species when not given a choice.

More L. testaceipes were recovered from grain sorghum than from Johnsongrass, Rogers barley, Tascosa wheat, Cimmaron oats and Elbon rye (Walker et al. 1973). However, the largest peak density of greenbugs (295.2) was also on grain sorghum. The next largest number of parasites were produced on Johnsongrass which supported a relatively low peak greenbug population (35.8). Although barley supported a relatively high peak greenbug population (145.2), it ranked third in aphids parasitized.

## MATERIALS AND METHODS

### Components of Greenbug Resistance in Sorghum

The sorghum entries selected were placed in two groups, each of which was tested similarly (except where noted) but separately. Table 1 lists the sorghum selections used, their species designation and their origin. All showed some degree of resistance in previous tests except BOK-8 which was a susceptible check obtained from the Oklahoma Agriculture Experiment Station breeding program. IS-809 (probably PI-221613) was selected from material originally obtained from the sorghum collection in India. The pedigree of Shallu Grain (SA-7536-1) involves S. virgatum (Hack) Stapf. and is given in part in Wood et al. (1969b). The resistant entries represent five species of sorghum from a wide geographical range.

Greenbug cultures were maintained on Redlan susceptible sorghum in a growth chamber at 23.9 to 29.4°C alternating temperature and 12 h photoperiod during the higher temperature. Biotype C was utilized in all tests.

Nonpreference was measured by randomly planting the selections of Group I in a circular arrangement in each of 10 15 cm pots. (In the case of Group II, the selections were each randomly planted twice in a circular arrangement in each of 10 15 cm pots.) One week after emergence each entry was thinned to one plant. After releasing 40 adult apterate greenbugs in the center of each pot, they were covered with circular plastic cages with cloth-covered holes and placed in a growth chamber at 23.9 to 29.4°C alternating temperature and 12 h photoperiod during the higher

Table 1. Species designation and sources of sorghum selections rated for nonpreference, antibiosis and tolerance to the green-bug biotype C, Schizaphis graminum (Rond.).

Sorghum Selection	Species	Origin or Source
Group I		
BOK-8	<u>Sorghum bicolor</u> (L.) Moench	Oklahoma
Piper sudangrass	<u>S. sudanense</u> (Peper) Stapf.	Kansas
PI-264453	<u>S. bicolor</u>	Spain
PI-308976	<u>S. sudanense</u>	Kenya
PI-229828	<u>S. nigricans</u> (Ruiz & Pav.) Snowden	S. Africa
PI-220248	<u>S. sudanense</u>	Sicily
IS-809	<u>S. bicolor</u>	India
Shallu Grain	Partly Tunis grass <u>S. virgatum</u> (Hack) Stapf.	Texas
Group II		
PI-302178	<u>S. nigricans</u>	Portugal
PI-302231	<u>S. verticilliflorum</u> Stapf.	Australia
PI-226096	<u>S. verticilliflorum</u>	Africa

temperature. Four days later the number of adults on the plants of each entry was noted. The entire procedure for Groups I and II was repeated with alate greenbugs.

Antibiosis was evaluated by two methods. In the first, each entry was planted individually in 10 cm pots. One week after emergence the plants were thinned to one per pot, infested with 5-10 adult apterate greenbugs, covered with plastic cages and placed in a growth chamber at the conditions indicated above. The following day the adults were removed leaving nymphs 24 h old or younger. After four days the number of greenbugs was reduced to one per plant and their progeny counted and removed every 48 h until death. Ten replicates in each Group were completed. In the second method of evaluating antibiosis, each entry was planted and infested as before leaving five nymphs of known age per plant. When the greenbugs were five days old, they were removed and weighed. Ten replicates for each Group were completed.

To measure tolerance each entry was planted individually in 10 cm pots. Three days after emergence the plants were thinned to one per pot. The following day plant height from soil to tip of longest leaf was measured. One plant of each entry was then infested with ten apterate adult greenbugs and another was left uninfested. All plants were covered with plastic cages. Those in Group I were placed in a greenhouse where the temperature averaged ca 23.9°C, and those in Group II were placed in a growth chamber at the conditions for the nonpreference and antibiosis tests. Every 48 h all nymphs were removed and the number of adults maintained at 10 individuals. After 10 days the height of all plants was again noted and the differences between this measurement and the measurement at the time of infestation calculated. Infested plants were also

rated on the basis of 1 for no greenbug damage to 6 for plant death. Five replicates were completed for Group I and six for Group II.

#### Direct Observation of Parasite Preferences

The response of Lysiphlebus testaceipes females to sorghum seedlings was observed by two methods.

In the first method, three seedlings of RS-610 sorghum in a 10 cm pot were infested with biotype C greenbugs and three seedlings in another pot were kept uninfested. Each of two trials consisted of four, 30 min releases of single female L. testaceipes of unknown age into a clear plastic chamber (28 cm by 45 cm by 30 cm high with cloth-covered holes) containing both pots. Plants in the second trial were greenbug-infested four days longer than plants in the first trial. During each release the number of landings and the duration of each visit was recorded. The position of the pots was reversed between releases.

In the second method to observe parasite response to plants, leaves of three-wk-old BOK-8 seedlings were separately ground in water and in ethanol with a mortar and pestle. Single filter paper disks ca 0.6 cm diam which had been soaked in either the extract or solvent were placed on a sheet of clear, backlighted plastic at two points of an equilateral triangle. At the third point was placed a BOK-8 leaf disk ca 0.6 cm diam. Over the disks was placed the lid of a large, plastic Petri dish, thus forming a chamber into which 10 female L. testaceipes of unknown age were individually released. Each parasite was observed ca 15 min. The test was completed separately with dry paper and with filter paper disks moist with the solvent.

To observe the response of L. testaceipes to aphids, adults were collected from mummies of greenbug and corn leaf aphid, Rhopalosiphum



maidis (Fitch), attached to dead, field-collected sorghum plants. Ten aphids of each species were placed in each of 20 Petri dishes. Ten female parasites of unknown age which emerged from greenbugs were released individually in 10 of the Petri dishes and 10 female parasites of unknown age which emerged from corn leaf aphids were released individually in the other 10. The number of times each parasite approached an aphid and performed oviposition thrusts (Fig. 1) was recorded according to the species of aphid attacked. Each female was observed for 30 min.

#### Release-Capture Observations of Parasite Preferences

Into a growth chamber at 26.7°C and 12 h photoperiod were placed eight two-wk-old plants of three sorghum entries (BOK-8, PI-264453 and IS-809), individually in 10 cm pots, half of which were infested with biotype C greenbugs. In each pot was placed a 30.4 cm wooden garden stake coated on both sides at the upper 15.2 cm with "Tanglefoot". An unknown number of unsexed L. testaceipes of unknown age were released daily into the chamber for one week, at the end of which the number of parasites trapped was noted for each pot.

Ten two-wk-old plants of each of three sorghum entries (BOK-8, IS-809, and PI-264453) individually in 10 cm pots were placed under an organdy-covered cage 89 cm by 176 cm by 119 cm tall in a greenhouse where the temperature averaged ca 29.4°. One half of the plants of each entry were infested with biotype C greenbugs. Two 15.2 cm wooden garden stakes coated on all sides of the upper 10.1 to 13.3 cm with "Tanglefoot" were placed at opposing edges of each pot. An unknown number of unsexed L. testaceipes of unknown age were released daily under the cage for two weeks at which time the number trapped per pot was noted.

For the following four tests, organdy-covered cages 43.2 cm by

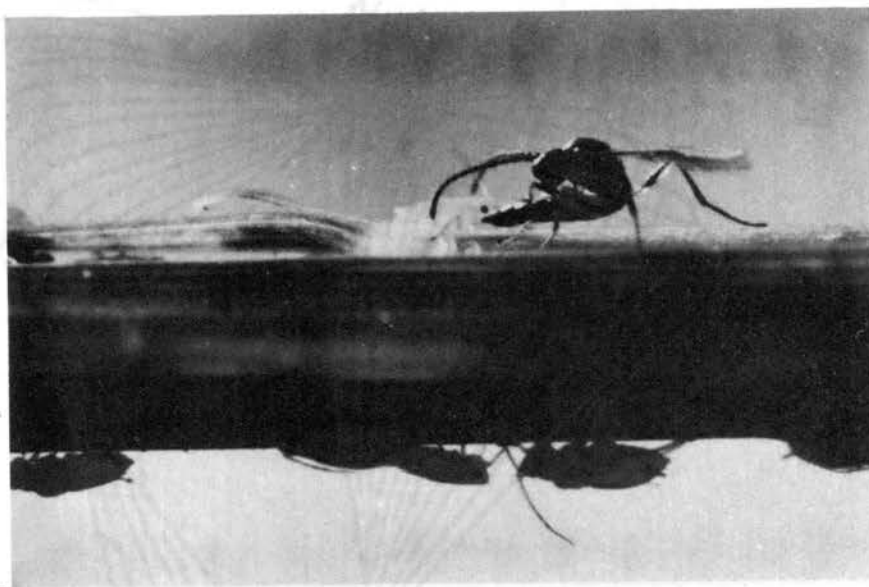


Fig. 1. Female Lysiphlebus testaceipes (Cresson) ovipositing in a greenbug, Schizaphis graminum (Rondani).

71.1 cm by 53.3 cm high were used. These were located in a greenhouse where the temperature averaged ca 29.4°C.

Ten aphids were placed on each of five 2-wk-old plants of IS-809 and BOK-8 sorghum entries. After placing the pots under the cage, five hundred unsexed L. testaceipes of unknown age were introduced and the number trapped on single "Tanglefoot"-coated lower leaves was counted three days later.

The above test was repeated with the exception that the cage was fitted with a black sailcloth cover.

Ten artificial sorghum plants (constructed by attaching sorghum-like plastic leaves to a plastic green stem) and 10 2-wk-old RS-610 sorghum seedlings in 10 cm pots were infested with biotype C greenbugs. After caging the pots, an unknown number of unsexed L. testaceipes of unknown age was introduced and the number trapped on single, "Tanglefoot"-coated lower leaves was counted four days later.

Four Petri dish halves were coated on the inside with "Tanglefoot". Ten biotype C greenbugs were placed in the center of two of them and 10 artificial greenbugs (painted sandgrains) were placed in the center of the other two. An unknown number of unsexed L. testaceipes of unknown age was released under the cage covering the dishes. The number of parasites trapped was counted 24, 48 and 72 h later.

#### Parasite Preference for Small Grain Species

In order to determine plant species preferences, one greenbug susceptible variety or selection was chosen from each of five plant species. The varieties or selections and their species are listed in Table 2. Each entry was randomly planted in the corners or center of each of five 34.5 cm by 49.5 cm flats and individually in each of five 15 cm pots. A

Table 2. Species designation of greenbug, Schizaphis graminum (Rond.), susceptible varieties or selections of small grain species rated for preference by the parasite Lysiphlebus testaceipes (Cresson).

Crop Variety or Selection	Species
Rogers barley	<u>Hordeum vulgare</u> L.
Chilocco oats	<u>Avena sativa</u> L.
Balboa rye	<u>Secale cereale</u> L.
BOK-8 sorghum	<u>Sorghum bicolor</u> (L.) Moench
Triumph wheat	<u>Triticum aestivum</u> L.

one-to-two peat moss-vermiculite mixture was substituted for soil to impede interspecies migration of greenbugs. The plants were fertilized weekly with a "Hyponex" solution. Two weeks after emergence the plants were thinned to six per species, trimmed to ca 15 cm high, and infested with 50 greenbugs. Each pot was covered with a circular plastic cage with cloth-covered holes into which were released two female L.

testaceipes 0 to 24 h old. Each flat was covered with an organdy-covered cage 38 cm tall into which were released 20 female parasites 0 to 24 h old. Pots and flats were arranged in a split-plot design on a table covered with black sailcloth to reduce interference of extraneous light sources. Lighting was provided by two double fluorescent tubes. Temperature averaged ca 23.9°C, humidity ca 40 percent RH and photoperiod ca 12 h. After 24 h all parasites were removed and the cages on the flats replaced with cylindrical plastic cages over each plant species to prevent aphid migration. After nine days the plants were cut, the number of mummies and adult and late instar greenbugs per species per pot or flat counted and the harvested material placed in ventilated quart ice cream cartons in a growth chamber at 23.9°C and with a 12 h photoperiod. After about one week the number of emerged parasites was noted.

#### Y-Tube Olfactometer Tests

Parasites for all tests were maintained on biotype C greenbugs on Redlan sorghum in a greenhouse.

A Y-tube olfactometer was constructed to determine the extent of olfactory responses of L. testaceipes to sorghum seedlings. The exterior of the apparatus is shown in Fig. 2. Air entered the system and was drawn through two columns (A). One contained ca 70 cm<sup>3</sup> of activated charcoal to remove impurities and the other ca 70 cm<sup>3</sup> of indicator silica

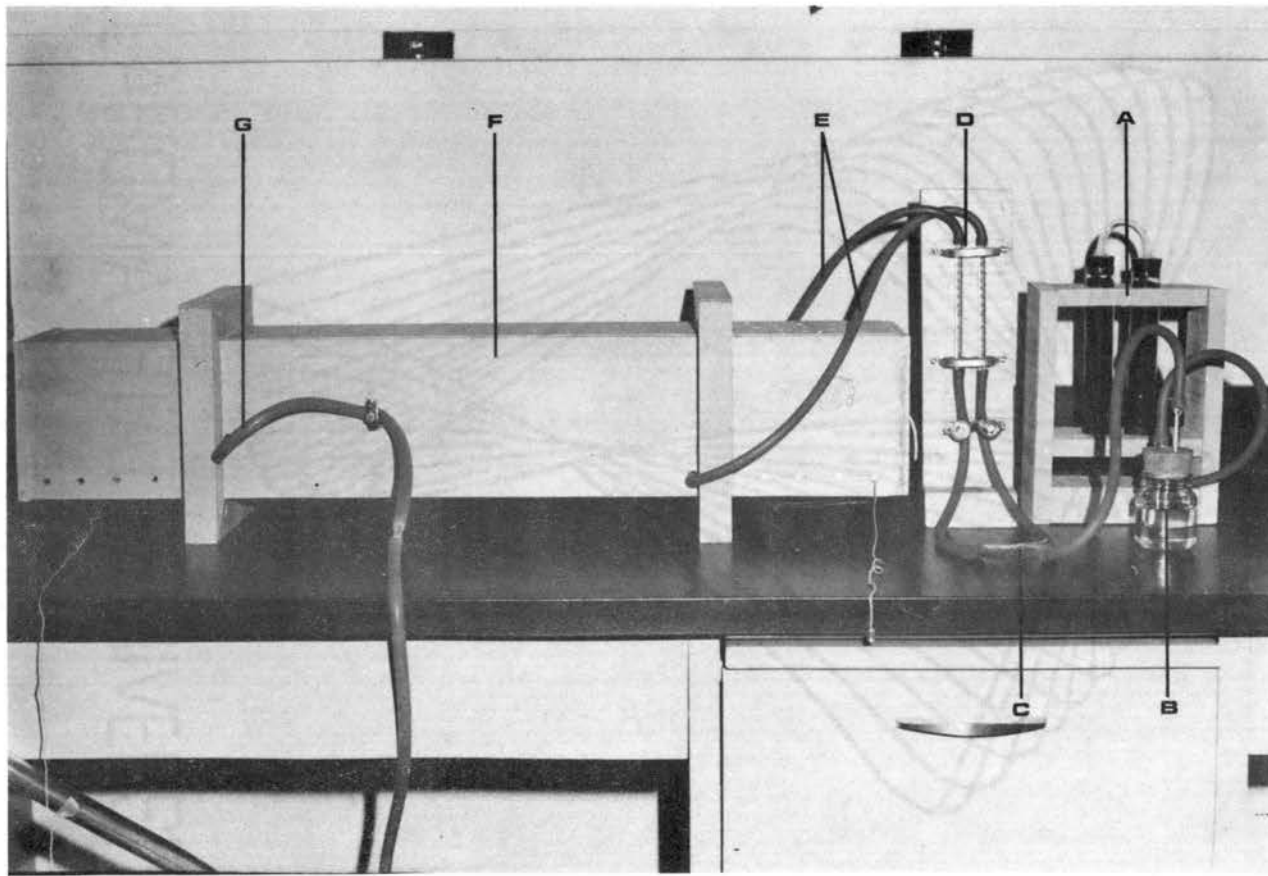


Fig. 2. Exterior of a Y-tube olfactometer used to test the response of Lysiphlebus testaceipes (Cresson) to excised sorghum leaves and greenbugs.

gel to remove moisture. In one test the silica gel was replaced with activated charcoal and the air bubbled through distilled water (B). In all other tests the air stream was split (C) after being cleaned and dried. The streams passed through flow meters (D) with a range of 0.2 to 90 ml/min and an accuracy of  $\pm 5$  percent or  $\pm 2$  mm of the scale (whichever was greater). Flow was regulated with clamps. The air stream (E) entered the test chamber (F); the combined stream exited (G) and was then drawn into a vacuum pump.

In Fig. 3 the top of the test chamber was removed exposing the interior. Air entering the chamber passed through tubing (A) and was thence drawn over the test material at B. These compartments were constructed of 4 cm sections of 0.7 cm outside diameter (O.D.) glass tubing pushed into shortened #5 black rubber stoppers. Parasites were barred entry by pieces of organdy cloth over the tube ends in the stoppers. The air streams next entered the trap compartments (C) (consisting of 6.8 cm sections of 2.7 cm O.D. glass tubing) and then moved to the Y-tube arms (D) (attached with shortened #5 stoppers) each of which had a curved length of 12.0 cm and O.D. of 0.7 cm. The air streams united and passed through the Y-tube stem (E) (8.0 cm long by 1.1 cm O.D.), a plastic coupler (F) (2.0 cm long) and into the release compartment (H) (9.0 cm long by 2.7 cm O.D.) via its stem (G) (4.5 cm long by 1.1 cm O.D.). Air left the system through a stem (I) 4.5 cm long 1.1 cm O.D. Parasite escape was prevented by a piece of organdy cloth stretched over the stem (I) opening.

To determine the region of mixing of the air streams at the Y-tube arms junctions, indicator silica gel was placed inside the arms, junction and stem. One arm was connected to the activated charcoal and silica gel

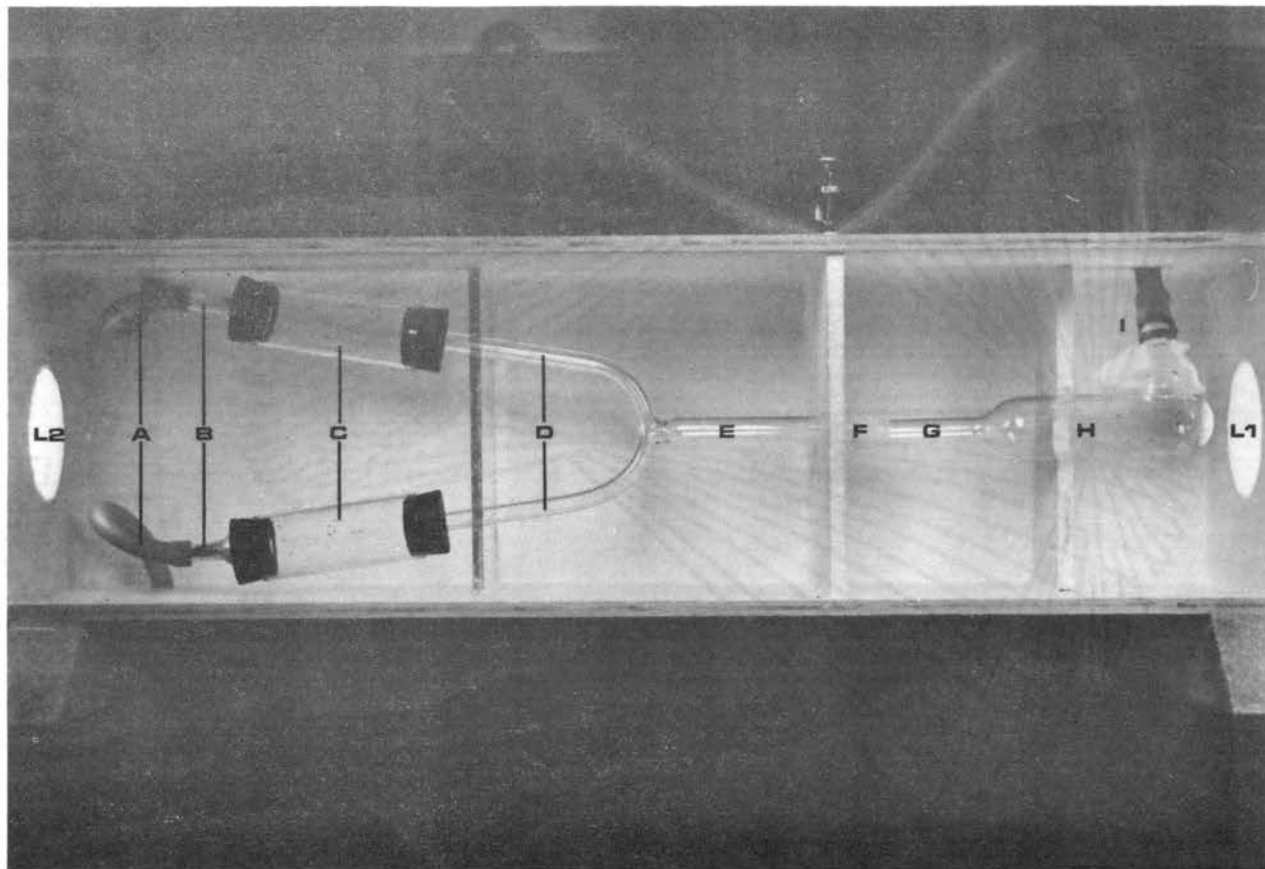


Fig. 3. Interior of a Y-tube olfactometer used to test the response of Lysiphlebus testaceipes (Cresson) to excised sorghum leaves and greenbugs.



and the other placed in a tube over hot water. The vacuum pump was run with flow adjusted at 50 ml/min until a change of color in the silica gel had proceeded beyond the arms junction of the Y-tube. The air streams appeared to unite in a relatively sharp line in the center of the Y-tube junction with a small degree of flaring beyond this area. However, the air streams tended to stay separated for a distance (ca 1.0 cm). It was judged that air mixing backward up the arms did not occur and that, because of the sharp line of air stream junction, a genuine choice by the insects was possible.

To complete a single trial within a test, the parasites were captured with a mouth aspirator and allowed to escape into the release compartment (Fig. 3, H). Light L1 was turned on, the lid placed on the chamber, the vacuum pump started and the flow adjusted. After several minutes of operating under test conditions, light L1 was extinguished and light L2 turned on. When 10 to 30 min had elapsed (depending upon response rate), flow was stopped and the number of parasites present in each arm trap (Fig. 3, C) noted.

Glassware was rinsed with acetone between all trials. Every 5 to 10 trials, glassware was washed, rinsed with distilled water and dried at ca 60°C. All trials were run at  $27 \pm 1^\circ\text{C}$ . Relative humidity of the ambient air was neither monitored nor controlled. It was thought that the moisture content of the test air stream was relatively constant after passing through the column of silica gel.

Early testing indicated a slight bias to one arm of each Y-tube, so they were placed in the test chamber in the same alignment for each trial. The test material was alternated from side to side. All tests consisted of 20 trials except where indicated.

An initial test was completed at an unknown flow rate greater than 50 ml/min using 50 unsexed parasites of unknown age per trial. The insects were given a choice of blank versus an excised leaf of one-to-two-wk old BOK-8 sorghum plants placed in the test material compartment (Fig. 3, B). Three additional tests were run at 50, 25 and 10 ml/min air flow using 25 female parasites 24 h old or younger per trial (the test at 50 ml/min consisted of 14 trials). Test choice was as above. Females of known age were obtained by placing cut sorghum plants with attached mummies in ventilated quart fruit jars. All parasites were removed with an aspirator. Newly emerged parasites were collected at the desired age interval.

Twenty-five females 24 h of age or younger per trial were obtained from mummies on sorghum which had been heavily infested with greenbugs and subsequently heavily parasitized. Emerging parasites were attracted to light in large numbers and rapidly collected for testing. Two tests were completed: in the first, an excised leaf from one-to-two-wk old BOK-8 sorghum plants was tested as above; in the second, the leaf was placed inside the trap compartment (Fig. 3, C).

Four additional tests were completed with a flow of 25 ml/min using 25 females per trial and excised leaves of one-to-two-wk old BOK-8 sorghum plants. In three of them parasites were 0 to 6 h old and were given the following choices: sorghum versus blank (air dried, 35 trials); sorghum versus blank (air bubbled through distilled water as described above); and sorghum versus a moist filter paper strip (19 trials). In the fourth test parasites were 6 to 12 h old and were given the choice of sorghum versus blank.

In two final tests more than 200 greenbugs were substituted for

excised sorghum leaves. In one test 50 unsexed parasites of unknown age were used per trial at an unknown flow rate greater than 50 ml/min. In the second, 25 females 24 h old or younger were used per trial at 50 ml/min flow.

## RESULTS AND DISCUSSION

### Components of Greenbug Resistance in Sorghum

The relative nonpreferences of the greenbug for the eleven entries are shown in Table 3. After four days 74 percent of the adult greenbugs were located on plants. The susceptible check, BOK-8, was most preferred, since 40 percent of the recovered apterate and alate adults were on this entry. In Group I PI-264453 and Piper sudangrass appeared intermediate in nonpreference although Piper was not statistically different from more nonpreferred entries when alate greenbugs were used. The remaining eight entries were statistically most nonpreferred by both greenbug forms when compared to BOK-8. There was a high positive correlation coefficient of 0.92 between the nonpreference of alate and apterate greenbugs. Nonpreference in sorghum to alate greenbugs could be more important earlier in the growing season when greenbugs first enter fields. If the nonpreference is effective, even in the absence of a more preferred host, colony formation could be avoided. Although the nonpreference of apterate greenbugs in the field is of doubtful importance, the similarity in nonpreference to alate greenbugs could permit the use of the usually more accessible and less mobile wingless aphids in future studies.

The antibiotic effects of the entries are shown in Table 4. On the basis of average weight of 5-day-old greenbugs, the entries could be separated into two aggregations: those not statistically different from the susceptible check (Piper sudangrass, PI-308976 and PI-264453) and those significantly lower (PI-229828, PI-220248, IS-809, Shallu Grain,

Table 3. Nonpreference of apterate and alate biotype C greenbugs for sorghum selections.

Sorghum Selection	Avg No. Apterate Greenbugs	Avg No. Alate Greenbugs
Group I		
BOK-8	9.1	10.9
Piper sudangrass	4.5	4.2
PI-264453	5.8	5.8
PI-308976	2.7	2.8
PI-229828	1.0	1.6
PI-220248	1.7	2.2
IS-809	1.5	2.9
Shallu Grain	1.6	2.1
LSD=0.05	1.7	2.7
Group II		
BOK-8	8.5	6.3
PI-302231	2.9	2.1
PI-226096	2.0	1.6
PI-302178	3.0	2.1
LSD=0.05	1.9	1.7

Table 4. Antibiosis of sorghum selections to biotype C greenbugs.

Sorghum Selection	Avg Weight (mg) <sup>a/</sup>	Avg Nymphs/ Adult	Avg No. Days Lived	Avg No. Days to Reproduc-tivity	Avg Days Repro- ducing
Group I					
BOK-8	.169	44.9	35.4	6.4	20.0
Piper sudangrass	.162	15.6	34.0	8.6	15.6
PI-264453	.143	20.2	32.0	7.6	15.2
PI-308976	.144	18.6	36.6	8.8	16.6
PI-229828	.105	12.9	37.2	9.2	18.6
PI-220248	.099	9.7	30.6	9.8	12.2
IS-809	.085	11.5	35.2	9.2	15.0
Shallu Grain	.082	9.8	31.2	9.2	12.2
LSD=0.05	.031	7.9	9.0	1.5	6.1
Group II					
BOK-8	.161	55.0	36.4	6.7	23.5
PI-302231	.067	16.3	30.1	10.6	13.5
PI-302178	.069	7.8	29.9	10.6	15.4
PI-226096	.049	6.9	24.1	9.1	9.3
LSD=0.05	.031	10.9	7.2	1.4	8.2

<sup>a/</sup> Greenbugs 5 days old at weighing.

PI-302231, PI-302178 and PI-226096). No significant differences occurred within these aggregations. The average number of progeny per adult on BOK-8 was significantly greater than that of the other selections indicating some antibiosis in all the resistant selections. The two aggregations indicated by nymphal weights were not statistically discernible on the basis of average number of progeny. However, the heaviest and largest number of nymphs were produced on the same selections (except for PI-302231). Similarly the lightest and fewest nymphs were produced on the same selections. Longevity of adult greenbugs was significantly affected in comparison to BOK-8 only by confinement on PI-226096. Greenbugs on BOK-8 started reproducing significantly sooner than on the other entries with the exception of PI-264453. The duration of reproduction was significantly shorter than BOK-8 only on PI-220248, Shallu Grain, PI-302231 and PI-226096, although no entry enabled a longer period than BOK-8. In general greenbugs tended to live about the same number of days after cessation of reproduction compared to BOK-8 except for PI-302178. Replication may not have been adequate to detect significant differences in all antibiosis measurements, particularly the longevity and duration of reproduction. However, the nymphal weights, progeny per adult and time until first reproduction were in relatively close agreement.

Average plant height differences between infested and uninfested plants were significant for five entries (including the check) and non-significant for six entries (Table 5). Neither tolerance nor nontolerance appeared restricted to tall or short entries since PI-264453 and Piper sudangrass are both tall and IS-809 and BOK-8 are both short. The plant injury scores were not entirely in agreement with the height differences although BOK-8, Piper sudangrass and PI-302231 indicated the least

Table 5. Tolerance of sorghum selections to the biotype C greenbug as measured by differences in beginning and ending height of plants when uninfested and infested for 10 days and by plant injury score.

Sorghum Selection	Avg Plant Height Difference (cm)			Avg Plant Injury Score
	Uninfested	Infested	Percent Difference <sup>a/</sup>	
Group I				
BOK-8	20.8	7.5	65*	4.8
Piper sudangrass	24.6	9.0	63*	3.8
PI-264453	21.3	17.6	17	2.2
PI-308976	24.3	16.3	30*	2.4
PI-229828	23.6	17.6	24	1.2
PI-220248	30.5	21.2	30*	1.2
IS-809	16.5	13.9	17	1.0
Shallu Grain	20.6	19.4	6	1.4
LSD=0.05				2.4
Group II				
BOK-8	12.5	3.7	70*	4.8
PI-302231	9.6	5.6	42*	4.2
PI-302178	8.8	7.7	12	1.5
PI-226096	7.1	6.2	13	1.8
LSD=0.05				1.6

<sup>a/</sup>Where \* occurs, the difference between the mean height of uninfested and infested plants was significantly different at  $P=0.05$ .



tolerance by both measurements. In general the injury ratings agreed with the measurements for nonpreference and antibiosis.

The susceptible BOK-8 indicated the least resistance of all the entries (Table 6). Piper sudangrass demonstrated low tolerance, but indicated some nonpreference and antibiosis (as did all resistant entries). Tolerance appeared to be the chief resistance component of PI-264453. While intermediately tolerant PI-220248 and PI-302231 indicated relatively high degrees of nonpreference and antibiosis, PI-308976 suggested a relatively high degree of nonpreference and an intermediate degree of antibiosis and tolerance. The remaining five entries (PI-229828, IS-809, Shallu Grain, PI-302178 and PI-226096) all appeared to possess comparatively high degrees of all three components.

Painter (1951) suggested that the ability of an insect to attack a previously nonpreferred host would necessitate pre-imaginal olfactory conditioning or a mutation affecting the insects' nervous mechanism concerned with the plant response. A change to an antibiotic host would involve mutations of genes governing the insects' physiology. Much more complex changes would be necessary for a host change if both nonpreference and antibiosis were present. On this basis it would appear that entries PI-229828, PI-220248, IS-809, Shallu Grain, PI-302231, PI-302178 and PI-226096 should each carry highly permanent resistance. Tolerance implies a biological relationship in which neither host nor insect is adversely affected. For this reason Beck (1965) does not classify it as a form of resistance in the strict sense. Whatever the classification, tolerance permits the production of a crop despite an insect infestation and, because of its unique host-pest relationship, there should be reduced selection pressure on the insect in favor of genetic mutations

Table 6. Relative <sup>a/</sup> degrees of greenbug biotype C resistance components expressed in sorghum selections.

Sorghum Selection	Nonpreference	Antibiosis	Tolerance
Group I			
BOK-8	+	+	+
Piper sudangrass	++	++	+
PI-264453	++	++	+++
PI-308976	+++	++	++
PI-229828	+++	+++	+++
PI-220248	+++	+++	++
IS-809	+++	+++	+++
Shallu Grain	+++	+++	+++
Group II			
BOK-8	+	+	+
PI-302231	+++	+++	++
PI-302178	+++	+++	+++
PI-226096	+++	+++	+++

<sup>a/</sup> + denotes low or no component expression; ++ denotes intermediate component expression; +++ denotes high component expression.

enabling adaptations to resistant entries. As a result, entries PI-229828, IS-809, Shallu Grain, PI-302178 and PI-226096 should have an added degree of resistance permanence. However, it should be noted that since there is a relationship among nonpreference, antibiosis and tolerance (when based on injury scores) in this study, it cannot be stated conclusively that these factors are separate entities and not different expressions of the same plant trait. If the latter is true, resistance would not be assumed to be as permanent. It would seem doubtful that all sources and components of greenbug resistance are controlled by the same inheritance factors.

#### Direct Observation of Parasite Preferences

The observed landings of female L. testaceipes are shown in Table 7. In general, parasites landed more frequently (at least within trials) on plants not infested with greenbugs. However, after landing, more time was spent on infested plants than on uninfested plants. Perhaps plant characteristics are more important in landing while the presence of hosts acts as a flight arrestant. Both the average number and duration of landings were greater for trial 2. This may indicate that the presence of more aphids stimulates greater parasite activity. However, the parasites used in trial 2 may have been different from those used in trial 1 in some respect such as age.

No tested female parasites exhibited any recognizable response toward sorghum leaf disks or dry or moist extract- or solvent-soaked filter paper disks when confined in the circular test chamber. Possible explanations include: plants elicit no response; color, texture, or olfactory factors are unimportant in host habitat finding or unoperative in the absence of other visual stimuli (form, for instance); plant

Table 7. The number and duration of observed landings of individual female Lysiphlebus testaceipes (Cresson) on greenbug infested and uninfested sorghum seedlings.

Trial	Landings of Single Females <sup>a/</sup>			
	Greenbug Infested		Greenbug Uninfested	
	Avg No.	Avg Duration (min)	Avg No.	Avg Duration (min)
1	.25	2.50	2.75	.92
<sup>b/</sup> 2	2.75	2.66	4.00	1.82

<sup>a/</sup> Individual females observed for 30 min.

<sup>b/</sup> Plants in Trial #2 were infested 4 days longer than those in Trial #1.

characteristics are operative at a distance; concentrations of olfactory substances were overwhelming to the insects' receptors (because of the enclosed conditions); the parasites utilized were unresponsive due to other factors (i.e., age); the insects' receptors were damaged during transfer. Successive tests seem to indicate the first explanation to be incorrect. Color, texture or olfactory factors apparently do not play a role in stimulating directed search patterns since females were observed to walk directly on leaf disks without hesitating. However, plant characteristics may act together in attracting the parasite from a distance, thus functioning as the stimulus for the first step of host habitat finding proposed by Doutt (1959) and Stary (1964). Certainly this is plausible since in the preceding test the presence of aphids did not result in more stops. It is doubtful that concentrations of plant olfactory constituents were large enough to mask a response, particularly since, as noted above, the females were noted to walk over the leaf disk without stopping. Intrinsic factors of the parasite (such as old age), while possible, are not probable since the tests were run on two separate days. Damage to the insects' receptors, although certainly possible, is not probable since parasites in the next test were handled similarly but responded to aphids. Neither greenbugs nor corn leaf aphids appeared preferred either by females emerging from mummies of greenbugs or corn leaf aphids (Table 8). More oviposition thrusts were made by parasites which had emerged from corn leaf aphids. As mentioned earlier, L. testaceipes has been recorded from many hosts in many habitats. It has been suggested that different strains or biotypes of the parasite exist for each of the different hosts. The present test indicates that L. testaceipes present on different aphid species on sorghum are of the same

Table 8. The average number of oviposition thrusts of individual female Lysiphlebus testaceipes (Cresson) emerging from mummies of greenbugs and corn leaf aphids when given a choice of greenbugs or corn leaf aphids.<sup>a/</sup>

Aphid Parasitized	Aphid From Which Parasite Emerged	
	Greenbug	Corn Leaf Aphid
Greenbugs	10.3	15.7
Corn leaf aphids	12.7	14.5
LSD=0.05	5.0	5.0

<sup>a/</sup> Individual females were observed for 30 min.

strain in terms of host selection but that degree of activity may be influenced by host.

#### Release-Capture Observations of Parasite Preferences

The average number of parasites trapped at greenbug-infested and uninfested sorghum plants are shown in Table 9. In an analysis of variance for each experiment F tests indicated no significant differences between entries or infestations. Thus the parasite did not demonstrate any preference for greenbug susceptible or resistant entries and this was not affected by being infested or uninfested. However, the experimental error was high as shown by significant differences between replicates. The position of replicates, and positions within replicates, indicated that the path of movement of the sun played a large role in determining where the parasites were recovered in the greenhouse. Although differences are apparent between numbers of parasites trapped in the growth chamber and greenhouse, the differences may not be real. An effort was made to release approximately the same number of parasites in each test although this was not checked. It is possible that the volume of the containers in which the tests were conducted is more important since the greenhouse cage was at least twice as large as the growth chamber. Personal observations during the maintenance of parasite cultures in covered 15 cm pots and 34.5 cm by 49.5 cm flats indicated that fewer parasites were required for the pots than the flats in producing similar numbers of mummies per plant. It should be pointed out that because of the long duration of these tests that the number of greenbugs on susceptible and resistant entries probably differed. Uninfested plants became infested in some cases.

The number of L. testaceipes trapped on greenbug-susceptible and

Table 9. Lysiphlebus testaceipes (Cresson) trapped on greenbug resistant and susceptible sorghum plants uninfested and infested with greenbugs.

Sorghum Selection <sup>a/</sup>	Avg No. Parasites Trapped/Plant <sup>b/</sup>	
	Greenbug Uninfested	Greenbug Infested
	<sup>c/</sup> Growth Chamber	
BOK-8	16.25	6.25
PI-264453	12.75	13.00
IS-809	13.00	9.75
	<sup>d/</sup> Greenhouse	
BOK-8	5.6	9.6
PI-264453	8.2	6.8
IS-809	6.2	5.2

<sup>a/</sup> BOK-8 is greenbug susceptible and PI-264453 and IS-809 resistant.

<sup>b/</sup> Parasites were trapped on "Tanglefoot"-coated stakes placed in the pots.

<sup>c/</sup> Test conducted in a growth chamber at 26.7°C and 12 hr photo-period.

<sup>d/</sup> Test conducted in a greenhouse where temperature averaged ca 29.4°C.



resistant entries in covered and uncovered cages are shown in Table 10. More parasites were trapped on greenbug-susceptible BOK-8 than on resistant IS-809 in both uncovered and covered cages although differences within tests were not significant. Fewer parasites responded under darkened conditions, indicating that parasites may be inactive (relative to host habitat finding) under reduced light or that sight plays a large role in locating the host's plant. Parasites in closed vials have been observed to be relatively inactive in dark situations. Sekhar (1960) similarly observed L. testaceipes to rest on the sides of cages at night even in the presence of a preferred host. The lower leaves of plants were coated with "Tanglefoot" in an attempt to increase the recovery of released parasites. Only about 1/3 of the parasites were trapped on plants in the uncovered cage while only 4.6 percent were trapped in the covered cage. Unrecovered parasites may have died before responding (since their age was unknown), may have responded but escaped trapping, may not have responded, or may have responded more phototaxically than phytotaxically. It is possible that a combination of the above factors was responsible.

Significantly more parasites were trapped on real than on artificial sorghum plants (Table 11). This could have been due to plant characteristics or to the aphids with which they were infested or to both. Since a greenbug infestation had not previously shown any significant effect, the present response might be due more to plant characteristics, including olfactory substances, color, texture, form, etc. Although the artificial plants were constructed to resemble real plants as nearly as possible, it would be impossible to exactly duplicate real plants in all respects except olfactory substances. However, it is possible that olfaction was more important in the differential response, although some

Table 10. Lysiphlebus testaceipes (Cresson) trapped on greenbug resistant and susceptible sorghum seedlings infested with greenbugs in covered and uncovered cages.<sup>a/</sup>

Sorghum Selection <sup>b/</sup>	Uncovered		Covered
	Avg No. Parasites <sup>c/</sup>	% Parasites Recovered	% Parasites Recovered
BOK-8	17.8	17.8	3.4
IS-809	15.0	15.0	1.2
LSD=0.05	9.1	11.8	3.8

<sup>a/</sup>Parasites were trapped on "Tanglefoot"-coated lower leaves.

<sup>b/</sup>BOK-8 is greenbug-susceptible and IS-809 is resistant.

<sup>c/</sup>The average number of parasites (of five replicates) recovered from 500 released.

Table 11. Lysiphlebus testaceipes (Cresson) trapped on real and artificial sorghum seedlings and real and artificial greenbugs.

	Avg No. Parasites Trapped			
	Sorghum <sup>a/</sup>	Greenbugs <sup>b/</sup>		
		24 h	48 h	72 h
Real	57.0	0.0	0.0	12.0
Artificial	13.0	0.0	0.0	15.0
LSD=0.05	8.9			

<sup>a/</sup>Parasites were trapped on "Tanglefoot"-coated lower leaves.

<sup>b/</sup>Parasites were trapped on "Tanglefoot"-coated Petri dishes. No parasites were trapped until after 48 hr following release.

parasites were trapped on the artificial plants, suggesting at least a slight attractancy based on physical characteristics. It is probable that both chemical and physical stimuli influence the responses to plants.

No parasites responded to real or artificial greenbugs until after 48 h had elapsed (Table 11). During this period parasites were observed on the top and sides of the cage but not on the bottom. At the end of 72 h the average number of parasites trapped on real and artificial greenbugs was not significantly different. Dead parasites were also present on the bottom of the cage possibly indicating trapped parasites were not responding to aphids but becoming ensnared as they weakened and fell from the top and sides. This fact, together with no results until after at least 48 h, strongly suggests that L. testaceipes responds to aphids only at a relatively short distance.

The preceding preliminary direct and release-capture observation tests appeared to indicate that L. testaceipes first responds at a distance to its host's plant without regard to different selections of sorghum or to the presence of a greenbug infestation. After the parasite reaches the host habitat or plant, plant characteristics appear to no longer elicit a strong response while greenbugs do. The following tests were conducted to attempt to delineate more precisely the role of plant species and olfactory responses in host and host habitat finding.

#### Parasite Preference for Small Grain Species

Preliminary tests showed that releasing only 10 parasites per flat resulted in too few mummies and too many zero data points. Also, since greenbug reproduction is reduced by parasitism (Hight et al. 1972), fewer parasitisms resulted in greater greenbug numbers and, in many cases, plant death before mummification could occur. For these reasons, twice

as many parasites per replicate were introduced in the free choice treatment.

F-tests in analyses of variance indicated significant species effects over both choice treatments on the average numbers of greenbugs and mummies (Table 12). Significantly more adult and late instar greenbugs were present on Triumph and Rogers than on the other entries. Chilocco supported significantly fewer greenbugs than the other entries except BOK-8. The species differences of the average number of mummies over both choice treatments were probably due largely to differences in greenbug susceptibility of the entries, since, in general, there was a strong relationship between final greenbug counts and average number of mummies. However, Chilocco deviated greatly from the greenbug-to-mummy ratio, thus indicating some varietal effect on parasitism success. Percent emergence was not significantly affected by small grain species. The difference between total number of mummies produced in the choice treatments was nonsignificant. The volume of the cages for flats was ca 3.3 times that of pot cages on a per replicate basis. Since the magnitude of averages for the number of mummies are comparable, the searching success of L. testaceipes is approximately halved when the search volume increases 3.3 times.

Only Balboa produced a significant difference between choice treatments. Although Triumph approached significance, the reduction in mummies was attributable to a reduced greenbug population due perhaps to reduced aphid survival or migration. It is possible that spheres of influence of the entries overlapped and masked differences in parasite response.

Table 12. Effect of five small grain species on the host plant response and emergence of a greenbug parasite, Lysiphlebus testaceipes (Cresson).

Small Grain	Totals			Free Choice		No Choice	
	Avg No. Green-bugs	Avg No. Mum-mies	% Parasite Emergence	Avg No. Green-bugs	Avg No. Mum-mies	Avg No. Green-bugs	Avg No. Mum-mies
Triumph wheat	102.6	51.0	88.6	77.8*	45.0	127.4	57.0
Rogers barley	93.7	38.4	94.5	94.0	41.2	93.4	35.6
BOK-8 sorghum	36.2	15.3	77.1	35.2	17.6	37.2	13.0
Balboa rye	52.0	23.9	81.2	47.4	16.4*	56.6	31.4
Chilocco oats	36.3	7.4	85.1	44.0	4.6	28.6	10.2
LSD=0.05	23.9	13.7	24.7	32.4	18.2	32.4	18.2

\*Choice treatment differences within varieties significant at  $P=0.10$ .

### Y-tube Olfactometer Tests

Unsexed L. testaceipes of unknown age did not significantly respond to an air stream of unknown flow rate (greater than 50 ml/min) drawn over excised leaves of one-to-two-wk old sorghum plants (Table 13). In an attempt to reduce the variation (as shown by the large heterogeneity  $\chi^2$  values), only females 24 h old or younger were used and the flow rate was adjusted downward. At 50 ml/min the heterogeneity  $\chi^2$  was still significant at  $P=0.10$  while at 25 and 10 ml/min it was not. The relatively large heterogeneity  $\chi^2$  at 50 ml/min was attributed to the tendency of the air flow to change momentarily in one flow tube arm or the other. This did not occur as frequently at 25 and 10 ml/min. The air flow at 25 ml/min was most easily regulated and was utilized for subsequent testing with excised sorghum leaves. The percent response at 10 ml/min was slightly greater than at 25 or 50 ml/min. No responses were significant when using parasites emerging in relatively low numbers. However, parasites which emerged in large numbers and which were rapidly attracted to a light source for collection showed a significant response to sorghum leaves. Placing an excised leaf in view of the responding parasites did not significantly affect the percent choosing sorghum leaves. A possible reason for the greater responses could have been an increased proportion of young parasites being utilized. To test this, females 0 to 6 and 6 to 12 h old were given a choice of sorghum leaf versus blank (Table 14). Fewer 6 to 12 h old female parasites chose sorghum leaves. Although this difference was not significant, it may indicate a small effect of age on response. Testing with 12 to 18 and 18 to 24 h old females was not completed because of difficulties in obtaining a sufficiently large number of parasites. Parasites confined under lighted conditions for the longer

Table 13. Effect of flow rate, and parasite sex, age and rate of emergence on the reaction of Lysiphlebus testaceipes (Cresson) to one-to-two-week old excised sorghum leaves in a Y-tube olfactometer.<sup>a/</sup>

Flow Rate ml/min	Parasite Sex	Parasite Age	Rate of Emergence <sup>b/</sup>	% Parasites Choosing Leaf	Heterogeneity $\chi^2$	Pooled $\chi^2$
50 <sup>c/</sup>	Unsexed	Unknown	Low	52.95	38.63**	1.478
50	Female	≤ 1-day	Low	53.16	23.68*	.051
25	Female	≤ 1-day	Low	53.50	19.72	.845
10	Female	≤ 1-day	Low	54.84	22.25	2.42
25	Female	≤ 1-day	High	60.06	22.45	12.48**
25	Female	≤ 1-day	High	56.96 <sup>d/</sup>	20.77	5.69**

<sup>a/</sup> All runs consisted of 20 trials except for that at 50 ml/min which had 14 trials. Choices in all runs were excised leaf versus blank.

<sup>b/</sup> Rate of emergence refers to the rapidity at which parasites could be attracted to light and collected for testing.

<sup>c/</sup> The actual flow rate was unknown but was greater than 50 ml/min.

<sup>d/</sup> In this run, the excised leaves were placed in view of the reacting parasite instead of hidden as in previous runs.

\*\* $\chi^2$  significant at both  $P=0.10$  and  $0.05$ .

\* $\chi^2$  significant only at  $P=0.10$ .



Table 14. Effect of parasite age and relative air moisture on the reaction of female Lysiphlebus testaceipes (Cresson) to one-to-two-week-old excised sorghum leaves in a Y-tube olfactometer.

Parasite Age (h)	Relative Air Moisture	Choice vs Sorghum	% Parasites Responding	% Parasites Choosing Sorghum	Pooled $\chi^2$
0-6	Dry	Blank	44.57	60.20	21.93**
6-12	Dry	Blank	44.80	56.25	3.25*
0-6	Humid	Blank	26.40	47.73	.19
0-6	Dry	Moist Paper Strip	42.11	65.50	18.66**

\*\* $\chi^2$  significant at  $P=0.05$ .

\* $\chi^2$  significant at  $P=0.10$ .

time intervals survived very poorly.

When the air stream was bubbled through distilled water, there was no significant response of parasites to sorghum leaves (Table 14). Fewer parasites responded, the majority remaining in the release chamber (Fig. 3, H). This may indicate that parasites previously were responding to moisture being released by the cut leaf, that olfactory substances of sorghum leaves are not released in humid air, or that parasites are repelled by humid air. Females given a choice of an excised sorghum leaf versus a filter-paper moistened with distilled water chose leaves 5.30 percent more than those without a choice of moist filter paper. This indicated that female parasites were making a genuine response to sorghum leaf olfactory substances which may be more volatile in dry air. Parasites may have been repelled by moist air or by some factor of the filter paper although the latter seems unlikely.

Unsexed L. testaceipes of unknown age significantly responded to biotype C greenbugs (Table 15). Regulating air flow at 50 ml/min and utilizing females 24 h old or younger decreased the variation (nonsignificant heterogeneity  $\chi^2$ ) as well as the response, although the difference was not significant.

Significant responses of parasites to sorghum leaves in these tests range from 56.96 to 65.50 percent and averaged 59.69 percent. This agrees closely with the response of the ichneumonid parasite, Nemeritis canescens (Grav.), to oatmeal (58.5 percent), one food of the preferred hosts in the genus Ephestia (Thorpe and Jones 1937), and with response of Pimpla ruficollis Grav. to odor of oil of Pinus sylvestris L. (58.5 percent), a food of the pine shoot moth, Rhyacionia (Evetria) buoliana Schiff. (Thorpe and Caudle 1938). Since the olfactometers used in the

Table 15. Reaction of adult Lysiphlebus testaceipes (Cresson) to ≥ 200 greenbugs in a Y-tube olfactometer.

Flow Rate ml/min	Parasite Sex	Parasite Age	% Parasites Choosing Aphids	Heterogeneity $\chi^2$	Pooled $\chi^2$
> 50 <sup>a/</sup>	Unsexed	Unknown	59.69	36.76**	11.63**
50	Females	<u>≤</u> 24 h	55.68	8.65	3.18*

<sup>a/</sup> The actual flow rate was unknown but was greater than 50 ml/min.

\*\* $\chi^2$  significant at  $P=0.05$ .

\* $\chi^2$  significant at  $P=0.10$ .

latter and present studies were similar, and since responses to sorghum leaves and aphids were similar, it is possible that apparatus design restricted or encouraged parasite response. However, this would seem unlikely since Thorpe and Jones (1937) obtained a much greater response of N. canescens to Ephestia larvae with their apparatus. It seems probable, then, that L. testaceipes does respond to olfactory substances released by sorghum leaves and greenbugs, and that, when working simultaneously under field conditions, these factors may represent an important link in host finding.

During these tests, parasites were often observed with the abdomen lowered and the head and thorax elevated (Fig. 4). Associated with this stance was movement of the antennae which suggested sampling of the air for olfactory substances. This behavior may further indicate the possible importance of olfaction in host finding. Plant characteristics, such as color and form, may operate in conjunction with olfactory characteristics and must not be overlooked.

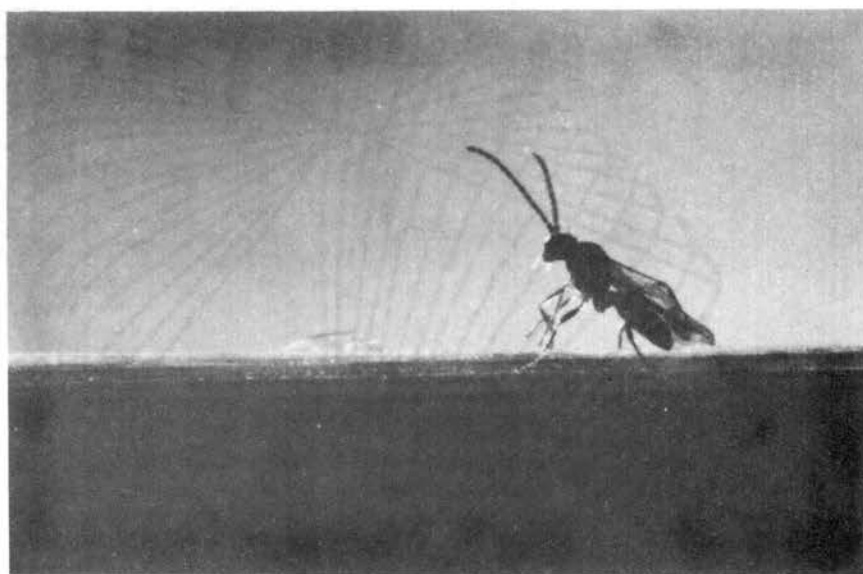


Fig. 4. Stance often assumed by Lysiphlebus  
testaceipes (Cresson).

## SUMMARY AND CONCLUSIONS

In tests to determine presence and extent of biotype C greenbug resistance components in selected sorghum entries, the susceptible check, BOK-8, indicated the least resistance of all the entries. Piper sudan-grass demonstrated low tolerance but indicated some nonpreference and antibiosis (as did all resistant entries). Tolerance appeared to be the chief resistance component of PI-264453. While intermediately non-tolerant PI-220248 and PI-302231 indicated relatively high degrees of nonpreference and antibiosis, PI-308976 suggested a relatively high degree of nonpreference and an intermediate degree of antibiosis and tolerance. Five entries (PI-229828, IS-809, Shallu Grain, PI-302178 and PI-226096) appeared to possess comparatively high degrees of all three components, and should, therefore, demonstrate a relatively high level of permanence of resistance to greenbugs. However, since in this study there is a relationship among nonpreference, antibiosis and tolerance (when based on injury scores), it cannot be stated conclusively that these factors are separate entities and not different expressions of the same plant trait. If the latter is true, resistance would not be assumed to be as permanent. It would seem doubtful that all sources and components of greenbug resistance are controlled by the same inheritance factors.

Female L. testaceipes landed more frequently on sorghum plants not infested with biotype C greenbugs but, after landing, spent more time on infested plants. Plant characteristics may be more important in

effecting landing while the presence of hosts may act as a flight arrestant.

No tested female L. testaceipes exhibited any recognizable response toward sorghum leaf disks or dry or moist extract- or solvent-soaked filter paper disks even when walking on them. Although a number of explanations are possible, it may be that plant characteristics act in attracting parasites from a distance.

Neither greenbugs nor corn leaf aphids appeared preferred by female L. testaceipes emerging from mummies of either biotype C greenbugs or corn leaf aphids. L. testaceipes emerging from different aphid species on sorghum are apparently of a single strain.

L. testaceipes did not demonstrate any preference for greenbug susceptible or resistant sorghum entries and this was not affected by being greenbug biotype C infested or uninfested. This was true in both growth chamber and greenhouse tests. The position of the sun was implicated in the high variance in the greenhouse.

Fewer L. testaceipes were trapped on plants under covered cages than under uncovered cages. The parasite is probably inactive under reduced light. Only about 32.8 percent of the released parasites were trapped on plants in the uncovered cage while only 4.6 percent were recovered in the covered cage.

Significantly more L. testaceipes were trapped on real than on artificial sorghum plants. Although the artificial plants could not exactly duplicate real plants, they did trap some parasites indicating at least a slight attractancy based on physical characteristics.

No L. testaceipes responded to real or artificial greenbugs until after 48 h had elapsed since release. The parasite probably only

responds to greenbugs at a relatively short distance.

Small grain species significantly affected numbers of adult and late instar greenbugs and mummies. Differences in species total mummy counts appeared closely related to total greenbug numbers. Significantly more aphids and mummies were produced on Triumph wheat and Rogers barley than on BOK-8 sorghum, Balboa rye and Chilocco oats. When parasites were given a choice, significantly fewer mummies were produced only on Balboa. No small grain species tested had a significant effect on percent parasite emergence.

Unsexed L. testaceipes of unknown age did not significantly respond in a Y-tube olfactometer to an air stream of unknown flow rate (greater than 50 ml/min) drawn over excised leaves of sorghum plants. Utilization of parasite females 24 h old or younger and regulation of flow rates reduced the variation but did not increase the response. Females 24 h old or younger which emerged in large numbers and which were rapidly attracted to a light source for collection showed a significant response to sorghum leaves. Similar responses were shown for females 0 to 6 h and 6 to 12 h old thus indicating the possible importance of parasite age. Humidifying the test air eliminated the response of 0 to 6 h old female L. testaceipes. Females given a choice of an excised sorghum leaf versus a filter paper strip moistened with distilled water chose leaves 5.30 percent more than those without a choice of moist filter paper. The parasites may have been repelled by moist air.

Both unsexed L. testaceipes of unknown age and females 24 h old or younger responded significantly in Y-tube olfactometer tests to biotype C greenbugs. It seems probable that L. testaceipes responds to olfactory substances released by sorghum leaves and greenbugs, and that, when



working simultaneously, these factors may represent an important link in host finding.

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## VITA

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