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Prey Habitat Location by the Cassava Mealybug Predator *Exochomus flaviventris*: Olfactory Responses to Odor of Plant, Mealybug, Plant–Mealybug Complex, and Plant–Mealybug–Natural Enemy Complex

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Exochomus flaviventris *Mader is considered to be the most active predator of the cassava mealybug* Phenacoccus manihoti *Matile–Ferrero in Central Africa. The response of experienced gravid female coccinellids to the odor of cassava plant (var. Zanaga), unparasitized mealybugs, plant–mealybug complex with or without feeding prey (parasitized or not), and plant–mealybug complex with or without conspecific coccinellids was investigated in a Y-tube olfactometer. The odor of uninfested cassava plants was not more attractive than clean air. Dual-choice tests revealed that mealybug-infested plants were preferred to mealybugs alone and mealybug-damaged plants and were the major sources of volatiles that attract females coccinellids to the microhabitat of its prey. The emission of volatile chemicals did not appear to be limited to the infested parts of the plant but did occur systemically throughout the plant. The presence of conspecific coccinellid larvae or adult males did not modify the attractiveness of the mealybug-infested plants. However, when an infested plant with conspecific predator females (alone or with conspecific males) was compared to an infested plant or infested plant with conspecific males,* E. flaviventris *females showed a preference for the last two sources of odor. The uninfested plant with conspecific males was also preferred to the uninfested plant with conspecific females. In addition, the odor of conspecific males was preferred over that of conspecific females. Female*

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predators preferred the plant infested with unparasitized mealybugs over the plant infested with mealybugs previously parasitized. These results showed that E. flaviventris *females use herbivore-induced plant volatiles during foraging and can detect via olfaction the presence of conspecific gravid females and parasitized prey, thus assessing patch suitability from a distance.*

KEY WORDS: *Exochomus flaviventris*; *Phenacoccus manihoti*; cassava; Coccinellidae; mealybug; tritrophic interactions; olfactometer; foraging behavior; volatile chemicals; prey location.

INTRODUCTION

As natural enemies of phytophagous insects function and develop in a multitrophic context, effective integrated pest management of insect pests can be achieved by improving the understanding of the plant effects up the trophic system and the mechanisms that mediate tritrophic interactions (Price, 1986; Thomas and Waage, 1996; Cortesero *et al.*, 2000).

Semiochemical, chemical, and physical factors mediate tritrophic interactions (Price, 1986). Semiochemically mediated interactions can influence pest populations only through natural enemies (extrinsic defense), while chemically and physically mediated interactions can directly affect herbivore population dynamics (intrinsic defense) (Thomas and Waage, 1996; Cortesero *et al.*, 2000). Several studies have emphasized on these three categories of tritrophic interactions during the last decade (Hare, 1992; Vet and Dicke, 1992; Turlings *et al.*, 1995; Dicke, 1999; Sabelis *et al.*, 1999). These studies showed strong linkages between intrinsic and extrinsic defense systems, thereby underlying the importance of managing plant attributes from a tritrophic perspective (Thomas and Waage, 1996; Cortesero *et al.*, 2000).

Plant chemical signals emitted as a result of herbivore damages play an important role in the ability of natural enemies to detect hosts or prey, as shown with insect parasitoids and predatory mites (Vet and Dicke, 1992, Dicke and Vet, 1999; Cortesero *et al.*, 2000). Their role in the orientation of insect predators toward their prey is less well documented (Cortesero *et al.*, 2000), although there is evidence of their use in case of lacewings (Flint *et al.*, 1979; Zhu *et al.*, 1999), anthocorids (Dwumfour, 1992; Drukker *et al.*, 1995; Venzon *et al.*, 1999), thrips (Shimoda *et al.*, 1997), and coccinellids (Obata, 1986; Zhu *et al.*, 1999).

The role of plant chemical signals in coccinellids has been relatively neglected despite the biological value of these predators (Hamilton *et al.*, 1999; Zhu *et al.*, 1999; Cortesero *et al.*, 2000). Prior to the 1980s, it was generally accepted that visual cues and physical contacts play a major role in prey search by coccinellids (Allen *et al.*, 1970; Wratten, 1973). Since the 1980s, the evidence for host-derived and plant volatile chemical involvement in searching behavior of predaceous coccinellids has been well documented. Coccinellids appeared to be arrested by the odor of their prey or their by-products (e.g., feces and honeydew) over very short distances, i.e., less than a few centimeters (Carter and Dixon, 1984; Van den Meiracker *et al.*, 1990; Heidari and Copland, 1993; Sengonca and Liu, 1994). However, Obata (1986), Hammond (1988), Liu and Sengonca (1994), Hattingh and Samways (1995), Ponsonby and Copland (1995), and Hamilton *et al.* (1999) demonstrated the response to prey odors over distances greater than a few centimeters and the orientation toward prey using chemical cues associated with prey presence or produced by plants in response to herbivore damage. Ponsonby and Copland (1995) stated that, like parasitoids, predaceous coccinellids have a hierarchical host finding mechanism which involves (i) host habitat location based on olfactory and visual responses, (ii) infested host plant location based on optomotor anemotaxis (iii), and host patch location based on visual cues, plant topography and morphology, and photo- and geotaxes.

Exochomus flaviventris Mader (Coleoptera: Coccinellidae) is a polyphagous predator indigenous to sub-Saharan Africa. In Central Africa, it is the most active predator of the cassava mealybug, *Phenacoccus manihoti* Matile–Ferrero (Homoptera: Pseudococcidae), a major pest of cassava, *Manihot esculenta* Crantz (Euphorbiaceae) (Fabres and Kiyindou, 1985; Iziquel and Le Rü, 1989). The cassava–mealybug and mealybug–predator bitrophic systems have been studied extensively both in the laboratory and in the field (Fabres and Kiyindou, 1985; Kiyindou *et al.*, 1990; Reyd and Le Rü, 1992; Calatayud *et al.*, 1994). Although there are few data available on the tritrophic interactions among cassava, cassava–mealybug, and the coccinellid, there is indication that olfactory cues are picked up by *Diomus* sp. and *Exochomus* sp. (Hammond, 1988; Van den Meiracker *et al.*, 1990). However, there is still no clear evidence of olfactory orientation toward cassava–mealybug patches by *Exochomus* coccinellids and data on the foraging behavior of these ladybirds are lacking at the habitat level.

In the present study, we investigated whether volatile chemical cues are involved in habitat orientation, prey community location, and prey location by females of *E. flaviventris*. The volatile chemical cues might originate from the prey itself, the plant itself, and plant–prey interactions (Vet and Dicke, 1992). Two recent studies showed that arthropod predators and parasitoids avoid prey patches with conspecific or heterospecific using volatile cues (Janssen *et al.*, 1995, 1997). We therefore further study the attractiveness of cassava–mealybug complex with and without larva or adult (female or male) coccinellids to determine if the presence of conspecifics can affect the foraging behavior of the beetles. We also test the attractiveness of parasitized and nonparasitized cassava–mealybug complex because parasitization by the parasitoid (*Apoanagyrus lopezi* De Santis, Hymenoptera, Encyrtidae) is responsible for the decrease in production of chemical volatiles emitted by mealybugs and/or plant–mealybug host complexes (Souissi *et al.*, 1998).

MATERIALS AND METHODS

Plants

Cassava plants [*M. esculenta* cv. Zanaga (MM79)] were obtained from 20-cm cuttings, planted at two-thirds of their length in soil held in plastic pots. They were watered twice a week. Plants 9–10 weeks old (20–30 cm in height and 9 or 10 leaves) were used in this study.

Insects

Stock cultures of *P. manihoti* and *E. flaviventris* were obtained from scattered field populations in 1996 in Pointe Noire, Republic of Congo. *E. flaviventris* was fed on mealybugs which were fed on two local varieties of cassava, Moundele Pakou and N'dombi, Pointe Noire. The insects were maintained in three separate greenhouses [21–33°C, 12L:12D, and 50–95% relative humidity (RH)]. These two varieties are different from the cassava variety used in the experiments.

Olfactometer Setup

The response of the predatory beetle to different odors was investigated in a Y-tube olfactometer as described by Souissi *et al.* (1998). It consisted of a Y-shaped 2.5-cm-diameter glass tube. The base and the two arms of the Y-tube measured 28 and 13 cm, respectively. Each arm was connected to a flowmeter and an odor source container made of a glass cylinder (25 cm in diameter and 40 cm high), large enough to hold a whole potted cassava plant. The soil was covered with parafilm. Dry air from a bottle was passed through a vial of distilled water before entering the two arms of the Y-tube olfactometer. The air circulated in each olfactometer arm at a flow rate of 10 liters/h. Female predators were able to walk upwind toward the arms of the tube and sometimes performed short flight attempts. The experiment was done at 26 ± 2°C and 75 ± 5% RH in a painted white box under a 35-W fluorescent tube.

Bioassay

The experiments were carried out with 10- to 18-day-old experienced adult females, previously mated. Under natural conditions, adult emergence usually occurs on the plant on which the larva have fed and, often, in contact with prey residues (wax exuvia, honeydew). The preoviposition period is 7–10 days (Mitsipa, unpublished); all test female insects were mature and ready to oviposit. All the test beetles were starved for 22–24 h before the test, introduced individually at the base of the olfactometer, and given 3 min to walk toward the end of one of the arms of the Y-tube. A female was supposed to choose a particular odor if it crossed the line 4 cm after the separation of the two branches and remained in one branch for at least 20 s. After testing five females, the olfactometer was washed with ethanol, rinsed with distilled water, and dried and connections to the odor source containers were exchanged to remove any positional bias. Tests were carried out for 2 to 7 h after the beginning of the photophase, which corresponded to the most active period of *E. flaviventris* females (Kiyindou, unpublished). For each choice situation, 10 females were tested per day and 4 replications on different days were made with a different set of plants for each replicate, so that 40 females in total were submitted to each choice situation. A chi-square test ($\alpha = 0.05$) was performed to test the homogeneity among replicates before pooling the data. The females not showing any response (less than 5%) were ignored. The proportions of females in each branch of the olfactometer were compared using a chi-square test at the level $\alpha = 0.05$.

Fifteen odor sources were tested.

(1) No airflow.
(2) Clean airflow from an odor source container holding a pot with soil covered with a sheet of parafilm.
(3) An uninfested cassava plant used as a standard clean cassava odor source.
(4) A cassava plant with 20 fourth-instar mealybugs in groups of 5 on four different leaves. The leaves were chosen randomly and the mealybugs were given 3 days to acclimatize prior to the experiment.
(5) An herbivore-damaged plant consisting of a cassava plant that had been infested with mealybugs for 3 days, but from which mealybugs, wax, and honeydew were removed with a paintbrush. The leaves were also washed with distilled water prior to the test.
(6) Twenty fourth-instar mealybugs that were removed from their host plants approximately 1 h before the test.
(7) Twenty fourth-instar mealybugs that were removed from their host plant approximately 24 h prior to the test.
(8) Uninfested clean leaves removed from infested plants 72 h after the infestation. Plant infestation was done by choosing one leaf at random and infesting it with 20 fourth-instar mealybugs; the leaf was then enclosed in a fine plastic bag to avoid colonization of the

remaining leaves by mealybugs and contamination of clean leaves by odors emitted from the infested leaf.

(9) Clean leaves from a clean plant.

For sources 8 and 9, uninfested leaves from each plant were taken with their petiole and placed in a glass vial (10 × 2 cm) filled with 20 ml distilled water and sealed with parafilm. The leaves in the vials were placed in the upstream glass cylinder of the olfactometer.

(10) A cassava plant infested for 3 days with 20 fourth-instar mealybugs and 6 fourth-instar larvae of *E. flaviventris* present for the previous 24 h.

(11) A cassava plant infested for 3 days with 20 fourth-instar mealybugs and 6 adult mated male beetles present for the previous 24 h.

(12) A cassava plant infested for 3 days with 20 fourth-instar mealybugs and 6 adult mated female beetles present for the previous 24 h.

(13) A cassava plant uninfested with six adult mated male beetles present for the previous 24 h.

(14) A cassava plant uninfested with six adult mated female beetles present for the previous 24 h.

(15) A cassava plant infested for 3 days with 20 parasitized fourth-instar mealybugs. The plant was infested with 20 mealybugs that had been previously exposed to 10 mated female *A. lopezi* during a 24-h period. More than 95% of the hosts were parasitized under these conditions (van Baaren and Nénon, 1996).

The following experiments were conducted.

Experiment I: Attractiveness of the Airstream and Control of Directional Bias. The experiment was designed to assess whether an airstream elicited an attraction of *E. flaviventris* and to ensure that the two arms of the Y-tube were equally chosen: 1 vs 2 and 2 vs 2 were compared.

Experiment II: Attractiveness of the Host Plant, the Prey, or Both. The experiment was designed to assess the attractiveness of the host plant, the prey, or both: 2 vs 3, 2 vs 4, 2 vs 5, 2 vs 6, and 2 vs 7 were compared.

Experiment III: What Does E. flaviventris *Prefer? and Is the Release of Chemicals Systemic*? The experiment was designed to assess the preference of *E. flaviventris* females and the systemic release of herbivore-induced synomones from uninfested leaves of the infested plant: 4 vs 6, 4 vs 5, 6 vs 5, and 8 vs 9 were compared.

Experiment IV: How Does E. flaviventris *Assess the Quality of the Patch*? The experiment was designed to assess if *E. flaviventris* uses volatiles to avoid prey patches with conspecific or competitor: 4 vs 10, 4 vs 11, 4 vs 12, 13 vs 14, and 4 vs 15 were compared.

RESULTS

Attractiveness of the Airstream and Control of Directional Bias (Fig. 1)

When an airstream and the absence of an airstream were compared, a significantly higher number of adult female beetles (34 vs 6) oriented toward the arm with an airstream, indicating an upwind orientation. The response of beetles to an odorless airstream (22 vs 18) revealed the absence of preference for either arm of the oflactometer, showing that the olfactometer was not biased.

Attractiveness of the Host Plant, the Prey, or Both (Fig. 1)

Female predators showed no preference for uninfested plant and unparasitized mealybugs (24 h) compared to clean air but oriented significantly

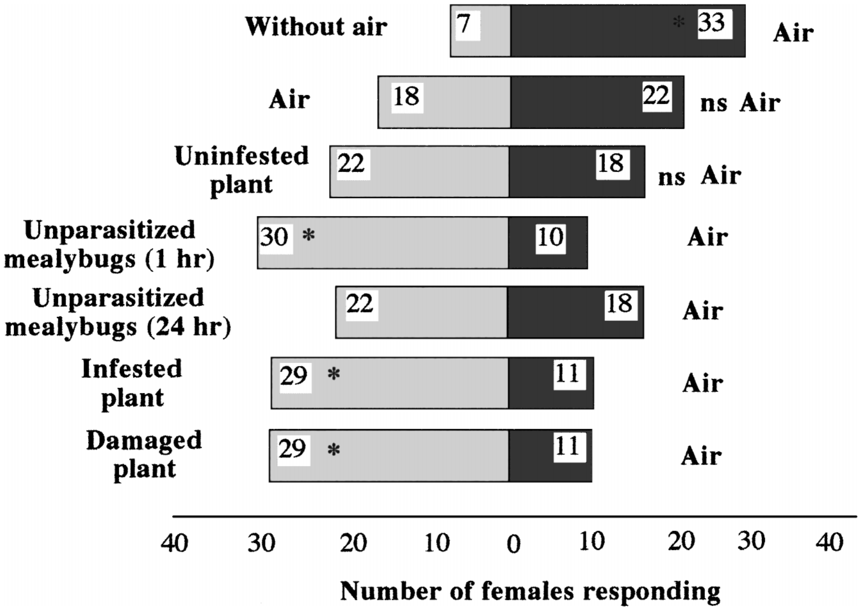

Fig. 1. Olfactory responses of experienced *E. flaviventris* females to air, tested versus no air, air, an uninfested plant, unparasitized mealybugs (1 or 24 h), a mealybug-infested plant, and a damaged plant in a Y-tube olfactometer. *Significantly different; ns, not significantly different ($P = 0.05$; χ^2 test). The numbers at the right and left indicate the number of females that made a choice for each of the two odor sources offered.

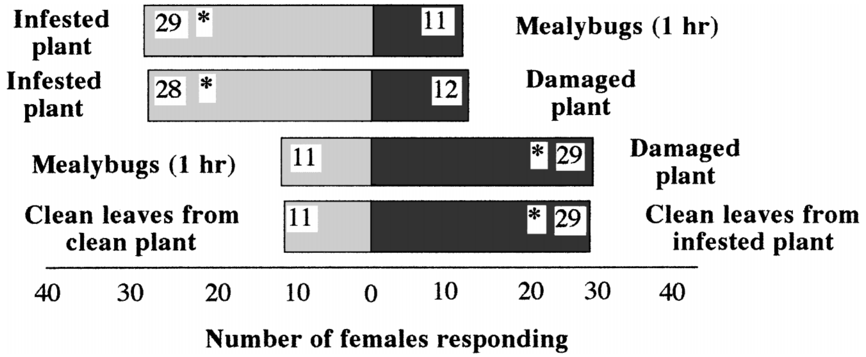

Fig. 2. Olfactory responses of experienced *E. flaviventris* females to an infested plant tested versus unparasitized mealybugs (1 h) and a damaged plant, to unparasitized mealybugs (1 h) tested versus a damaged plant, and to clean leaves from a clean plant tested versus clean leaves from an infested plant. *Significantly different; ns, not significantly different ($P = 0.05$; χ^2 test). The numbers at the right- and left indicate the number of females that made a choice for each of the two odor sources offered.

toward unparasitized mealybugs (1 h), infested plant, and damaged plant compared to clean air.

What Does *E. flaviventris* Prefer? and Is the Release of Chemicals Systemic? (Fig. 2)

When infested plant was compared to damaged plant or unparasitized mealybugs (1 h), the predators had a preference for the first source of odor, 29 vs 11 and 28 vs 12, respectively. However, the odor of damaged plant was preferred to the odor of unparasitized mealybugs removed from the plant 1 h prior to the test (29 vs 11).

Female *E. flaviventris* significantly preferred odors from volatiles from clean leaves removed from an infested cassava plant to volatiles from clean leaves removed from an uninfested plant (29 vs 11).

How Does *E. flaviventris* Assess the Quality of the Patch? (Fig. 3)

The odor of an infested plant and that of an infested plant with conspecific predator larvae were compared. *E. flaviventris* females showed no preference for either source of odor (22 vs 18). The same situation was observed on the response of volatiles from an infested plant vs an infested plant with conspecific predator males alone (16 vs 24). But when the odor of an

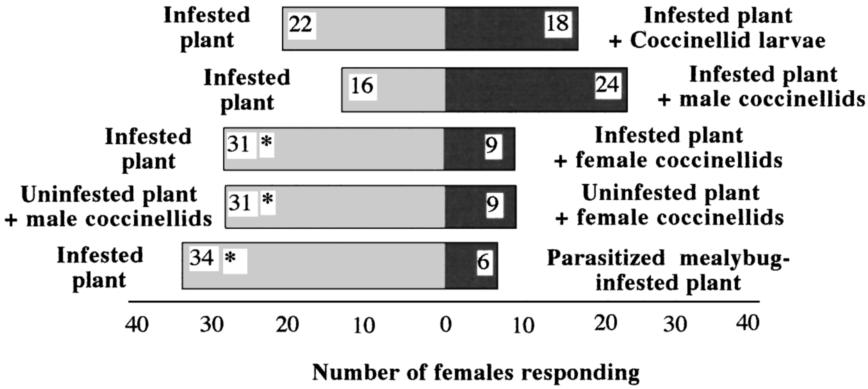

Fig. 3. Olfactory responses of experienced *E. flaviventris* females to an infested plant tested versus an infested plant + coccinellid larvae or male coccinellids or female coccinellids or a parasitized mealybug-infested plant (3 days) and to an uninfested plant + male coccinellids versus an uninfested plant + female coccinellids. *Significantly different; ns, not significantly different ($P = 0.05$; χ^2 test). The numbers at the right and left indicate the number of females that made a choice for each of the two odor sources offered.

infested plant and that of an infested plant with conspecific female predators were compared, *E. flaviventris* females were significantly more attracted to the first source of odor (31 vs 9). On the other hand, an uninfested plant with conspecific males was preferred to an uninfested plant with conspecific females (29 vs 11). In addition, female predators preferred an infested plant over a plant infested with parasitized mealybugs from 3 days (34 vs 6).

DISCUSSION

Experienced mated female *E. flaviventris* had a typical upwind orientation and a positive odor-conditioned response. Similar observations were reported by Ponsonby and Copland (1995) for *Chilocorus nigritus* F. (Coleoptera: Coccinellidae). In contrast, Hattingh and Samways (1995) reported that the location of *Aspidiotus nerii* Bouché (Hemiptera: Diaspididae) patches by *C. nigritus* was facilitated by olfactory stimulation because patch discovery is more rapid in the presence of prey odor when the response is not source oriented. The discrepancies between these results are likely due to the different experimental procedures. As were Ponsonby and Copland's (1995), our experiments were carried out only with experienced female beetles and each female was individually tested during a short period of time (3 and 10 min). In the case of Hattingh and Samways (1995), experiments were carried out with 40 adult beetles of both sexes placed in the olfactometer at the same time for a very long period (5 to 200 min). Great variability of behavior among insects was observed because of sex and age (unspecified age). Moreover, the searching behavior of each adult beetle might have been influenced by the presence of conspecifics.

Experienced female beetles were not attracted by uninfested plants, which indicate that chemicals emitted by plants alone are not efficient cues for foraging *E. flaviventris*. On the other hand, mealybug-infested plants, damaged plants, and unparasitized mealybugs (removed at 1 h) significantly attracted female predators. The attraction of *E. flaviventris* might have resulted from an increased production of volatiles or a change in the volatile blend (Dicke *et al.*, 1990; Paré and Tumlinson, 1997; Turlings *et al.*, 1998). Changes in chemicals produced by cassava plants infested by *P. manihoti* have been reported by Calatayud *et al.* (1994). High attractiveness of mealybug-infested cassava has also been demonstrated for the two encyrtids *A. lopezi* and *Apoanagyrus diversicornis* Howard, parasitoids of *P. manihoti* (Nadel and Van Alphen, 1987), and for the two encyrtids *Aenasius vexans* Kerrich and *A. diversicornis*, parasitoids of another cassava mealybug, *Phenacoccus herreni* Cox and Williams (Bertschy *et al.*, 1997). The weak responses observed for damaged plants and mealybugs alone compared with infested plants indicate that predators discriminate among these three sources of odor and show that the mealybug-infested plant is the primary source of the volatile chemicals that attract *E. flaviventris*.

The attractiveness of unparasitized mealybugs (1 h) was weak compared with that of infested plants or damaged plants. This might have been due to volatiles emitted from the cassava plant but not from the mealybugs themselves. The time interval (1 h prior to testing) was not sufficient to dissipate plant volatile substances contaminating mealybugs. Read *et al.* (1970) reported similar results with females of the braconid *Diaeretiella rapae* (M'Intosh), which were attracted to the cabbage aphid *Brevicoryne brassicae* (L.) freshly removed from collards (15 min before the test). Our results indicate that experienced female ladybirds were not attracted to a long-range distance by mealybug by-products (wax and honeydew kairomones) but directly by mealybug-induced plant volatiles. Besides, female predators were attracted by undamaged leaves of the infested plant, which indicates that the release of mealybug-induced plant volatiles is not restricted to a damaged site but occurs systemically throughout the plant. Similar results were reported with the same host plant and herbivore (Nadel and van Alphen, 1987; Souissi *et al.*, 1998) and in other tritrophic systems (Dicke *et al.*, 1990; Röse *et al.*, 1996; Cortesero *et al.*, 1997). The release of such induced compounds appears to be elicited by a factor present in the herbivore's saliva (Mattiacci *et al.*, 1994; Potting *et al.*, 1995). The importance of these volatile chemicals, reliable indicators of herbivore presence, for host and prey finding by natural enemies is well known in many other tritrophic systems (Dicke *et al.*, 1990; Takabayashi *et al.*, 1994; Wickremasinghe and van Emden, 1992; Steinberg *et al.*, 1993; Mattiaci *et al.*, 1994; Du *et al.*, 1996, Shimoda *et al.*, 1997; Venzon *et al.*, 1999). In a recent study, Ponsonby and Copland (1995) showed that experienced females *C. nigritus* are strongly attracted by *Solanum tuberosum* L. (Solanaceae) infested with *Abgrallaspis cyanophylli* (Signoret) (Homoptera, Diaspididae) in comparison with an uninfested plant. However, they could not determine the plant origin of the compounds because the herbivore-infested plant also contains herbivores and their by-products. To our knowledge, only Zhu *et al.* (1999) showed that the lady beetle *Coleomegilla maculata* (Degeer) can possibly use volatiles of corn origin to locate its prey. Our results confirm that the hierarchical host finding mechanism suggested by Ponsonby and Copland (1995) for predaceous coccinellids involves chemical cues that can operate from a certain distance. Furthermore, Ponsonby and Copland (1995) indicated that the involvement of plants in prey finding by coccinellids shows remarkable similarities to the implication of plants in host finding by other natural enemies. Likewise, Souissi *et al.* (1998) found that the major source of volatiles that attract *E. lopezi* females in the habitat of their hosts is the systemically released cassava volatiles induced by mealybug infestation. However, great differences exist between the foraging behavior of the parasitoid and that of the predator: the specialist parasitoid shows an innate response to the systemically released cassava volatiles induced by *P. manihoti* infestation, while the generalist predator needs first to learn about them (Makaya Makosso, unpublished). Thus, further work needs to be done to determine if systemically induced cassava volatiles that attract the specialist parasitoid are the same as those that attract the generalist predator.

Our results also showed that the attractiveness of mealybug-infested cassava was not modified by the presence of conspecific larvae. Hemptinne *et al.* (1992), Merlin *et al.* (1996), and Ruzicka (1997), working on *Adalia bipuntata* (L.), *Cryptolaemus montrouzieri* Mulsant, and *Coccinella septempuntata* L., respectively, proved that females of these three coccinellids were deterred from ovipositing at sites previously exposed to conspecific larvae. Nevertheless, Hemptinne *et al.* (1992) reported that "females appeared to react to a cue associated with larvae, which acts over a short distance...." Furthermore, these results were obtained in small experimental petri dishes where prey detection was achieved primarily by physical contact. Merlin *et al.* (1996) concluded that an oviposition-deterring pheromone is associated with wax filaments produced by conspecific larvae. Therefore, there is no discrepancy among these results. In fact, in our study, patch detection was achieved by odor without any physical contact.

This study has demonstrated that the presence of conspecific adult males on mealybuginfested cassava does not affect the attraction of experienced female *E. flaviventris*, whereas the presence of conspecific gravid females deters them. Chemical cues that convey information between two organisms of the same species are called pheromones (Dicke and Sabelis, 1988). Our results indicate that experienced mated female *E. flaviventris* produce pheromones that deter conspecific experienced mated females. Consequently, experienced females would be deterred over a distance from foraging on a mealybug-infested cassava where conspecific females are preying or laying eggs. This foraging behavior limits intraspecific competition by avoiding the exploitation of a patch habitat where conspecific gravid females are already present on the cassava plant. Hemptinne *et al.* (1992) suggested that gravid female ladybirds essentially assess prey patch quality in evaluating the presence of conspecific larvae by physical contact. Our results also indicate that gravid females ladybirds assess prey habitat quality in evaluating the presence of conspecific gravid females by olfaction. There are few other studies that report the avoidance of patches occupied by competitors. Janssen *et al.* (1995) reported that adult females of *Leptopilina heterotoma* (Thompson) (Hym. Eucoilidae) refrain from visiting patches occupied by another closely related parasitoid, even in the absence of other patches. Janssen *et al.* (1997) showed that females of the predatory mite, *Phytoseiulus persimilis* Athias–Henriot (Acari: Phytoseiidae), avoid patches where female conspecifics are present; however, they reported a quite different mechanism of avoidance, showing that the decreased attractiveness of a prey patch with conspecific odor is more likely due to odor produced by adult prey.

The attractiveness of cassava infested with parasitized mealybugs was significantly lower than that of cassava infested with unparasitized mealybugs. Souissi *et al.* (1998) reported that parasitized mealybugs probably cause less damage on a cassava plant than unparasitized ones, and as a result the amount of synomones produced by the plant might be equally reduced. This confirms that ladybirds, very mobile predators with a full set of sense organs, are able to detect small patches of prey even when the prey is scarce in the habitat and tend to oviposit particularly on favorable prey patches (Thompson, 1951; Hemptinne *et al.*, 1992; Ponsonby and Copland, 1995, Barbier *et al.*, 1996). Subsequently, a patch with a higher parasitization rate and producing less synomones than a healthy one indicates that the patch is an unsuitable breeding place. This foraging behavior prevents oviposition in patches where mealybugs have been parasitized and benefits the parasitoid. Eggs, larvae, and mummies of the parasitoid are all exposed at very vulnerable stages to the predation of ladybirds (larvae and adults) that forage on the plant. The avoidance of oviposition by gravid female coccinellids in patches where female parasitoids are already exploited is advantageous to the parasitoids as it allows the development of their offspring.

In conclusion, we have shown in this study the importance of herbivore-induced attractants in the tritrophic system involving *M. esculenta, P. manihoti*, and *E. flaviventris*. The systemically released cassava volatiles induced by mealybug infestation were the major source of volatiles that attract experienced gravid female coccinellids in the habitat of their prey. These results confirm earlier work by Ponsonby and Copland (1995) on a hierarchical host finding mechanism. The implication of plants in prey finding by coccinellids is very similar to that in host finding by parasitoids and other predators. Our results also indicate that experienced gravid female coccinellids are able to assess mealybug patch suitability for oviposition from a certain distance, by evaluating the olfactory presence of conspecific gravid females and by avoiding parasitized patches, whose attractions are lower than that of healthy patches. This foraging behavior is likely to maximize the fitness of the two natural enemies and consequently favors both the predator and the parasitoid. However, our data were obtained under laboratory conditions that are far less complex than field conditions. Future research will be conducted under more complex conditions, for instance, in glasshouses, to estimate at what spatial scale the volatiles are effective in coccinellid foraging behavior. We are currently investigating how the foraging behavior of adult coccinellids is influenced by experience (associative learning) and by environmental factors of the cassava agroecosystem.

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