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Within-Plant Migration of the Predatory Mite *Typhlodromalus aripo* from the Apex to the Leaves of Cassava: Response to Day–Night Cycle, Prey Location and Prey Density

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Abstract Under attack by herbivores, plants produce a blend of “herbivore-induced plant volatiles (HIPV)” that help natural enemies of herbivores locating their prey, thereby helping plants to reduce damage from herbivory. The amount of HIPV emitted by plants increases with herbivore density and is positively correlated with the intensity of the olfactory response of natural enemies. In this study, we determined the effects of density or within-plant distribution of the herbivorous mite *Mononychellus tanajoa* on movement of the predatory mite *Typhlodromalus aripo* out of apices of cassava plants. Proportions of *T. aripo* that migrated out of apex, and distances traveled were significantly higher when *M. tanajoa* was further away from the apex—i.e. on middle or bottom leaves of cassava plants—than when present on top leaves, or absent from the plant. This supports previous field observations that *T. aripo* is not a sit-and-wait predator but uses HIPV to search and locate its prey within cassava plant.

Keywords Phytoseiidae · *Mononychellus tanajoa* · herbivore-induced plant volatiles (HIPV) · tritrophic interactions · olfactory response

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Introduction

In biological control programs involving the use of predators or parasitoids against herbivorous arthropods, plants have been often considered as passive players in that their impact on predator–prey (or parasitoid–host) interactions is not made explicit in developing control strategies. During the last two decades, ecologists have become fully aware that plants can effectively defend themselves against herbivorous arthropods, either directly, by limiting feeding by herbivores; or indirectly, by promoting the effectiveness of natural enemies of the herbivores (Price et al. 1980; Dicke and Sabelis 1988; Sabelis et al. 1999a,b,c; Cortesero et al. 2000; Sabelis et al. 2001, 2005). Direct defenses include plant structures (such as thick cuticle, ‘slippery’ cuticle surfaces, leaves covered by a dense layer of trichomes, or by glandular trichomes), that reduce feeding by the herbivore, and secondary plant compounds that inhibit digestion, intoxicate or deter the herbivore. The indirect strategy is based on a “mutualistic” association between plants and the herbivores’ natural enemies, in which plants attract natural enemies through chemical lures, provide them with alternative food such as exudates, pollen or nectar. Plants can also develop shelters, called “domatia”, that protect natural enemies against harsh environmental conditions or against relatively large hyper-predators (e.g. Sabelis et al. 1999a).

It is well known by now that, in response to attack by herbivores, plants can produce a blend of “herbivore-induced plant volatiles (HIPV)” that attract natural enemies of the herbivores and arrest them on or near the plants under attack. These HIPV help the natural enemies in locating their victims (Dicke and Sabelis 1988; Dicke et al. 1998), thereby reducing herbivore load of the plant. The strength of the attraction of natural enemies to plants, and the efficacy of natural enemies against the herbivores are generally enhanced by the existence of domatia on the plants. For example, plants with domatia are more likely to be inhabited by a predatory mite and, generally, have many more predators per leaf compared with sympatric plants lacking these structures (Grostal and O’Dowd 1994; Rozario 1995). As a consequence, plants with domatia harbour less herbivorous mites compared to plants that lack domatia (Agrawal 1997). Predators in domatia help the plant to defend itself against herbivores and in turn, domatia protect predators from their arthropod natural enemies or abiotic stress (Walter and O’Dowd 1992; Norton et al., 2001).

The apex (i.e. the growing point) of a cassava plant plays a role similar to that of domatia, as the predatory mite *Typhlodromalus aripo* De Leon hides in the apex during the day and comes out to actively forage for the herbivorous mite *Mononychellus tanajoa* (Bondar), on young cassava leaves during night hours (Onzo et al., 2003). Hiding in the apex is thought to protect the predatory mite against harsh environmental conditions such as low relative humidity and direct exposure to ultraviolet (UV) radiations, especially UVB, which are harmful to the predator (Onzo et al., in preparation). Previous studies (Gnanvossou et al. 2001, 2003) showed that *T. aripo* is attracted to volatiles emitted by cassava leaves or apices infested by *M. tanajoa*. It is still not clear, however, if density and within-plant location of *M. tanajoa* on cassava plants affect both the proportion of *T. aripo* that migrate from the apex at night and the distance covered by the migrating predators during their foraging bouts along cassava plants. In a tritrophic system consisting of the kidney bean plant, the two-spotted mite *Tetranychus urticae* Koch

and the predatory mite *Phytoseiulus persimilis* Athias-Henriot, Maeda and Takabayashi (2001) found that the amount of HIPV emitted by the plant changed in relation to changes in *T. urticae* density on the plant. They also showed that the intensity of the olfactory response of *P. persimilis* correlates positively with the amount of volatiles emitted by the plant. Such a mechanism may well influence the movement of *T. aripo* out of the apices of cassava plants at night. If this is the case, the quantity of HIPV emitted by a cassava plant should be proportional to the density of *M. tanajoa* per plant and the olfactory response of *T. aripo* should be proportional to the quantity of HIPV emitted by the cassava plants under attack by *M. tanajoa*. We therefore, hypothesize that: (1) the number of *T. aripo* that leaves the apex to forage on cassava leaves during night hours increases with prey population on the plant; and (2) the distance traveled by *T. aripo* during its foraging bouts increases with the distance of the prey patch to the apex of the cassava plant. Here, we present the results of experiments aimed at testing these two hypotheses.

Materials and Methods

Two experiments were conducted in a screenhouse at IITA-Benin Station (Cotonou). Cassava cuttings (20 cm long) of the variety “Agric” were planted singly in plastic pots (14 cm diameter at the base, 20 cm at the top and 17.5 cm high), filled with c. 3.8 kg of topsoil collected from a field that was in fallow for more than 4 years. The potted plants were transferred to the screenhouse just after planting and placed on 350×180×76 cm (*L*×*W*×*H*) iron benches which were separated from each other by a distance of 65 cm. To accommodate all treatments and replicates, each bench was divided into two compartments. Each compartment accommodated one replicate of a treatment. Where needed, plants were thinned to one stem per cutting at two weeks after planting to establish a uniform plant size across treatments and replicates.

Experiment 1: Effects of Prey Location on Foraging by *T. aripo*

This experiment was designed to test whether the location of *M. tanajoa* within a cassava plant influences the movement of *T. aripo* out of the apex, in response to HIPV emitted by the leaves. The hypothesis is that the further the prey patch is from the apex of the cassava plant, the lower the amount of volatiles that would reach the predator and the weaker the response of *T. aripo* to the chemical cues. The predator’s response can be measured by the number of *T. aripo* that emigrated from the apex of the cassava plant. With this experiment we also intended to test the ability of *T. aripo* to track the origin of the HIPV to discover an *M. tanajoa* patch within the cassava plant. This could be measured by the distance covered by foraging *T. aripo* in response to different positioning of *M. tanajoa* patches within the cassava plant.

For this experiment, potted cassava plants bearing at least ten leaves were used, and the treatments were based on the location of *M. tanajoa* within the cassava plant. The cassava canopy was, therefore, divided into three parts as follows: top leaves, middle leaves and bottom leaves. Taking the apex as the starting point, top leaves were represented by leaf 1 and 2; middle leaves by leaf 5 and 6; and bottom leaves by leaf 9 and 10.

The four treatments of these experiments consisted of: (1) control with no *M. tanajoa* on plants; (2) plants with top leaves infested with *M. tanajoa*; (3) plants with middle leaves infested with *M. tanajoa*; and (4) plants with bottom leaves infested with *M. tanajoa*. Each treatment was replicated three times and each replicate was represented by four potted cassava plants. The four plants in each replicate were placed at least 80 cm apart. Treatments and replicates were assigned randomly to bench compartments.

For the treatments with *M. tanajoa* (i.e. treatments 2, 3, and 4), 200 adult *M. tanajoa*—originating from wild populations and reared on potted cassava plants in a screenhouse for 2 to 3 weeks before use—were added to the cassava plants 72 h before the day of observation, when potted cassava plants were 8 weeks old. This time period is enough to induce damage to cassava leaves as a consequence of mite feeding activities (Gnanvossou et al. 2001). To prevent the mites from dispersing throughout the plant, a double-side sticky tape was fixed around the stem, just above the petiole of the highest infested leaf, and also below the petiole of the lowest infested leaf. In this manner, mite-feeding activities were restricted, almost exclusively, to the infested leaves.

In each treatment, 15 adult female *T. aripo*—collected from a cassava field on the previous day—were released on each cassava plant around noon of the day when the observations were initiated. After releasing the predator on the plants, the double-sided sticky tape was removed from the plants to allow free movement of the predatory mites. The experiment was repeated twice, between 29 June and 03 August 2006; and between 05 September and 25 October 2006.

Experiment 2: Effects of Prey Density on Movement of *T. aripo* Out of Apex of Cassava Plants

This experiment was intended to test whether the number of *T. aripo* moving out of the apex at night depended on *M. tanajoa* density on the leaves. The hypothesis here is that the response of *T. aripo* to HIPV emitted by *M. tanajoa*-infested cassava plants will increase with increasing *M. tanajoa* density on the plants, as the amount of HIPV increases with prey (=herbivore) density on the plant (Gnanvossou et al. 2001).

The three treatments of this experiment consisted of: (1) control with no *M. tanajoa* on the plants; (2) high prey density (i.e. predator-to-prey ratio of c. 1:200); and (3) low prey density (i.e. predator-to-prey ratio of c. 1:20). Each treatment was replicated three times and each replicate was represented by six potted cassava plants. The six plants in each replicate were at least 80 cm apart. Treatments and replicates were assigned to bench compartments at random.

Three weeks after planting, all plants were pruned to ten leaves; thereafter, plants assigned to the high prey density treatment were infested with ten adult female *M. tanajoa* that were placed on the youngest leaves. Plants assigned to the low prey density treatment were similarly infested but one week later (i.e. four weeks after planting) than the high prey density treatment. To determine the number of *T. aripo* to be released to meet the required predator-to-prey ratio, mean *M. tanajoa* density on each category of plants (i.e. low or high density) was estimated from a sub-sample of ten plants per prey density treatment level, at one week after the last

infestation (i.e. 5 weeks after planting). On the next day around 1000 hours in the morning, 15 adult female *T. aripo* were added to each plant. Observations of the within-plant movement of predators started 1 day later. Female *M. tanajoa* used in this experiment had been collected from cassava fields in southern Benin and maintained on potted cassava plants for two weeks, while *T. aripo* were collected from a cassava field one day before their addition to the experimental cassava plants. The experiment was conducted between 05 September and 12 October 2006.

Data Collection and Analysis

For experiment one—i.e. *M. tanajoa* location within cassava plant—six plants were sampled per treatment (two per replicate) at 2200 hours on the day of *T. aripo* release, and at 2000 hours the following day. For experiment two—i.e. *M. tanajoa* density on cassava plant—nine plants (three per replicate) were sampled per treatment at 2000 hours and at 0000 hours on the day following *T. aripo* addition. For each selected plant, the apex was removed and immediately placed into an individual glass vial containing 70% ethanol. The apices were later dissected under a binocular microscope to facilitate *T. aripo* counting—mobile stages only. The leaves were removed, with their petiole, starting from leaf 1 (i.e. the nearest leaf to the apex), down to the lowest. All leaves were immediately checked under binocular microscope and all stages of *M. tanajoa* and *T. aripo* on the leaves were counted and recorded separately for leaf position per plant.

To determine whether *T. aripo*'s emigration from the apex was related to the location of *M. tanajoa* within the cassava plant, or to the density of *M. tanajoa* on the plant, the proportions of *T. aripo* that emigrated from the apex and was effectively found on leaves were calculated per plant and per treatment. In addition, the distance covered by the foraging *T. aripo* (i.e. the mean leaf position visited by the predator below the apex), was calculated as a weighted leaf number (L), using the following formula (Onzo et al. 2003):

$$L = \frac{\sum_{x=0}^y xN(x)}{\sum_{x=0}^y N(x)}$$

with x =leaf position (ranging from the apex (leaf 0) to the y th leaf below the apex), y =total number of leaves on the plant ($10 < y < 12$), and $N(x)$ =number of mobile *T. aripo* on leaf x .

For experiment one (i.e. *M. tanajoa* location within cassava plant), proportions of emigrated *T. aripo* and distances covered (i.e. weighted leaf numbers) were compared among *M. tanajoa* locations, sampling days and sampling hours (nested within sampling day), using analysis of variance (SAS 2003). For experiment two (i.e. *M. tanajoa* density on cassava plant), proportions of emigrated *T. aripo* and distances covered were compared among *M. tanajoa* density levels and sampling hours. When differences were statistically significant, treatment means were separated using the Student–Newman–Keuls multiple range test. Data on proportion were arcsine-square root-transformed before the statistical analysis.

Results

Effects of Prey Location on Foraging by *T. aripo*

The migration of *T. aripo* from the apex to cassava leaves during night foraging bouts depended on within-plant location of *M. tanajoa* on the cassava plant (Table 1). The proportions of *T. aripo* out of the apex during the night hours were significantly lower when *M. tanajoa* were not present on the plant, or were present on the top leaves, than when *M. tanajoa* was located on the middle or bottom leaves of the cassava plants. The proportions of *T. aripo* that migrated from the apex were similar when *M. tanajoa* were located on bottom or middle leaves and also similar when *M. tanajoa* were not present on the plant or present on the top leaves (Table 2).

The distance traveled by foraging *T. aripo* on cassava plants (i.e. the mean leaf position visited by the predator below the apex), also varied with the within-plant location of *M. tanajoa* (Table 1). This distance was significantly longer when *M. tanajoa* was located on the bottom leaves and middle leaves than when *M. tanajoa* was absent or located on the top leaves of cassava plants (Table 2).

Day, hours nested within day, and the interactions between day and within-plant location of *M. tanajoa* on cassava plants had no significant effects either on distance traveled by *T. aripo* or on the proportion of *T. aripo* that foraged at night (Table 1).

Effects of Prey Density on Foraging by *T. aripo*

The proportions of *T. aripo* that emigrated from apices of cassava plants at night did not differ among the three *M. tanajoa* density ranges tested (Table 3). Distance traveled by foraging predators at night also was not affected by the three *M. tanajoa* densities tested (Table 3). Hours and interaction between hours and density of *M. tanajoa* per plant did not significantly affect proportions of *T. aripo* emigrating from the apices, but the interaction term was bordering significance (Table 3). The latter result implies that *M. tanajoa* density might have an effect depending on the time of the day. Inspection of the data (Table 4) suggests that an effect on emigration of *T. aripo* out of the apex becomes manifest only at high *M. tanajoa* density. Average distance traveled by *T. aripo* away from the apex was lower when *M. tanajoa* density per plant was high compared with the low *M. tanajoa* density treatment, or when the plants were not infested with *M. tanajoa*; however, for both variables the differences were not statistically significant (Table 4).

Table 1 Effects of *M. tanajoa* Location Within Cassava Plants on Migration of *T. aripo* Out of Apex of Cassava Plants: ANOVA on Proportions of *T. aripo* Out of Apex and Distance Covered Within Cassava Plants

Source of variation	df	Proportion of <i>T. aripo</i> on leaves			Distance foraged by <i>T. aripo</i>		
		MS	F	P	MS	F	P
<i>Mt</i> location	3	0.224	5.52	0.002	4.975	4.48	0.006
Hours (day)	2	0.041	1.00	0.373	2.565	2.31	0.105
Day	1	0.000	0.01	0.924	2.042	1.84	0.179
Day × <i>Mt</i> location	3	0.040	0.99	0.401	0.191	0.17	0.915

Table 2 Effects of *M. tanajoa* Location Within Cassava Plants on Migration of *T. aripo* Out of Apex of Cassava Plants: mean (\pm SE) Separation Using Student–Newman–Keuls Multiple Range Test

<i>M. tanajoa</i> location	Proportion of <i>T. aripo</i> on leaves	Distance foraged by <i>T. aripo</i>
No <i>M. tanajoa</i>	0.036 \pm 0.015b	0.313 \pm 0.103b
On top leaves	0.044 \pm 0.018b	0.375 \pm 0.118b
On middle leaves	0.116 \pm 0.026a	0.903 \pm 0.328ab
On bottom leaves	0.110 \pm 0.018a	1.271 \pm 0.235a

Discussion

This study is among the few that have tested the role of HIPV in prey location by a predator species on whole plants under semi-field conditions. Several studies have been conducted in recent years to test the attraction of *T. aripo* to various odor sources, but most of them were laboratory-conducted olfactometer studies (Gnanvossou et al. 2001, 2003). Our study is the first that has attempted to explain how *T. aripo* locates its prey mite *M. tanajoa* within an intact cassava plant.

The series of greenhouse experiments presented in this study showed that, although the predatory mite *T. aripo* stays in the apex of cassava plants, it actively searches for and locates patches occupied by its main prey *M. tanajoa*. Indeed, both the proportion of *T. aripo* that emigrated from the apex at night and the distance covered by *T. aripo* while foraging along the stem of the cassava plant increased with the distance of the prey patch to the apex of the plant. In contrast, migratory movement of *T. aripo* out of the apex of the cassava plant is not affected by the density of *M. tanajoa* on the plant. Both the proportion of *T. aripo* that emigrated out of the apex and the distance traveled by *T. aripo* foraging at night were not statistically different among the three treatments. The relatively small proportion of *T. aripo* that emigrated from the apex of *M. tanajoa*-free plants and the relatively short distance that they traveled confirm that when the plant is not attacked by *M. tanajoa*, the olfactory stimuli that attract *T. aripo* out of the apex to the leaves are absent or very weak (Gnanvossou et al. 2001).

That *T. aripo* was able to locate a prey patch within the cassava plant, suggests that the predator could perceive the volatile cues emitted by the *M. tanajoa*-infested cassava leaves. Moreover, the differences in the migratory responses of *T. aripo* to the within-plant location of *M. tanajoa* suggest that the perception of the volatile cues by the predator is influenced by the distance that separates the odor source (i.e.

Table 3 Effects of *M. tanajoa* Density on Migration of *T. aripo* Out of Apex of Cassava Plants: ANOVA on Proportions of *T. aripo* Out of Apex and Distance Covered Within Cassava Plants

Source of variation	df	Proportion of <i>T. aripo</i> on leaves			Distance foraged by <i>T. aripo</i>		
		MS	F	P	MS	F	P
<i>M. tanajoa</i> density	3	0.001	0.01	0.990	0.775	1.15	0.324
Hours	1	0.006	0.10	0.758	0.001	0.00	0.972
Hours \times Mt density	3	0.168	2.71	0.077	1.138	1.69	0.195

Table 4 Effects of *M. tanajoa* Density on Migration of *T. aripo* Out of Apex of Cassava Plants: mean (\pm SE) Separation Using Student-Newman-Keuls Multiple Range Test

<i>M. tanajoa</i> density	Proportion of <i>T. aripo</i> on leaves	Distance foraged by <i>T. aripo</i>
No <i>M. tanajoa</i>	0.125 \pm 0.024a	1.023 \pm 0.224a
Low <i>Mt</i> density	0.119 \pm 0.031a	1.097 \pm 0.205a
High <i>Mt</i> density	0.148 \pm 0.046a	0.706 \pm 0.144a

the infested leaf) from the apex of the cassava plant. However, our data showed counterintuitively that the more distant the odor source, the higher the proportion of *T. aripo* that move out of the apex. Indeed, we would have expected that the closer the origin of the stimuli to the apex, the higher the perception of the cues and, consequently, the stronger the response from the predator. One possible explanation of this counterintuitive result may be that the closer the prey patch to the apex the higher the chance that *M. tanajoa* mobiles may reach the apex and arrest any migrating *T. aripo*. Whereas *M. tanajoa* is known to avoid leaves with *M. tanajoa* and *T. aripo*—possibly due to a predator-induced alarm pheromone of the spider mite—(Magalhães et al. 2002; Onzo et al. 2003), this may not have occurred in the experiments presented here because the apex was free of *M. tanajoa* at the time when *T. aripo* was released. So, *M. tanajoa* may well migrate from the top leaves to the apex in search for more nutritious leaves, thereby arresting *T. aripo* in the apex.

The non-significant impact of prey density on the responses of *T. aripo* to cues emitted from cassava plants infested by *M. tanajoa* is somewhat surprising, because average *M. tanajoa* density per plant is nearly 20 fold higher in the high density treatment than in the low density treatment. With such differences in prey density, we expected the quantity of volatiles emitted by the cassava plant to be much higher in the high density treatment than in the low density treatment (Maeda and Takabayashi 2001), and that the olfactory response of the predator should increase with the quantity of HIPV emitted. More surprising is the lack of differences in the responses of the predators between *M. tanajoa*-free plants and *M. tanajoa* infested plants. An explanation for this finding could be that the flux of infochemicals was not efficiently directed towards the apex of the cassava plant, e.g. due to the turbulence of air movement in the greenhouse. However and as shown in Tables 3 and 4, there is an almost significant effect of the interaction between hours and *M. tanajoa* density on the proportion of *T. aripo* out the apex, and this is an indication that the pattern of *T. aripo* migration is not similar during the two sampling hours. Indeed, scrutiny of the data showed that whereas *M. tanajoa* density did not significantly affect proportions of *T. aripo* out of the apex at 2000 hours, the sampling at 0000 hours showed that the proportions of migrating *T. aripo* were positively affected by *M. tanajoa* density. The average proportions of *T. aripo* that emigrated at 2000 hours were 0.39, 0.31 and 0.21, respectively on plants without *M. tanajoa*, on plants with low and plants with high *M. tanajoa* densities. In contrast, at 0000 hours the proportions were 0.20, 0.26 and 0.39, respectively on plants without *M. tanajoa*, on plants with low and on plant with high *M. tanajoa* densities. So, even though not significant, there is a trend for the proportion of *T. aripo* that emigrated from the apex to be higher when *M. tanajoa* density is high (see Tables 3 and 4).

Although not significant, the distance traveled by migrating *T. aripo* at high *M. tanajoa* density was shorter than distances traveled at low *M. tanajoa* density or when the plants were *M. tanajoa*-free (Table 4). An explanation for this finding could be that the predators were more efficient in finding cassava leaves with high *M. tanajoa* densities and skip visiting leaves lower in the plant.

Whereas the proportion of *T. aripo* that foraged on the cassava leaves were lower in our experiments than what is observed in the field (see Onzo et al. 2003), the study presented here shows and confirms that *T. aripo* is not a sit-and-wait predator. It also provides support for a role of HIPV in the prey searching strategy of *T. aripo* within cassava plants. However, because we used potted cassava plants of relatively small size, the response of *T. aripo* to volatile cues emitted by *M. tanajoa*-infested leaves may be different, had we used field plants of larger size that permit marked segregation of patches with the prey mite *M. tanajoa*. Despite these limitations, this study has improved our understanding of the foraging behavior of a predatory mite that plays a key role in the biological control of the cassava green mite in Africa (Yaninek and Hanna 2003; Hanna et al. 2005). In addition, these semi-field experiments constitute a major step toward testing the role of HIPV in sustaining predator-prey systems under field conditions. This is particularly important as most studies dealing with predator responses to prey odours are done under very artificial settings and their relevance to natural systems is often overlooked.

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