Population dynamics of cassava green mite and its predator, Typhlodromalus aripo in Benin, West Africa

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Citation for published version (APA):

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Dynamics of refuge use: Diurnal, vertical migration by predatory and herbivorous mites within cassava plants

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Published in: Oikos (2003) 101: 59-69

Plants may protect themselves against herbivorous arthropods by providing refuges to predatory arthropods, but they cannot prevent herbivores from taking countermeasures or even from reaping the benefits. To understand whether plants benefit from providing self-made refuges (so-called domatia), it is not only necessary to determine the fitness consequences for the plant, but also to assess (1) against which factors the refuge provides protection, (2) why predatory arthropods are more likely to monopolise the refuge, and (3) how herbivorous and predatory arthropods respond to and affect each other in and outside the refuge. In this article, we focus on the last aspect by studying the dynamics of refuge use of a predatory mite (Typhlodromalus aripo) and its consequences for a herbivorous mite (Mononychellus tansjoja) on cassava plants in Benin, West Africa. The refuge, located in-between the leaf primordia of the cassava apex, is thought to provide protection against abiotic factors and/or intraguild predators. To test whether the predator waits for prey in the apex or comes out, we sampled predator-prey distributions on leaves and in the apex at 4 hour-intervals over a period of 24 hours. The predatory mites showed pronounced diurnal changes in within-plant distribution. They were in the apices during the day, moved to the young leaves during night and returned to the apices the next morning. Nocturnal foraging bouts were more frequent when there were more herbivorous mites on the leaves near the apex. However, the foraging predators elicited an avoidance response by mobile stages of their prey, since these were more abundant on the first 20 leaves below the apex during late afternoon, than on the same leaves during night. These field observations on cassava plants show that (1) during daytime predatory mites monopolise the apical domatia, (2) they forage on young leaves during night and (3) elicit avoidance by within-plant, vertical migration of mobile stages of the herbivorous mites. We hypothesize that cassava plants benefit from apical domatia by acquiring protection for their photosynthetically most active, young parts, because predatory mites (1) protect primordial leaves in the apex.
(2) reduce the densities of herbivorous mites on young leaves, and (3) cause herbivorous mites to move down to less profitable older leaves.

**Key words** Tritrophic system, foraging behaviour, domatia, refuge, diurnal migration, predator avoidance, *Typhlodromalus aripo*, *Mononychellus tanajoa*, Phytoseiidae, Tetranychidae

Plants may defend themselves indirectly against herbivorous arthropods by promoting the effectiveness of predators, e.g. by providing specialized plant structures (domatia) that act as a refuge from abiotic factors and/or intraguild predators (Walter, 1996; Norton et al., 2001). However, the plant cannot directly control whether the refuges it provides are used only by predators or also by other organisms that are detrimental to the plant, such as herbivores and disease-vectors. Despite this potential 'misuse', plants may still benefit because any herbivore seeking protection in the refuge would increase the chance of encountering a predator seeking protection too (Sabelis et al., 1999). But this argument holds under the assumption that there are predators around, that they make use of the plant's refuges, that – in case there are no prey in the refuges – the predators come out to prey on herbivorous arthropods, yet return frequently enough to the refuges to scare off others from using it. Thus, to understand the impact of plant domatia on plant fitness (Agrawal and Karban, 1997), it is important to analyse the dynamics of refuge use by predatory arthropods and how this depends on the density of herbivorous arthropods and their response to the predators in and outside the domatia. As yet, these questions have not been addressed and there is a paucity of data on the dynamics of refuge use, even though – in theory (e.g. McNair, 1986) – its population dynamical consequences can be profound.

In this article, we analyse refuge use by predatory mites on cassava plants and its consequences for herbivorous mites. Cassava has no obvious domatia-like structures on leaves. Instead, the cassava plant apex serves as a refuge by harbouring (sometimes large) numbers of the predatory mite, *Typhlodromalus aripo* De Leon (Acari: Phytoseiidae) within the leaf primordia (Bakker, 1993; Bakker and Klein, 1999). The herbivorous, prey mite, *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae) resides on the expanded leaves below the apex. Because the presence of *T. aripo* in the apex is known to reduce populations of *M. tanajoa* on the upper stratum of the cassava plant (Bakker, 1993), interaction between this predator and prey is likely, but the mode of interaction is not clear. Since the apex itself does not harbour prey, the predator has only three foraging options: (1) remain in the apex, and consume the herbivores that migrate into the apex (a sit-and-wait strategy), (2) actively move out of the apex and return after foraging on the leaves, or (3) a combination of (1) and (2). To determine which options are used by *T. aripo*, we monitored the within-plant distribution of *M. tanajoa* and *T. aripo*. Preliminary observations in the laboratory and in the field (Onzo, pers. obs.) showed that the prey, *M. tanajoa*, does not move to the apex.
when *T. aripo* is present in the apex, and that the predator emigrates from the apex to foliage on prey-occupied leaves below the apex. These observations led to the following more specific questions:

1. What is the temporal (seasonal, diurnal) pattern of predator emigration from the apex?
2. Given that prey requirements of predatory mites varies with development and sex, which stages contribute most to the emigration?
3. Does predator emigration depend on prey (herbivore) density on the leaves?
4. How does the prey (herbivore) respond to predator emigration from the apex?

Answers to these questions were obtained by monitoring the within-plant distribution of predator and prey mites at 4 hour-intervals for a period of 24 hours, and by repeating these assessments at 3-month intervals, starting three months after planting and continuing until 12 months after planting.

**MATERIAL AND METHODS**

**Study organisms**

Cassava, *Manihot esculenta*, Crantz (Euphorbiaceae) is a woody semi-perennial shrub that can reach up to 5 m in height under favourable conditions. It was introduced into Africa from Latin America by Portuguese traders late in the 16th century (Jones, 1959) and is now commonly grown in regions between latitudes 30°N and 30°S, in areas receiving 750 to 3000 mm rainfall a year. The plant is renowned for its ability to tolerate low soil fertility and drought conditions and is grown in Africa mostly by small-scale farmers on plots of less than 0.5 ha (Dorosh, 1988). Cassava is propagated from vegetative cuttings (stems) and is harvested from 8 to more than 36 months after planting (Cock, 1985). Its starchy storage roots provide staple food to several hundred million people living in the tropics, who also consume the young tender leaves as vegetables (Jones, 1959; Sylvestre and Arraudeau, 1983; Herren and Bennet 1984). Much of the photosynthetic capacity of cassava resides in the young expanded leaves below the apex.

The cassava green mite, *M. tanajoa*, was accidentally introduced into Africa from Latin America in the early 1970s. It was first discovered near Kampala in Uganda in November 1971 (Nyiria, 1972), from where it has spread across the cassava belt in Africa and has within 14 years become the most serious cassava pest in many regions of the continent, (Yaninek *et al*., 1989a; Yaninek and Schulthess, 1993). This mite feeds on the content of parenchyma cells by inserting its chelicerae into the abaxial surface of cassava leaves. In the absence of predatory mites, *M. tanajoa* prefers to feed on young, expanded cassava leaves below the apex and on leaf primordia in the apex of the plant. Feeding causes chlorosis and leaf stunting (Yaninek *et al*., 1989b; Nyiria, 1972) and if severely attacked, leaves may drop. Yield losses due to *M. tanajoa* range can be up to 80% depending on variety, cultural practices, and local agro-ecological conditions (Yaninek *et al*., 1989a; Yaninek and
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Typhlodromalus aripo is a predatory mite introduced into Africa in 1993 from the Neotropics for the classical biological control of M. haematostoma. It is now established in a large part of the cassava belt in Africa and is shown to have a significant positive effect on cassava yield (Yaninek and Hanna, 2003). Little is known about the biology and ecology of T. aripo, except that it is unique in being the only phytoseiid species that resides in the cassava apex and it is seldom found on cassava leaves (during daytime) (Bakker, 1993). The cassava apex functions much like acarodomatia, specialized protective structures found exclusively on leaves where leaf veins bifurcate (Walter, 1996). That the apex of cassava plants can act as a domicium for the predatory mite T. aripo, was an entirely new discovery (Bakker and Klein, 1999). Not all cassava varieties are equally suitable to harbour T. aripo in their apices. Varieties with hairy apices appear to be more attractive for the predator than varieties possessing ‘glabrous’ apices (Hanna et al., 2000).

Study sites

Our observations were made at two locations in southern Benin, West Africa: one in Mono Province near the town of Sé (6°32.23’N, 1°49.11’E), and the other in Atlantique Province near the town of Houëgbô (6°48.23’N, 2°11.13’E). Both sites were located in the humid coastal Savannah Forest Mosaic zone characterized by a bimodal rainfall pattern that begins in late March and ends in November (c. 1200 mm/year), and a dry season from December to early March. At both sites, a single introduction of T. aripo led to establishment and widespread distribution for c. 4 years prior to the experiments.

Experimental design

Field plots, 0.35 ha in size, were planted with the cassava variety ‘Agric’, the most common cultivar in southern Benin, one at the Houëgbô field site on May 14, 1998 and one at the Sé field site on May 20, 1998. Each field plot was divided into four parallel sections of 50 m length and 15 m width, separated by 3 m bare ground as a buffer zone. Cassava was inter-cropped with maize during the first rainy season, which is a common practice in Benin. In each field, there were 20,000 maize plants per hectare (i.e. 1 m between rows and 0.5 m within rows), and 10,000 cassava plants per hectare (1 x 1m), planted two weeks later. In each section, there were a total of 750 cassava plants. Two months after planting, all cassava plants were thinned to one stem per cutting. Maize was harvested in August and cassava was thereafter the only crop in the field. Weeding was undertaken as needed. No fertilizers were used.

Samples were taken at three-month intervals starting in August 1998, three months after planting, and ending in May and June 1999 in Houëgbô and Sé respectively, when cassava plants were 12 and 13 months old. A total of four samples were collected from each field. Care was taken to select sampling days at which no rainfall occurred, because rain showers can cause noticeable and immediate changes in predator and prey numbers.
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(A. Onzo, pers. obs.). For the same reason, sampling was limited to a 24-hour period, because at this time scale it is expected that the numerical changes due to predation and growth would be minor.

During a sampling day, the number of predators and prey were counted at 4 hour intervals during a 24-hour period, from 12:00h until 8:00h the following morning. Each sample consisted of 20 randomly selected cassava plants, 5 per field section. Starting from the apex, every other leaf from the second fully unfolded leaf to the 20th leaf was collected from each cassava plant (plants can have up to 50 leaves). The apices were placed directly into separate vials containing 70% alcohol. Similarly, leaves with their petioles intact were placed individually in separate plastic bags (one leaf per bag). Apex and leaf samples were labelled with their plant number, node position, sampling period and name of the site. Leaf samples were transported in a cool box and stored in a freezer until processed. Eggs and mobile stages of predatory and herbivorous mites were counted under a dissecting binocular microscope (Wild M3B). Only the mobile stages of phytoseiids were preserved in 70% alcohol and mounted in Hoyer's solution for identification with the aid of a phase-contrast compound microscope (Wild Leitz Diaplan (Schweiz) AG). Voucher specimens are stored at the IITA Station in Benin.

Temporal variation in prey and predator distribution

Changes on total number of mobile mites (prey or predator) on the even-numbered leaves among the first 20 leaves were analysed, using the data set consisting of 20 randomly selected plants per sampling hour and 6 sampling hours per sampling day. To detect differences between sampling hours, an ANOVA (PROC GLM, SAS Institute, 1999) was carried out and a Student-Newman-Keuls (SNK) multiple range test was applied to identify significant differences between time of day. In addition, we used a Rayleigh test to detect diurnal changes in mite distributions (Batschelet, 1981). To this end, the sampling hours (\( t \)) were first transformed into angles (\( \phi \)) expressed in radians and the length of the mean vector \( r \) and the rectangular \( X \) and \( Y \) coordinates of the mean vector were calculated using the following equations (Batschelet, 1981; pp.10-14; 54-58):

\[
X = (\Sigma n \cos \phi) / n \quad \text{and} \quad Y = (\Sigma n \sin \phi) / n
\]

\[
r = [(\Sigma n \cos \phi)^2 + (\Sigma n \sin \phi)^2]^{1/2} / n
\]

with \( n \) = mean total number of mites found per plant part (leaves or apex) during the 24 hour cycle and \( n \) = the mean number of mites present per plant part (leaves or apex) at a certain sampling hour (\( t \)). The mean angle, \( \phi \), (corresponding to the peak hour of abundance), was calculated from the rectangular coordinates \( X \) and \( Y \) of the mean vector as follows:
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\[ \phi = \begin{cases} \arctan(Y/X) & \text{if } X > 0 \\ 180^\circ + \arctan(Y/X) & \text{if } X < 0 \end{cases} \]

Under the null hypothesis, the distribution over sampling hours is random, whereas under the alternative hypothesis the mites aggregate in the upper 20 leaves at certain hours of the day. The same analysis was applied to the number of predators inhabiting the apex. Seasonal trends were not statistically analysed. Instead, we compared the numerical results of the Rayleigh tests on the various sampling dates to detect trends over the sampling dates spanning a total period of circa one year.

By monitoring predator abundance in the apex and on leaves, predators foraging on stems were ignored. Hence, the number of predators on leaves underestimates the true number foraging on the plant. As a remedy, the real number of predators outside the apex \((E)\) on a given sampling day was estimated as the difference between the peak and trough numbers of predators inside the apex. The proportion of predators emigrated from the apex \((i.e.\ predators\ found\ on\ leaves)\) is estimated as the ratio of the number collected on leaves and \(I\). Because sampling of predators required destructive removal of leaves and apex, these calculations were not made on individual plant basis. Instead, means were calculated per plant per cassava field section \((20\ plants\ per\ field,\ i.e.\ 5\ plants\ per\ section,\ 4\ sections\ per\ field)\).

**Stage distribution among the predator emigrants**

To test which developmental stages took part in the emigration from the apex, changes in the stage distribution (larvae, nymphs, adult males and adult females) were determined by comparing proportions in each stage in the apex at different sampling hours, as well as in the population collected from leaves. Because of the excessive amount of work involved in mounting specimens for determining stage and sex, the stage distributions were determined only at 12:00h and 20:00h and only in two of four field sections \((1\ and\ 3)\) in each of the two field sites. From these stage distributions the proportion of males among adults was calculated \((to\ test\ the\ hypothesis\ that\ males\ move\ less\ than\ females)\) and arcsine-transformed to obtain continuous and normal distributions. This transformed variable was subjected to an ANOVA with sites \((Houégbô\ and\ Sé)\), sampling dates, sampling hours or plant part \((apex\ or\ leaves)\), the interaction between the latter two and the residual error as sources of variation.

**Predator emigration from the apex, prey density on leaves and prey response**

To determine whether the frequency of \(T.\ aripo\) emigration from the apex was related to the abundance of \(M.\ tanajoa\) on leaves, two relationships were examined. First, we analysed the proportion of predators \((p)\) emigrated from the apex at peak emigration time \((i.e.\ 20:00)\)
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h) in relation to the mean number of herbivorous mites (all stages including eggs) on all the even-numbered leaves among the first 20 leaves together \( (\bar{n}) \). The relationship was described by a negative exponential function \( p(n) = 1 - \exp(-k.n) \), where \( k \) is a constant equal to the slope in a log(1-p) vs. \( n \) plot. Second, for prey and predator separately, the centre of the distributions of mobile mites (all stages except the eggs) over leaves was calculated as a weighted leaf number \( (L) \) using the following formula:

\[
L = \sum_{x=2}^{20} xN(x)/\sum_{x=2}^{20} N(x)
\]

with \( x = \) leaf number (from first to 20th leaf below the apex) and \( N(x) = \) number of mites on leaf \( x \). The estimates of \( L \) for predator and prey were tested through regression analysis to detect whether changes in predator distribution coincide with changes in prey distribution. In this way, it was investigated how emigration of predators from the apex was influenced by prey density on the leaves and how the distribution of prey over the leaves was influenced by predator emigration.

RESULTS

Temporal variation in prey and predator distribution

Populations of both \( M. tanajoa \) and \( T. aripo \) in apices and on leaves of cassava plants showed significant variation between sampling days and sampling hours within sampling days.

The prey mite, \( M. tanajoa \), was absent from the apex on all sampling dates except for the August sampling in the field site at Sè. Here, it showed up in low, yet significantly different numbers compared to all other sampling dates (Table 1). On the first 20 leaves below the apex, however, total densities of \( M. tanajoa \) always exceeded zero and were highest in August (Houëgbo) or November (Sè) and lowest in May (Houëgbo) or June/August (Sè).

There were significant effects of sampling hour on \( M. tanajoa \) abundance in the top 20 leaves for all sampling days (thus in all seasons) and for Houëgbo as well as Sè (Table 1; Figure 1). According to the Rayleigh tests applied to average distributions over the four sampling dates, \( M. tanajoa \) was most abundant on the top 20 leaves around 15:30h in Sè and 17:30h in Houëgbo, with the earliest 'highest-abundance' occurring at 14:00h in Sè and the latest 'highest-abundance' occurring at 21:30h in Houëgbo in November (Table 2). This strongly indicates a diurnal pattern of vertical migration of \( M. tanajoa \) within the cassava plant. No other obvious seasonal trends in diurnal migration patterns were detected.
Table 1 Analysis of Variance for densities of mobile stages of *M. tanajina* and *T. aripo* in apices and on every other leaf within the top 20 leaves on cassava plants, in Houegbo and Sè field sites. Densities were log-transformed and, then, analysis was performed with PROC GLM (SAS, 1999).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th><em>M. tanajina</em></th>
<th>T. aripo</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Houègbo field site</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Apex</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hour</td>
<td>5</td>
<td>0.002</td>
<td>1.00</td>
</tr>
<tr>
<td>Date</td>
<td>3</td>
<td>0.002</td>
<td>1.00</td>
</tr>
<tr>
<td>Hour*Date</td>
<td>15</td>
<td>0.002</td>
<td>1.00</td>
</tr>
<tr>
<td>Error</td>
<td>456</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td><strong>Leaves</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hour</td>
<td>5</td>
<td>1623.90</td>
<td>15.93</td>
</tr>
<tr>
<td>Date</td>
<td>3</td>
<td>11655.31</td>
<td>114.36</td>
</tr>
<tr>
<td>Hour*Date</td>
<td>15</td>
<td>929.5</td>
<td>9.12</td>
</tr>
<tr>
<td>Error</td>
<td>47&quot;6</td>
<td>101.91</td>
<td></td>
</tr>
<tr>
<td>Sè field site</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Apex</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hour</td>
<td>5</td>
<td>0.079</td>
<td>2.87</td>
</tr>
<tr>
<td>Date</td>
<td>3</td>
<td>0.768</td>
<td>27.89</td>
</tr>
<tr>
<td>Hour*Date</td>
<td>15</td>
<td>0.052</td>
<td>1.88</td>
</tr>
<tr>
<td>Error</td>
<td>456</td>
<td>0.028</td>
<td></td>
</tr>
<tr>
<td><strong>Leaves</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hour</td>
<td>5</td>
<td>3.99</td>
<td>13.86</td>
</tr>
<tr>
<td>Date</td>
<td>3</td>
<td>66.52</td>
<td>230.97</td>
</tr>
<tr>
<td>Hour*Date</td>
<td>15</td>
<td>1.59</td>
<td>5.51</td>
</tr>
<tr>
<td>Error</td>
<td>47&quot;6</td>
<td>0.29</td>
<td></td>
</tr>
</tbody>
</table>

Overall population densities of *T. aripo* found in the cassava apices in both field sites were high compared to other field sites not included in this study; with the lowest densities occurring in May in Houègbo and January in Sè. During the day nearly all *T. aripo* were found in the apex and very few were found on leaves. At night, the numbers of *T. aripo* in the apex dropped (Table 1), whereas there were more *T. aripo* recovered among the samples taken from the first 20 leaves below the apex (Table 1; Figure 1). Rayleigh tests further revealed that *T. aripo* predators were most abundant in the apex around 11:00h in both field sites with 8:56h (in May at Houègbo) and 12:40h (in August at Sè) as the earliest and the latest, respectively. On the leaves, however, they were most abundant around 22:30h (in Sè) and 21:00h (in Houègbo), with 18:08h (in August in Houègbo) and 22:56h (in August at Sè) as the earliest and the latest, respectively (Table 2). This all strongly indicates a diurnal pattern of vertical migration of the predatory mites within the cassava plant. No obvious seasonal trends in diurnal migration patterns were observed.
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**Figure 1** Mean number (mean + SE) of *M. tanajoa* (eggs + mobile stages) and *T. aripo* (mobile stages) found in apex and on the even-numbered among the top 20 leaves within cassava plants at 4-hour-intervals during a 24-hour period, starting from 12:00h to 8:00h the following morning. In Houègbo, samples were taken in August 1998, November 1998, January 1999 and May 1999; while in Sè, samples were taken in August 1998, November 1998, January 1999 and June 1999. Means represent averages over the four sampling days. Since only 10 leaves have been sampled, number of *T. aripo* on the top 20 leaves was obtained by multiplying by 2 the number found of the 10 leaves sampled. Note that arrows indicate presence of *M. tanajoa* in apices (albeit usually in very low numbers). For each plant part, bars with the same lower case letter are not significantly different (PROC GLM; Student-Newman-Keuls multiple range test, SAS, 1999).

In summary, *T. aripo* exhibited the following diurnal pattern: the predators remained in the apex during the daylight sampling hours (12:00h, 16:00h and 08:00h), and moved out to forage on cassava leaves during the night hours (20:00h, 00:00h and 04:00h). This can be concluded because the numbers of predators observed in the apex at the first two daytime sampling hours were approximately equal to those observed in the apex on the last sampling hour the next day (*i.e.* 8:00h); thus, the decrease in numbers of *T. aripo* during the night must be due to emigration. Therefore, the 'daytime' numbers of predators in the apex were taken as a reference to calculate the proportion of predators that did not leave the apex during the night hours. At Houègbo and across all sampling dates, 32.3% of *T. aripo* were found in cassava apices at 20:00h, 36.4% at 00:00h and 71.2% in the apices at 04:00h. At Sè, the pattern was quite similar: 30.4% of *T. aripo* were in apices at 20:00h, 45% at 00:00h and 64% at 04:00h. The percentage of predators that emigrated from the apices and were recovered on the leaves at 20:00h was rather low: 16.7% (SE = 4.5,
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For Houègbó and Sè, these low rates of recovery of T. aripo on the leaves are most likely the result of many T. aripo individuals moving from leaf to leaf via the stems, which were not included in the samples. Specimens also could have been lost especially during handling of the leaves in the field and in the laboratory.

Table 2 Peak hours of abundance of mobile stages of M. tanajoa and T. aripo in the top 20 leaves within cassava plants and T. aripo in the apex of cassava plants during a sampling day at the sites Houègbó and Sè.

<table>
<thead>
<tr>
<th>Months</th>
<th>M. tanajoa on leaves</th>
<th>T. aripo on leaves</th>
<th>T. aripo in apex</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Peak hour</td>
<td>Rayleigh test (%)</td>
</tr>
<tr>
<td>Houègbó</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aug</td>
<td>536.9</td>
<td>19:56</td>
<td>4.229*</td>
</tr>
<tr>
<td>Nov</td>
<td>300.5</td>
<td>21:36</td>
<td>11.090*</td>
</tr>
<tr>
<td>Jan</td>
<td>304.9</td>
<td>15:36</td>
<td>67.598*</td>
</tr>
<tr>
<td>May</td>
<td>76.1</td>
<td>14:04</td>
<td>0.909ns</td>
</tr>
<tr>
<td>Average</td>
<td>304.5</td>
<td>17:32</td>
<td>8.060*</td>
</tr>
</tbody>
</table>

| Sè | | | | | | | | |
| Aug | 338.4 | 15:40 | 3.969* | 1.8 | 22:56 | 0.867na | 23.4 | 12:40 | 0.396ns |
| Nov | 1161.3 | 14:00 | 1.570ns | 6.3 | 22:16 | 1.640ns | 124.3 | 11:52 | 17.078* |
| Jan | 710.3 | 16:00 | 27.045* | 0.5 | 20:00 | 0.080na | 58.6 | 10:00 | 3.830* |
| June | 386.7 | 14:28 | 7.323* | 14.1 | 22:28 | 1.316ns | 97.0 | 10:48 | 12.160* |
| Average | 649.1 | 15:20 | 6.756* | 5.6 | 22:32 | 0.921ns | 75.7 | 11:16 | 7.751* |

n: total sample size; Rayleigh test statistic;*: test significant at 0.05; na: test not significant at 0.05; ns: test not applicable because sample size is too low.

Table 3 Percentage of each T. aripo life stages present (1) in the apex of cassava plants at 12:00h, (2) as (1) but now at 20:00h, and (3) in the top 20 leaves within cassava plants at 20:00h, at the sites Houègbó and Sè.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Larva</th>
<th>Nymph</th>
<th>Male</th>
<th>Female</th>
<th>Larva</th>
<th>Nymph</th>
<th>Male</th>
<th>Female</th>
<th>Larva</th>
<th>Nymph</th>
<th>Male</th>
<th>Female</th>
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<tr>
<td>Houègbó</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<td></td>
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<td>14.29</td>
<td>50.00</td>
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<tr>
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<td>24.09</td>
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<td>2.13</td>
<td>22.34</td>
<td>27.66</td>
<td>47.87</td>
<td>0.00</td>
<td>15.79</td>
<td>10.53</td>
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<tr>
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<td>15.63</td>
<td>37.50</td>
<td>46.88</td>
<td>0.00</td>
<td>27.27</td>
<td>45.45</td>
<td>27.27</td>
<td>0.00</td>
<td>22.22</td>
<td>33.33</td>
<td>44.44</td>
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<tr>
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<td>18.72</td>
<td>25.62</td>
<td>53.94</td>
<td>2.42</td>
<td>21.21</td>
<td>36.36</td>
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<td>0.00</td>
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<td>26.09</td>
<td>54.35</td>
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<tr>
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<td>28.94</td>
<td>44.56</td>
<td>5.76</td>
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<td>40.29</td>
<td>34.53</td>
<td>6.71</td>
<td>18.79</td>
<td>22.82</td>
<td>51.68</td>
</tr>
</tbody>
</table>
Stage distribution among the predator emigrants

Since adult female predatory mites have much higher prey requirements, than males and all juvenile stages, one would expect females to dominate among the emigrants response. In fact, all mobile stages of the predator were found foraging out of the apices during the night, except for the larvae in Houègbo (Table 3). The proportion of male predatory mites in the apex at 12:00h was lower than at 20:00h ($F = 28.35$, df = 1, $P < 0.006$), regardless of the field site ($F = 1.05$, df = 1, $P > 0.38$), the sampling date ($F = 8.04$, df = 3, $P > 0.06$), and with no significant interactions between sampling date and field site ($F = 0.60$, df = 3, $P > 0.65$) or, between sampling date and sampling hour ($F = 1.56$, df = 3, $P > 0.33$). In addition, the proportion males in the apex population at 20:00h differed from that in the leaf-inhabiting population of predatory mites at the same time ($F = 9.14$, df = 1, $P < 0.04$), regardless of field sites ($F = 0.92$, df = 1, $P > 0.40$), sampling dates ($F = 1.10$, df = 3, $P > 0.47$), with no significant interactions between sampling date and field site ($F = 0.77$, df = 3, $P > 0.57$) or between sampling date and plant part ($F = 0.48$, df = 3, $P > 0.71$). Scrutiny of the data showed that during night hours, males tend to stay more frequently in the apex compared with females, which tended to move more frequently to the leaves, thereby skewing the sex ratios in the apex and on the leaves. This conclusion was confirmed by calculating the percentage emigrated of each stage from the numbers of that stage present in the apex at 20:00h and at 12:00h. It was estimated that in Houègbo, 40% of larvae, 54% of nymphs, 41% of adult males and 76% of adult females moved out of the apex during the night hours, clearly indicating that females migrated more frequently out of the apex than any other stage. This pattern also held in a qualitative sense for the other field site (Sè), but here the emigration rates were much higher for all stages: 80% of the larvae, 78% of the nymphs, 67% of the adult males and 85% of the adult females.

Predator emigration from the apex in relation to prey density on leaves

Emigration of *T. aripo* from the apex increased with an increasing prey density on the leaves. The relationship between the proportion of *T. aripo* that moved out of the apex and the total density of *M. tanajoa* (all stages on the even-numbered leaves among the first 20) is significant for the field site at Sè (Figure 2), but not significant for the field site at Houègbo, albeit qualitatively similar ($\log(1-p) = -1.21 - 0.00006n; R^2 = 0.0002; P = 0.93$; df = 60; here, $p$ = proportion of predators emigrated from the apex at peak emigration time (*i.e.* 20:00h) and $n$ = mean number of herbivorous mites (all stages including eggs) on all the even-numbered leaves among the first 20 leaves together). The non-significance of the relation for Houègbo may be due to low *M. tanajoa* densities and consequently the smaller range of densities included in the regressions.

Prey response to predator emigration

The data on *T. aripo* emigration from the apex showed that this predator species moved out of the apex towards the leaves in the same period where *M. tanajoa* tended to move
down to lower leaves in the cassava plant. We asked whether the extent of the downward movement of *M. tanajoa* was related to the rate of *T. aripo* emigration out of the apex. Regressing the weighted leaf numbers (*L*) of the prey to those of the predator revealed a significant correlation between *L* of *M. tanajoa* and *L* of *T. aripo* for the period of 20:00h to 00:00h at the field site in Sè (Figure 3). This shows that *M. tanajoa* moved down to yet lower leaves, when *T. aripo* also moved further down from the apex. Because these changes in vertical distribution occurred simultaneously, this suggests predator avoidance behaviour by *M. tanajoa*. The other field site (Houègbo), however, did not show such a relation between *L* of predator and *L* of prey (intercept = 10.09; slope = 0.07; \( R^2 = 0.001; \) df = 159; \( F = 0.17; P = 0.68 \)). One reason for the absence of the prey’s response at Houègbo may be the lower *M. tanajoa* densities (up to 600 in Houègbo vs. up to 1200 in Sè). Another reason may be that the densities of *T. aripo* at Houègbo were lower (on average, at mid-day, over the four sampling dates together, 20.1 mobile *T. aripo* per plant in Sè vs. 10.8 mobile *T. aripo* per plant in Houègbo). See Discussion for a third possible reason.

![Figure 2](image)

**Figure 2** Relationship between the proportion of *T. aripo* emigrated from the apex at 20:00h and total number of *M. tanajoa* on the 10 even-numbered leaves sampled among the top 20 cassava leaves at the field site in Sè \( \log(1-p) = -1.61 - 0.00084u; R^2 = 0.15; P < 0.004; \) df = 54 where \( p \) = proportion of predators emigrated from the apex at peak emigration time (i.e., 20:00 h) and \( u \) = mean number of herbivorous mites (all stages including eggs) on all the even-numbered leaves among the first 20 leaves together.
DISCUSSION

This study shows the temporal dynamics of how the predatory mite *T. aripo* uses the apex of a cassava plant as a refuge. During the day the predatory mite resides in the plant apex. It does not wait for its prey to move into the apex in search for fresh leaves, as hypothesized by Bakker (1993). Instead, predatory mites leave the apex during the night to forage for prey on the young leaves. The decision to leave the apex appears to depend on prey availability on leaves: the proportion of predators out of the apex increases with increasing prey density on the first 20 leaves. Moreover, the physiologically most active life phase, *i.e.* the adult female – due to prey requirements for egg production – dominates among the emigrants. Finally, the prey (*M. tanajoa*) responds to a higher predator density on young leaves at night by moving to lower leaves with a lower predator density and they move up in the plant again when the predatory mites seek shelter in the plant apex during the day.

Figure 3 Relationship between the weighted leaf numbers (*L*) for *M. tanajoa* (y-axis) and those of *T. aripo* (x-axis) for samples taken at 20:00 hours and 00:00 hours at the field site in Sê. The line represents a regression equation with intercept = 8.54, slope = 1.004; and $R^2 = 0.276$ (df = 159; $F = 60.18; P < 0.001$)
The reasons why *T. aripo* stays in the apex during the day are not fully elucidated yet. The apex may provide a refuge to cope with harsh climatic conditions during the day, such as low humidity, high temperature, rain or UV-radiation (van der Geest, 1985; Yaninck et al., 1989a; Barcelo, 1981; Bakker, 1993; Grostal and O'Dowd, 1994; Mebelo, 1999; Sabelis et al., 1999). In fact, plant-feeding mites are known to avoid UV-radiation and realistic levels of UV-radiation are known to cause mortality in spider mites (Barcelo, 1981). Another reason to hide in the apex may be to avoid predation (Sabelis et al., 1999; Norton et al., 2001). Leaf-dwelling predatory mites, such as *Typhlodromus manihoti*, can feed on *T. aripo* juveniles (S. Magalhaes, University of Amsterdam, unpublished data). Hence, if the two phytoseiid species co-occur on leaves of the same plant and *T. manihoti* forages for prey on leaves, *T. aripo* may lower the risk of intraguild predation by hiding in the apex. A nice example of such avoidance by ovipositing away from enemy-occupied sites was given by Faraji (2001) for another predatory mite, *Iphiseius degenerans* (Berleese).

Another puzzle waiting to be solved is why *T. aripo* on the one hand migrates more frequently when there is more prey on the leaves, yet did not move further down in the plant than leaf 10. A possible reason is that the predators stay put where they first find prey. Indeed, on cassava plants, *M. tanajoa* densities begin to decline beyond leaf 10. Even if the mobile stages of *M. tanajoa* move down in response to predator emigration from the apex, there are still immobile stages (eggs, moultng stages) left behind and they may well arrest the downward-migrating predatory mites. In any case, we do not expect that the distance migrated away from the apex is constrained by *T. aripo*’s ability to return to the apex before sunrise. They can in principle reach the apex by moving against gravitational forces (negative geotaxis). Moreover, frequent within-plant migration over considerable distances has been observed in other predatory mites. For example, in sweet pepper plants *I. degenerans* moves up to flowers where it feeds on flower thrips and pollen, and down to the leaves to lay a single egg quite distant from the flowers, and this procedure is repeated several times per day (Faraji et al., 2000). Another reason why *T. aripo* may avoid moving deeper down in the plant is to avoid interference with intraguild predators that typically inhabit the lower part of the plant. This is not likely however, because such intraguild predators (e.g. *T. manihoti, Euseius pastor* (Pritchard and Baker)) were absent or rare, especially at the field site in Sè (Onzo, pers. obs.; Hanna and Sabelis, unpubl. data). In short, refuge use by *T. aripo* appears to be subject to a trade off between lower predation (and hence less energy available for reproduction) when in the refuge, and greater survival by avoiding intraguild predators and exposure to detrimental abiotic conditions such as low humidity and UV-radiation.

If predatory mites emigrating nocturnally from the apex are arrested by feeding on eggs and moultng stages of their prey on the young leaves, then this provides an explanation for why the mobile stages of this prey avoid predation by moving further down in the plant. Thus, the gain for the mobile prey mites to move down in the plant at night exists by virtue of other stages of the prey mites that cannot move and stay put.

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Dynamics of refuge use: Diurnal, vertical migration by mites within cassava plants

higher in the plant. They also gain by moving up the next morning, because the young leaves provide better food resources and harbour fewer predators during the day. Thus, nocturnal emigration of *T. aripo* from the cassava apex may well trigger diurnal vertical migration of *M. tanajoa*, as a mode of predator avoidance behaviour. Behavioural experiments under controlled conditions showed that such migration responses of *M. tanajoa* could be induced by odours emanating from *T. aripo* (Magalhães et al., 2002). Avoidance responses of other species of spider mites to predator-associated odours have been reported earlier by Grostal and Dicke (1999) and Pallini et al. (1999).

Whereas diurnal vertical migration was evident from the observations at the field site in Sé, it was not in Houëgbo. Two reasons for this difference have been given earlier, but there is third possibility related to the higher density of endemic predators of *M. tanajoa* in Houëgbo (c. 4 *Lusius justus* (Pritchard and Baker) per plant in Houëgbo vs. only 0.02 per plant in Sé). Experiments under controlled conditions showed that vertical migration of the adult females of the prey (*M. tanajoa*) is not a fixed, diurnal pattern because it can be induced by predator odours (and thus depends on the presence of predators) and because the direction of the prey’s response (to move up or down in the plant) depends on the type of predator (leaf-dwelling or apex-inhabiting), as well as on the position of the predator (*i.e.* the odour source) in the plant (Magalhães et al., 2002). Thus, it is entirely possible that the prey at the field site in Houëgbo showed a response to two or more predator species and that this response was not a simple downward migration in the plant, because the prey faces a dilemma ‘being in between two fires’.

The diurnal pattern of refuge use by predatory mites, such as *T. aripo*, may have important population dynamical consequences, as can be seen within the framework of a Lotka-Volterra type model. While in the refuge, the predators give up predation opportunity and thereby also reproduction, but are hypothesised to gain in terms of survival from abiotic or biotic causes. If refuge seeking by the predators is the one and only modification, this is likely to destabilise the equilibrium of the strongly coupled (Lotka-Volterra-type) interactions within local predator-prey populations (Sabelis et al., 1991). However, the herbivorous mites are at least partially free of *T. aripo* predators during the whole day. During daytime, they can feed on the young leaves when predators hide in the apex and hence predation risk is low, and – during night-time – their mobile stages move down to feed on the older leaves, thereby escaping from the nocturnally foraging predatory mites. This avoidance response of the prey alone is well known to have a stabilising effect on the equilibrium of strongly coupled predator-prey interactions and this may counteract the destabilising effect of a predator refuge (*e.g.* Sabelis et al., 1991). In any case one would expect the prey refuge to cause prey and predator populations to persist for a longer time on a given plant. This is not necessarily disadvantageous to the cassava plant for four reasons. First, the predatory mites may keep the density of herbivorous mites, and thereby plant damage, low. Second, the presence of predatory mites in the apex causes the herbivorous mites to refrain from feeding on the leaf
primordia. Third, the predatory mites reduce the density of herbivorous mites on the young leaves near the apex and especially these leaves are of great importance to the photosynthetic capacity of the cassava plant. Fourth, the predatory mites force the herbivorous mites to feed on older (and less profitable) leaves, which causes their reproductive rate to decrease. Therefore, we hypothesize that the cassava plant gains by creating predator refuges in the apex, because in this way it protects its primordia and its young (= photo-synthetically most active) leaves. Testing this hypothesis will be an important future task.

**Acknowledgements**

We are grateful to B. Eklou, J. Goulodji, S. Dossou, D. Hounhagni, D. Gany and B. Bovis for enduring the hardships of collecting samples at night and for processing these samples. Many drivers of IITA-Bénin gave their valuable contributions to transport of the samples. We are also extremely grateful to Valentin Kpeegan and SéraphinDansou for allowing us to use their land. Sam Korie provided assistance on the statistical analysis of the data. Thanks are due to ArneJanssen and SaraMagalhães for their valuable comments on an earlier version of this manuscript and to PeterHambäck for suggestions to improve the structure of the text. This research was supported by the International Institute of Tropical Agriculture, with funds provided by the Danish International Development Agency and the Netherlands Foundation for the Advancement of Tropical Research.

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