ORIENTATION OF SUGARCANE ROOTSTALK BORER WEEVIL, *Diaprepes abbreviatus*, TO WEEVIL, FRASS, AND FOOD ODORS[1]

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Abstract—Adults of the sugarcane rootstalk borer weevil, *Diaprepes abbreviatus*, form aggregations on citrus trees, where they feed on new foliage. The relative roles of male and female weevils, frass, food, and combinations of these odor sources in aggregation formation were studied using a y-tube olfactometer. Female and male *D. abbreviatus* were attracted by food, males, females, and female or male frass. Females were most often attracted by damaged food (broken green beans), whereas males were similarly attracted to damaged food and either female frass, male frass, or heterosexual pairs. No enhancement of attraction by either sex was found when males and male frass were combined with damaged food.

Key Words—Olfactometer, pheromone, volatiles, aggregation, behavior, attractant.

INTRODUCTION

The sugarcane rootstalk borer weevil, *Diaprepes abbreviatus* (L.) is a major pest of sugarcane and vegetable crops in the West Indies and is a serious pest of citrus in Florida, responsible for the death of many trees in infested areas

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(Schroeder, 1981; Beavers et al., 1982; Cruz and Segrarra, 1992; Sirjusingh et al., 1992). The larvae destroy root systems of seedlings and mature citrus trees, while adult weevils feeding on new foliage may significantly reduce growth and productivity of trees (Schroeder and Beavers, 1977). Methods are needed for monitoring the distribution of the pest in infested areas and for control.

Adult weevils form aggregations of equal sex ratio on or near new growth on citrus trees and may remain on the same trees for weeks (Beavers et al., 1982; Jones and Schroeder, 1984). Evidence for chemical mediation of the formation of aggregations is somewhat contradictory. Schroeder (1981) suggested a male-produced pheromone attracts females and a female-produced pheromone attracts males to aggregation sites. Beavers et al. (1982) indicated that odor of young citrus foliage is the main cue effecting aggregation and that subsequently produced frass at an aggregation site may serve as a secondary attractant for the opposite sex. Jones and Schroeder (1984) implied that a male-produced pheromone released from frass is attractive to both sexes of *D. abbreviatus*. Utilization of the chemical cues that attract *D. abbreviatus* to aggregation sites could provide attractants to lure one or both sexes to traps and hence serve as a useful lure for monitoring or trapping out weevils.

The goal of this study was clarification of the chemical-stimuli that are of most significance in attracting *D. abbreviatus* weevils to aggregation sites. This knowledge is needed to pursue the isolation and identification of pheromones and kairomones to use as lures in traps.

METHODS AND MATERIALS

Weevils. Adult *D. abbreviatus* were collected by hand picking from a citrus grove in Lake County, Florida, during April–October 1995. Beetles were maintained in climatic chambers in the USDA-ARS laboratory in Gainesville, Florida, at 25°C, 40–60% relative humidity, and 16L:8D photoperiod. Freshly cut citrus foliage and fresh green beans were supplied as food sources for the first five days and then beans thereafter. Beetles were separated by sex using differences in the last abdominal sternite shape: triangular sternite for females and rounded sternite for males. Beetles of each gender were kept in Plexiglas frame and screened cages (30 × 30 × 30 cm) with a Plexiglas plate at the bottom. Up to 100 beetles were held in a cage. All beetles were used in these studies, either as attractant sources or subjects tested for attraction to a volatile source, were held at least seven days prior to testing to adjust to laboratory environmental conditions. Age of collected weevils was variable, and females probably were mated before collection, as indicated by the fact that all egg clutches laid on the first seven days following collection hatched ($N > 200$).

Bioassay. All experiments were conducted using two y-shaped glass tube olfactometer sets as described by Harari et al. (1994), in which each of the two olfactometer arms led to a spherical glass trap, followed by a glass bulb containing a volatile source. Air (350 ml/min) was pushed into the system, directed from the source of volatiles to the starting point of the tested beetle. Beetles were released individually at the starting point and walked against the air current toward the control and treatment airstreams. A positive response was recorded when a beetle crawled into the spherical glass trap, while a negative or no response was recorded when a beetle did not reach the trap within 20 min of release. After testing five weevils, the olfactometer was turned 180° in order to avoid bias from uncontrolled directional factors. Since mating is apparently a diurnal behavior that starts before first light and lasts all day (Schroeder and Beavers, 1985), experiments were begun in the scotophase (red light) 60 min before lights-on and were conducted until 150 min after the onset of the photophase of the light cycle. Only one type of treatment comparison was made in any of the olfactometers in a given day, and 25–55 weevils were tested to that comparison during the 3.5-hr test period of a given day. Each treatment comparison was repeated over a period of five to eight days to comprise an experiment. Olfactometers were rinsed daily with hot water and ethyl alcohol.

Treatment Comparisons. Bioassays were conducted to determine whether *D. abbreviatus* are attracted to food, frass of either sex, individual weevils of either sex, interacting same-sex or heterosexual pairs of weevils, or to combinations of either sex with their frass or food.

Green beans (*Phaseolus vulgaris* L.) (2), either intact or broken by hand, were tested as a food attractant. Fecal material of males or females (0.5 ± 0.1 g), deposited over the two days before the experiment, was collected 20 min before the experiment was commenced. Adult weevils when held together either as a unisex group or as a mixed sex group often interacted, including mounting and copulating attempts. Therefore, multiple adult weevils were used as attractant sources either as an interacting group or held separately. A group was composed of five or 10 weevils held together in the olfactometer glass bulb, while weevils held separately were each put into a small plastic screen cage (6 cm high × 1.5 cm diam) to prevent physical interaction. Five or 10 cages of individual weevils were placed within the olfactometer glass bulb as an attractant source. When weevils of either sex were used as the attractant source in one arm of the olfactometer, empty small screen cages were added to the other arm together with the second treatment as a control.

Insect Experiments. The olfactometer was first assessed as a means to bioassay the weevils' attraction by conducting an experiment with no volatile sources in both arms of the olfactometer. After movement of the weevils along the tubes to both arms was confirmed, three experiments were performed with

Table 1. Comparison Sets of Treatments for All Experiments Conducted
Using Two-Choice Olfactometer

Test category	Exp.	Source 1	Source 2	No. of replicates (no. of weevils)	
				Female response	Male response
System	1	blank	2 intact beans	6 (183)	6 (195)
control	2	blank	5 males	6 (178)	6 (189)
	3	blank	5 females	6 (175)	6 (170)
Food	4	2 intact beans	2 broken beans	8 (273)	5 (223)
	5	5 females	2 broken beans	5 (194)	6 (209)
	6	5 males	2 broken beans	5 (203)	5 (178)
	7	female frass	2 broken beans	5 (175)	5 (198)
	8	male frass	2 broken beans	5 (199)	5 (159)
	9	5 males + 5 females held together	2 broken beans	5 (195)	6 (184)
	10	male frass + 5 males + broken beans	2 broken beans	6 (196)	6 (193)
Frass	11	male frass	5 males	8 (258)	6 (189)
	12	female frass	5 females	5 (161)	5 (117)
	13	female frass	male frass	7 (245)	6 (218)
Weevils	14	5 females (separated)[a]	5 males (separated)	7 (287)	5 (187)
	15	5 females (separated) + 5 males (separated)	5 males + 5 females held together	6 (214)	5 (172)
	16	10 males (separated)	10 males held together	7 (268)	5 (195)
	17	10 males held together	5 males + 5 females held together	6 (168)	6 (177)

[a]Five males or five females kept individually separated in small screen cages.

no source of potentially attractive volatiles in one arm of the olfactometer (Table 1) and either intact green beans (experiment 1), separated males (experiment 2), or separated females in the other arm (experiment 3).

The relative role of damaged food as a weevil attractant was assessed in a second series of experiments (Table 1, experiments 4–10). These experiments involved the following comparisons: (1) intact green beans vs. broken green beans (experiment 4), (2) a group of female weevils held together vs. broken green beans (experiment 5), (3) a group of males held together vs. broken green beans (experiment 6), (4) female frass vs. broken green beans (experiment 7), (5) male frass vs. broken green beans (experiment 8), (6) a group of males and females held together vs. broken green beans (experiment 9) and (7) male frass,

a group of males held together, and broken green beans vs. broken green beans (experiment 10).

The relative role of weevil frass in male or female attraction was assessed in a third series of experiments (Table 1, experiments 11–13). These experiments involved the following comparisons: (1) male frass vs. males held separately (experiment 11), (2) female frass vs. females held separately (experiment 12) and (3) female frass vs. male frass (experiment 13).

The attractiveness of female and male weevils to other weevils and effects of interacting weevils on female and male weevil attraction was assessed in a fourth series of olfactometer experiments (Table 1, experiments 15–17). These experiments involved the following comparisons: (1) female weevils held separately vs. male weevils held separately (experiment 14), (2) female weevils held separately and male weevils held separately vs. a mixed group of male and female weevils held together (experiment 15), (3) male weevils held separately vs. male weevils held together (experiment 16), and (4) male weevils held together vs. a mixed group of male and female weevils held together (experiment 17).

Statistical Analysis. The results were analyzed as two-choice data. The choice of one arm was compared to the choice of the other after nonresponsive individuals (less then 10% in any experiment) were omitted from the calculation. G statistics (Sokal and Rohlf, 1969) were used for replicated goodness-of-fit tests. The heterogeneity of the replicates for each experiment was tested first and when it was found to be significant ($P < 0.01$) more tests were conducted. A second goodness-of-fit test was performed for the pooled data. Both tests were used to compute the significance of deviation from expectation (1 : 1) for each experiment ($\alpha = 0.05\%$).

RESULTS

The heterogeneity of the replicates was significantly high ($P < 0.05$) in only one experiment (Table 2, experiment 11), meaning that the replicates of that experiment differed significantly among different days.

Interactions of males, females, or males and females were frequently observed when weevils were held together as a group in one arm of the olfactometer. These interactions included female–female mounting, male–male mounting with copulatory attempts, and male and female mounting and copulating.

Both male and female weevils chose the treatment arms more often ($P < 0.05$) in all experiments comparing a potential odor source with a system control. This indicated that adult *D. abbreviatus* were capable of moving toward a source

TABLE 2. RESPONSE OF FEMALE *D. abbreviatus* TO DIFFERENT ATTRACTANT SOURCES IN *Y*-TUBE OLFACTOMETER[a]

Exp.	Total	Source 1	Attracted (%)	Source 2	Attracted (%)	G_h	G_D	G_t	df
1	183	blank	35	green beans	65	7.45	16.70	**	6
2	178	blank	37	males	63	10.15	13.05	**	6
3	175	blank	37	females	63	8.22	1.72	**	6
4	273	intact beans	38	broken beans	62	16.85	15.54	**	8
5	194	females	28	broken beans	72	0.22	37.53	**	5
6	203	males	36	broken beans	64	2.64	17.35	**	5
7	175	female frass	30	broken beans	70	1.33	21.54	**	5
8	199	male frass	37	broken beans	63	4.81	19.53	**	5
9	195	males + females held together	37	broken beans	63	0.86	13.05	**	5
10	196	male frass + males + broken beans	48	broken beans	52	9.44	0.27	ns	6
11	258	male frass	47	males	53	15.48	1.64	ns	8
12	161	female frass	68	females	32	0.62	20.46	**	5
13	245	female frass	53	male frass	47	0.85	1.71	ns	7
14	287	females (separated)[b]	38	males (separated)	62	4.04	15.07	**	7
15	214	female (separated) + male (separated)	48	males + females held together	52	9.50	0.20	ns	6
16	268	males (separated)	44	males held together	56	9.31	4.25	ns	7
17	168	males held together	53	males + females held together	47	4.81	0.55	ns	6

[a]Total: number of tested weevils; G_h: G test for heterogeneity; G_D: G test pooled data; G_t: G test total (**P < 0.05).
[b]Five males or five females kept individually separated in small screen cages.

of volatile attractant in the olfactometer and were attracted by intact green beans, males, or females (Tables 2 and 3; experiments 1, 2, and 3, respectively).

Female Response. Significantly more females (Table 2) were attracted to broken green beans than to intact green beans (P < 0.05) (experiment 4), and more females were attracted to broken green beans than to female frass (experiment 7), male frass (experiment 8), females (experiments 5), males (experiment 6) or males and females that were held together (experiment 9) (P < 0.05). The combination of broken green beans, males, and male frass was not more

TABLE 3. RESPONSE OF MALE *D. abbreviatus* TO DIFFERENT ATTRACTANT SOURCES IN *Y*-TUBE OLFACTOMETER[a]

Exp.	Total	Source 1	Attracted (%)	Source 2	Attracted (%)	G_h	G_D	G_t	df
1	195	blank	37	green beans	63	6.41	13.44	**	6
2	189	blank	37	males	63	2.53	12.79	**	6
3	170	blank	34	females	66	1.62	18.70	**	6
4	223	intact beans	37	broken beans	63	6.74	14.62	**	5
5	209	females	38	broken beans	62	10.61	12.91	**	6
6	178	males	37	broken beans	63	5.55	13.00	**	5
7	198	female frass	40	broken beans	60	1.20	6.86	ns	5
8	159	male frass	47	broken beans	53	2.51	0.71	ns	5
9	184	males + females held together	46	broken beans	54	8.06	3.63	ns	6
10	193	male frass + males + broken beans	48	broken beans	52	6.07	0.20	ns	6
11	189	male frass	63	males	37	3.63	12.80	**	6
12	117	female frass	31	females	69	2.34	14.02	**	5
13	218	female frass	54	male frass	46	2.07	1.77	ns	6
14	187	female (separated)*	47	males (separated)	53	2.11	0.61	ns	5
15	172	females (separated) + males (separated)	35	males + females held together	65	2.02	14.70	**	5
16	195	males (separated)	37	males held together	63	1.64	13.43	**	5
17	177	males held together	43	males + females held together	57	5.22	3.49	ns	6

[a]Total: number of tested weevils; G_h: G test for heterogeneity; G_p: G test pooled data; G_t: G test total (**$P < 0.05$).

[b]Five males or five females kept individually separated in small screen cages.

attractive to females than broken green beans alone (experiment 10) ($P > 0.05$). Females did not choose male frass more often than female frass (experiment 13). Females did not choose male frass over males (experiment 11) ($P > 0.05$), but significantly more females were attracted to female frass than to female weevils (experiment 12) ($P > 0.05$). More females were attracted to males than females held separately (experiment 14) ($P < 0.05$), but females were not attracted more to males and females held together than males and females held separately (experiment 15) ($P > 0.05$). Females also were not attracted more

to males held together compared to males held separately (experiment 16) or males held together compared to males and females held together (experiment 17) ($P > 0.05$) (Table 2).

Male Response. Significantly more males (Table 3) were attracted to broken green beans than to intact green beans (experiment 4), and more males were attracted to broken green beans than to females (experiment 5), or to males (experiment 6) ($P < 0.05$). Males, however, were not attracted more to broken beans than to female frass (experiment 7), male frass (experiment 8) or males and females held together (experiment 9) ($P > 0.05$). Broken green beans with males and male frass were not more attractive to males than broken green beans alone (experiment 10) ($P > 0.05$). Males were not significantly more attracted to male frass than to female frass (experiment 13) ($P > 0.05$), but males were significantly more attracted to male frass than to male weevils (experiment 11) and were attracted more to female frass compared to female weevils (experiment 12) ($P < 0.05$). Males were not attracted more to females held separately compared to males held separately (experiment 14) ($P > 0.05$). However, males were significantly more attracted to males and females held together than to males and females held separately (experiment 15) and to males held together compared to males held separately (experiment 16) ($P < 0.05$). Males were attracted similarly to males held together compared to males and females held together (experiment 17) ($P > 0.05$) (Table 3).

DISCUSSION

Plant volatiles that act as insect attractants are known to occur widely (Finch, 1980; Visser, 1986). Among the curculionids, the boll weevil, *Anthonomus grandis* Boheman, orients to volatile chemicals from its host plant, cotton, (Hardee et al., 1966) and responds to crushed cotton squares (Dickens, 1989). Male and female plum curculio, *Conotrachelus nenuphar* (Herbst.), are similarly attracted to host odor (Prokopy et al., 1995), and both males and females of the banana weevil, *Cosmopolites sordidus* (Germar), are attracted to chopped banana (Budenberg et al., 1993).

Beavers et al. (1982), using a bouquet of citrus foliage, reported that both male and female *D. abbreviatus* weevils were attracted to volatiles emitted by citrus foliage, whereas Jones and Schroeder (1984) did not find a significant difference between numbers of weevils attracted to traps containing a methanol extract of citrus leaves or unbaited traps. Both males and females in our study were attracted to food odors and were more attracted to damaged food compared to intact food. A heightened response to damaged plant tissue may explain aggregations of large number of weevils observed on a single tree (Beavers et al., 1982; Jones and Schroeder, 1984). Aggregation sites first may be occupied

by individual weevils that initiate feeding and, by damaging foliage, may attract more weevils to that tree, leaving nearby trees undisturbed.

In this study, male and female *D. abbreviatus* also were attracted to females and to males. While females were more attracted to males than to females, males were similarly attracted to males and to females. A similar situation may occur in the pepper weevil, *Anthonomus eugenii* Cano, where females are more attracted to males than to females but males cannot distinguish between females or males (Coudriet and Kishaba, 1988). Adults of the plum curculio also may respond positively to odor of the same or opposite sex (Prokopy and Cooley, unpublished data, cited in Prokopy et al., 1995). In olfactometer experiments by Beavers et al. (1982), *D. abbreviatus* weevils were attracted to but did not choose one sex over the other. This contradiction with our data may be explained by: (1) in our assay individual males or females may have been contaminated by frass or (2) the experiment of Beavers et al. (1982) was conducted in the scotophase while *D. abbreviatus* mating behavior occurs during the photophase (Schroeder, 1981; Schroeder and Beavers, 1985). Thus, the time of day of the bioassays by Beavers et al. (1982) may have led to a different pattern of attraction responses.

Male and female *D. abbreviatus* were more attracted to frass than to either males or females, and both were similarly attracted by male frass and female frass. These results are in agreement with those of Jones and Schroeder (1984), who reported that males and females were similarly attracted to traps baited with either male or female frass, and with those of Schroeder (1981) and Beavers et al. (1982), who assumed that an attractant in weevil frass attracts the opposite sex as well as the same sex. A pheromone released from frass is known for the boll weevil, (Tumlinson et al., 1969). Sex pheromones are released by both sexes in the pecan weevil, *Curculio caryae* (Horn), (Hedin et al., 1979), the cabbage looper, *Trichoplusia ni* (Hübner) (Lenczewski and Landolt, 1991), and the salt marsh caterpillar, *Estigmene acrea* (Drury), (Willis and Birch, 1982), among others.

Male attraction to female-released pheromone is common in insect species (Mayer and McLaughlin, 1990) and easily explained in the context of sexual selection theory, where males are expected to maximize their mating potential and females are expected to perform the less costly role in pair formation (Greenfield, 1980; Thornhill and Alcock, 1983). Female attraction to a male-produced pheromone is far less common (Mayer and McLaughlin, 1990). Two explanations (among others) for male signaling for females provided by Thornhill and Alcock (1983) are: (1) the female may benefit from better mate choice opportunities among males in aggregations, and (2) males offer something of value to females, such as advertising a food location. The latter may be accomplished by augmenting the attractiveness of the food odor by a volatile male sex pheromone released from the frass. Male *D. abbreviatus* may signal their location

as a potential mate and the location of food to attract females. Other males, as well as females, may be attracted to the combined plant volatiles and pheromones, resulting in aggregations. The observed female attraction to female frass may have evolved as a means of food location as well.

Male, but not female, *D. abbreviatus* weevils were more attracted to males held together as a group than to males held separately. Males, but not females, also were more attracted to males and females held together as a group than to females and males that were held separately. Homosexual male mounting was frequently observed among males that were held together as a group in the olfactometer experiments. This behavior often was observed in the laboratory among weevils held in cages and was twice seen on citrus foliage in the field. Homosexual male mounting in the laboratory took place while the mounted male continued copulating with a female or in the vicinity of a female or a mating pair ($N > 100$). The mounting male actually penetrated the lower male's genitalia with its aedeagus ($N > 100$). Thus, the lower male may have exhibited "female mimicry" behavior. According to Trivers (1985) and Alcock and Gwynne (1991) such a male may convey the message to a conspecific male that he is a receptive female, in order to promote his own mating opportunities. A male may carry such a message by emitting an odor that resembles the female pheromone or by acting like a female (Alcock and Gwynne, 1991). Male *D. abbreviatus* courting or copulating with a female may try to deceive a rival male by emitting a "female odor" and may allow a homosexual mounting in order to avoid mating competition. In our experiments the possibility of contamination of those males with a female-produced sex pheromone was not excluded. Male-courtship pheromones that resemble components of female-produced pheromone are known for the velvetbean caterpillar, *Anticarsia gemmatalis* (Hübner) (Heath et al., 1988), and the Oriental fruit moth, *Grapholitha molesta* (Busck) (Baker, 1983). In the case of the velvetbean caterpillar, male responses to male pheromone are interpreted as a secondary effect that may reduce the mating success of the courting male (Heath et al., 1988). *D. abbreviatus* "female mimicry" may be intended to draw the rival male away from the female in order to avoid fighting over mates. Release of a pheromone by males that mimics female sex pheromone as a mean of avoiding combat with other males is known in the rove beetle *Aleochara curtula* (Goeze) (Peschke, 1987), whereas a female mimicry behavior (pseudofemale behavior) with copulatory attempts is a widespread occurrence in cockroaches of the genera *Blaberus, Archimandrita,* and *Byrsotrias* (Wendelken and Barth, 1985).

The observed attractiveness of males to females, of females to males, and of each sex to their own sex, to their frass, and to food may be a result of responses to a bouquet of aromas comprised of a blend of pheromone and plant chemicals. The next step in understanding the role of each attractant in conjunction with the others as it occurs under field conditions may be to use distinct

components as attractants in traps in field cage experiments and then expand such tests to open field conditions.

The attractiveness of damaged food to males and even more so to females overshadowed the other attractant components in our olfactometer tests. Such results with female weevils is encouraging: developing lures for females may be more useful for reducing pest populations. Thus, it may be worthwhile to bait traps with food lures for *D. abbreviatus*, as has been implemented for monitoring and controlling populations of the scarabaeids *Maladera matrida* Argaman (Ben-Yakir et al., 1995), the Japanese beetle, *Popillia japonica* Newman (Fleming, 1969), and others (Reed et al., 1991).

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