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

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Temporal and spatial dynamics of an exotic predatory mite and its herbivorous mite prey on cassava in Benin, West Africa

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Quantitative knowledge of temporal and spatial distribution patterns of arthropod pests and their natural enemies in agricultural crops is essential for understanding their interactions, and is a prerequisite for the development of reliable sampling plans for estimation and monitoring of pest and natural enemy populations. Temporal and spatial distributions of the cassava green mite Mononychellus tanajoa (Bondar) (Acari: Tetranychidae) and its predator Typhlodromalus aripo DeLeon (Acari: Phytoseiidae) were determined in two cassava fields in Southern Benin, West Africa. Samples were taken monthly from August 1998 to June 1999 to follow predator and prey dynamics in cassava fields, from shortly after planting to harvest time. In addition, within-plant distribution of both predator and prey was determined in the upper 20 nodes of the cassava plant at four critical periods during the study. In both field sites, temporal trends in abundance of M. tanajoa and T. aripo were similar but with a slight delay in T. aripo response to changes in M. tanajoa densities. Overall temporal trends of T. aripo and M. tanajoa in both study sites were, as expected, related to seasonal rainfall pattern. Aggregation indices calculated using Taylor's power law indicated a clumped distribution for both predator and prey. Nonetheless, prey distribution was less aggregated after introduction of the predator than it was when no efficient predator was present in the system. Within-plant distribution of M. tanajoa showed an aggregation on young leaves; however, the highest densities shifted from the first fully developed leaf (c. leaf 4) to leaves 6 to 12 in the presence of the predatory mite T. aripo, which was almost exclusively found in apices of cassava plants. The shift in M. tanajoa distribution to lower parts is due to the foraging patterns of T. aripo, which searches for prey within the upper part of the cassava foliage during night hours and spends much of the daylight hours sheltered in the apex (apical domatium) of the plant. New enumerative and binomial sampling plans were developed for M. tanajoa and T. aripo on the basis of the new Taylor’s Power Law aggregation indices. Limitations of the proposed sampling plans in monitoring the population densities of T. aripo and M. tanajoa are discussed.
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Key words Acari, Phytoseiidae, Tetranychidae, Mononychellus tanajoa, Typhlodromalus aripo, Manihot esculenta, population dynamics, clumped distribution, aggregation, enumerative sampling, binomial sampling

Reliable sampling programs for estimating and monitoring the abundance of pests and their natural enemies are critical components of sound biological and/or chemical pest management programs (Wilson et al., 1989; Jones, 1990). Sampling programs must be founded on quantitative knowledge of the pest and the natural enemies with respect to their temporal and spatial distribution patterns (Taylor, 1984), their response to local environments, and their spatial coincidence (Greco et al., 1999), and their natural history and habitat requirements (Murdoch and Briggs, 1996). In this article we quantified the spatial and temporal dynamics of an herbivorous mite pest and its exotic phytoseiid predator on cassava (Manihot esculenta Crantz) under different climatic conditions in Benin (West Africa) to further our understanding of the effect of the natural enemy on population dynamics of the pest, and to develop sampling programs to estimate pest and natural enemy abundance.

The system explored in this article consisted of the cassava green mite, Mononychellus tanajoa (Bondar) (Acari: Tetranychidae) and the predatory mite Typhlodromalus aripo DeLeon (Acari: Phytoseiidae) on cassava plants in southern Benin. Both pest and predator are of neotropical origin. The pest, *M. tanajoa*, was accidentally introduced into Uganda (East Africa) in the early 1970’s (Nyiira, 1972) and from there it quickly spread over much of sub-Saharan Africa, causing extensive cassava crop losses and resulting in substantial negative impact on the livelihood of millions of inhabitants in 27 African countries (Yaninek, 1988). Ever since its discovery in Africa, *M. tanajoa* has been the subject of numerous studies with the goal of developing chemical and biological control programs, and sampling strategies for estimating and monitoring its population abundance. The greatest amount of effort devoted to developing control options for *M. tanajoa* in Africa has been the multi-national and multi-institutional classical biological control program led by the International Institute of Tropical Agriculture and partners in Africa, South and North America, and Europe (Yaninek and Hanna, 2003). This classical biological control campaign has resulted in the permanent establishment of two neotropical predatory mites Typhlodromalus manihoti Morales and *T. aripo* (Yaninek et al., 1998; Hanna and Toko, 2001; Janinek and Hanna, 2003). Of the two predatory mites, *T. aripo* has established and spread most quickly. Since its introduction in 1993, *T. aripo* has become the most effective natural enemy of *M. tanajoa* in terms of its impact on the densities of the pest and the extent of its geographical distribution in Africa, where it is now found in 20 countries in sub-Saharan Africa (Hanna and Toko, 2001; Janinek and Hanna, 2003).

Prior to the introduction of *T. aripo* into Africa, population dynamics studies had shown that *M. tanajoa* densities generally exhibited two peaks of abundance — early in the
Temporal and spatial dynamics of an exotic predator and its herbivorous prey on cassava

dry season and at the onset of the wet season – while remaining at low levels during the second half of the dry season and throughout much of the wet season (Yaninek et al., 1989b; Skovgard et al., 1993). Within-plant distribution studies showed that *M. tanajoa* is generally more abundant on young than on old cassava leaves, regardless of planting time or plant age (Braun et al., 1989; Yaninek et al., 1991; Nachman et al., 1993). Based on this within-plant distribution pattern, Yaninek et al. (1991) proposed the first fully developed leaf near the top of the foliage as the most appropriate sampling unit for estimating and monitoring *M. tanajoa* population abundance. The information on within-plant distribution and dispersion indices based on Taylor’s power law (Taylor, 1961) were used to develop a sampling program for *M. tanajoa* on cassava in Africa in the absence of effective natural enemies (Yaninek et al., 1991). It is well known that effective natural enemies can reduce the degree of aggregation of arthropod populations (Wilson et al., 1984; Braun et al., 1989) by ‘thinning’ of prey population densities through predation (Wilson et al., 1984) or through induced predator-avoidance behaviour (Onzo et al., 2003). The introduction and permanent establishment of *T. aripo* is thus expected to alter the temporal and spatial dynamics of *M. tanajoa* in Africa, necessitating additional studies to describe and quantify these dynamics, and use them for developing appropriate sampling programs for estimating and monitoring *M. tanajoa* and *T. aripo* abundance (Braun et al., 1989; Yaninek et al., 1991; Nachman et al., 1993; Skovgard et al., 1993).

Equally needed is information on *T. aripo* spatial dynamics throughout the cassava growing season and on the coincidence between population dynamics of the predator and the prey, which are presently lacking. Field and laboratory studies on acarine prey-predator systems generally show marked density oscillations of both populations that are, generally, prone to extinction. Experiments have confirmed, however, that spatial structure can promote persistence of predator-prey interactions at a larger spatial scale (Ellner et al., 2001). (1) through habitat complexity that gives rise to a game of hide and seek, thereby creating partial refuges for the prey (Price et al., 1980; Sih and Gleeson, 1995; Greco et al., 1999; Onzo et al., 2003), and (2) through various elements of the dispersal behaviour of both predator and prey (Sabelis et al., 1991).

The overall objective of this study is to obtain quantitative information on the spatial and temporal variation of *M. tanajoa* and *T. aripo* densities in cassava fields throughout a growing season, and use it to develop enumerative and binomial sampling plans for estimating densities of *T. aripo* and *M. tanajoa* in cassava fields.

**MATERIAL AND METHODS**

**Study sites**

Field experiments were conducted in two cassava fields, 0.35 ha each, at two locations in southern Benin, West Africa. One of the sites was located near the town of Sé (6°32.23' N,
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\(6^449.11^\circ \text{E}\) in Mono Province, whereas the other site was located near the town of Houëgbô (\(6^\circ48.23^\circ \text{N}, 2^\circ11.13^\circ \text{E}\)) in Atlantique Province. At both sites, a single introduction of \(T. \text{arpio}\) had led to its persistence for more than three years prior to the initiation of the experiments. The two fields were located in the humid coastal Savannah Forest Mosaic (SFM) zone, characterized by a bimodal rainfall pattern that begins in late March and ends in November. The rainy season is generally interrupted by a dry spell from mid-July until mid-September. Long-term average precipitation in this region is 1200 mm/year (Yaninek et al., 1996). Rainfall data collected at Toffo, 10 km West of the experimental site were used for the field site in Houëgbô. For the field site in Sè, rainfall data were collected at Kpinnou, 8 km North-West of the field site. Fields were planted with the cassava variety ‘Agric’, the most common cultivar in southern Benin. Each field was divided into four sections (blocks) of 50 m length and 15 m width, separated by 3 m buffer of cassava-free space. Cassava was inter-cropped with maize (local variety) in the first growing season, which is common practice in Benin. In each field, maize was planted first, at a density of 20,000 plants per hectare (i.e., 1 m between rows and 0.5 m within rows), and cassava was planted two weeks later at a density of 10,000 plants per hectare (1 x 1m spacing). Cassava was planted at the Houëgbô field site on 14 May, 1998 and at the Sè field site on 20 May, 1998. Cassava plants were thinned to one stem per plant at 2 months after planting. Maize was harvested in August and no other intercrops were planted thereafter. Weeding was undertaken as needed. No fertilizers were used in either of the two sites as addition of fertilizer is uncommon in small-holder cassava production in Africa.

Population dynamics

Previous field observations suggested that cassava generally remains free of \(M. \text{tanypa}\) and \(T. \text{arpio}\) for up to two months after planting; therefore, mite census started in August 1998, when cassava was three month-old, and continued through June 1999 when cassava was 12 month-old, which is the normal age of cassava harvest in Southern Benin. In each field, numbers of predators and prey were counted every month from 10 plants chosen per field section at random. On each plant the apex (i.e., the growing point) and the first fully developed leaf of the cassava plant (as described by Yaninek et al., 1991) were removed. The apices were put into individual vials containing 70\%\text{v} \text{o} \text{ ethanol}. Leaf samples were also placed individually in separate plastic bags and kept chilled during transit to the laboratory, where they were stored in a freezer until processed. Eggs and mobile stages (larvae + nymphs + adults) of predator and prey mites were distinguished and counted under a dissecting binocular microscope. Only mobile stages of phytoseiids were preserved in 70\%\text{v} \text{o} \text{ alcohol for subsequent mounting and identification to species.}

Monthly mean mite densities were calculated per plant for mobile stages of \(T. \text{arpio}\) in the apex, and for all stages of the \(M. \text{tanypa}\) population on the first fully developed leaf. These data were used to plot the population dynamics of predator and prey through time.
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together with the corresponding monthly rainfall intensity. A two-way analysis of variance (ANOVA) was used to compare densities of *M. tanajoa* and *T. aripo* between the two field sites and among blocks (nested within fields). All analyses were conducted using SAS statistical software (SAS Institute, 1999).

**Within-plant distribution of *M. tanajoa* and *T. aripo***

During the experimental period, the within-plant distribution of *M. tanajoa* was assessed four times corresponding to wet or dry periods prevailing in the area where the fields were located. Samples were taken in August, November, January, and May, corresponding respectively to rainy season, end of rainy season, early dry season and beginning of rainy season. From each field section, 15 cassava plants were randomly selected for each sample. Starting from the apex, each even-numbered leaf from the second fully unfolded leaf to the 20th leaf was selected from each cassava plant in the sample (plants can have up to 50 leaves). Apex and leaf samples were processed as described above. Spatial variations in mite densities were analysed using a random effect, 3-way nested ANOVA stratified by field and date to compare mean densities of *M. tanajoa* and *T. aripo* among blocks, among plants (nested within blocks) and among leaf node (nested within plant). Temporal changes in size and proportion of the variability of mite densities explained by variation among field sections (blocks), among plants and within plants (leaf node), were analysed using variance-component analysis, as in Hanna *et al.* (1996).

To compare mean densities of *M. tanajoa* per leaf node, the cassava canopy was divided into the following 5 strata: (1) leaf 2 and 4, (2) leaf 6 and 8, (3) leaf 10 to 12, (4) leaf 14 to 16, and (5) leaf 18 and 20. Analysis of variance was used to compare mean *M. tanajoa* densities among strata, stratified by field and by date. Differences in *M. tanajoa* densities among strata were compared with Student-Newman-Keuls multiple range test. Data were log-transformed to correct for the heterogeneity of error variance commonly found in arthropod count data. SAS statistical software (SAS Institute, 1999) was used for all the analyses.

**Measures of aggregation***

Aggregation pattern of *M. tanajoa* and *T. aripo* was evaluated using Taylor's Power Law (Taylor, 1961), a commonly used aggregation index based on the relationship between mean density and its corresponding variance and expressed by the following mathematical relationship:

\[ S = \alpha \bar{x}^b, \]  

(1)

where *S* is sample variance, *x* is sample mean, and *a* and *b* are estimated coefficients commonly used to characterize arthropod population distribution — *a* is a sampling factor and depends on sample size, while *b* is a measure of dispersion or aggregation.
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(Southwood, 1978) and is considered as the intrinsic property of the organism. Values of $b > 1$, $b = 1$ and $b < 1$ indicate aggregated, random and regular distributions respectively (Taylor, 1961). The $b$ coefficient is species-specific and can be a measure of the density dependence of aggregation (Taylor, 1984). However, both $a$ and $b$ determine the degree of aggregation of a species (Bancic, 1975; Hanna and Wilson, 1991).

Taylor’s coefficients were determined for mobile stages of both $M. tanaioa$ and $T. aripo$ with data from each field separately and for pooled data from both fields. To calculate these coefficients, leaf nodes with the highest mite densities, based on the within-plant distribution, were used as sampling units for each of $M. tanaioa$ or $T. aripo$ (Braun et al., 1989). However, to compare the aggregation pattern of $M. tanaioa$ after introduction of $T. aripo$ with the value reported by Yarinck et al. (1991) before the introduction of $T. aripo$ into Africa, Taylor’s coefficients were also determined for mobile stages of $M. tanaioa$ on the first fully developed leaves. Samples taken for the population dynamics were used for this purpose.

Parameters of Taylor’s power law were incorporated into the model proposed by Wilson and Room (1983) to describe the relationship between the proportion of infested sampling units and the mean density of $M. tanaioa$ or $T. aripo$ as follows:

$$P(l) = 1 - \exp [-\sin(\alpha)^{-1} / (\alpha^{-1} - 1)],$$

(2)

where $P(l)$ is the proportion of sampling units infested with one or more mites; $\alpha$ is the mean number of mites ($M. tanaioa$ or $T. aripo$) per sampling unit; and $a$ and $b$ are the corresponding Taylor’s coefficients. The goodness of fit of this model to the observed values was tested with a regression, forced through the origin, of the expected values against observed values.

**Developing a sampling plan for $M. tanaioa$ and $T. aripo$**

**Enumerative sampling plan**

Wilson and Room (1983) proposed to incorporate the parameters of Taylor’s power law into the general equation of Kariandinos (1976), to determine the number of samples ($N$) necessary to estimate mean density ($\alpha$) of predator or prey with a specified precision level ($D$). This leads to the following expression:

$$N = \left( Z_{\alpha} / D \right)^2 \alpha^{-2},$$

(3)

with $Z_{\alpha}$ being the standard normal deviate (1.96 for $N > 30$ and a confidence coefficient of 0.95); $D = 0.2$ and 0.3, being the fixed precision levels expressed as a proportion of the mean; $a$ and $b$ are Taylor’s coefficients.
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**Binomial sampling plan**

The binomial sampling plan is based on the relationship between the proportion of infested sampling units and the mean density of the species under consideration. To develop this sampling procedure, the Karandinos (1976) equation was again used as follows:

\[ N = \left( \frac{Z_n}{D_x} \right)^2 \frac{(1-p)}{p}, \]  

where \( N \) is the number of samples needed to estimate the mean density; \( Z_n \) is defined as before; \( p = P(I) \) in equation (2); \( D_x \) = precision level for \( p \) obtained by using equation (2) to find limits for \( p \) at \( x \pm D_x \), where \( D_x \) is a fixed proportion of the mean. Both sampling plans were developed only for mobile stages of predator and prey.

**RESULTS**

**Temporal changes in prey and predator densities**

Figure 1c shows quite large differences in the abundance of *M. tanajoa* and *T. aripu* between the two fields with lower densities at Houègbo than at Sè. It also shows variation among sampling dates. For each field and each sampling date, variation of predator and prey densities among blocks, among plants (within-blocks), and among leaf nodes (within plant), and the proportion of variability explained by each of these components are presented in Table 1. For *M. tanajoa*, each of these components had significant effects in both field sites except for the August samples at Houègbo where blocks had no effects on spatial distribution of *M. tanajoa*. At the Houègbo field site, among-block differences (within-field heterogeneity) explained 0 to 11.5% of spatial variation in total *M. tanajoa* densities. Among-plant (within-block) differences explained 8.6 to 29.9% of variation, while among-leaf-node differences explained 60 to 91% of variation. At the Sè field site where among-block differences explained 0.8 to 2.7% of variation in densities of *M. tanajoa* (eggs + mobiles), among-plant differences explained 1.3 to 8.8% while among-leaf-node differences explained 89 to 96% of spatial variation in densities of *M. tanajoa*.

For *T. aripu*, among-leaf-node differences explained nearly 100% of the spatial variation in predator densities at both field sites; whereas among-block and among-plant differences added very little to the spatial variability in predator densities, as the predator is restricted to the apex during the day.

Total densities of *M. tanajoa* (eggs + mobile stages) ranged from 0.7 to 21.7 and from 1.0 to 100.5 individuals on the first fully developed leaf at Houègbo and Sè, respectively. Densities of *M. tanajoa* were significantly higher in the field site at Sè than in the field site at Houègbo \((P < 0.001)\). *Mononychellus tanajoa* was rarely found in cassava apices. Changes in population size of *M. tanajoa* were closely related to rainfall pattern. Within the sampling
Table 1 Results from nested ANOVA of *M. tanajoa* and *T. aripo* densities in relation to blocks, plants and leaf node within cassava plants

<table>
<thead>
<tr>
<th>Date</th>
<th>Field</th>
<th>Among total <em>M. tanajoa</em></th>
<th>Among mobile <em>M. tanajoa</em></th>
<th>Among total <em>T. aripo</em></th>
<th>Among mobile <em>T. aripo</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>P</em> value</td>
<td><em>P</em> value</td>
<td><em>P</em> value</td>
<td><em>P</em> value</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Among blocks</td>
<td>Among plants</td>
<td>Among leaf node</td>
<td>Among blocks</td>
</tr>
<tr>
<td>Aug</td>
<td>Hou</td>
<td>0.1624</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.1286</td>
</tr>
<tr>
<td></td>
<td>Sè</td>
<td>0.0359</td>
<td>0.0004</td>
<td>0.0001</td>
<td>0.0338</td>
</tr>
<tr>
<td>Nov</td>
<td>Hou</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Sè</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
</tr>
<tr>
<td>Jan</td>
<td>Hou</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Sè</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
</tr>
<tr>
<td>May</td>
<td>Hou</td>
<td>0.0006</td>
<td>0.0002</td>
<td>0.0001</td>
<td>0.0000</td>
</tr>
<tr>
<td></td>
<td>Sè</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

Proportion of variation explained

<table>
<thead>
<tr>
<th>Date</th>
<th>Field</th>
<th>Among total <em>M. tanajoa</em></th>
<th>Among mobile <em>M. tanajoa</em></th>
<th>Among total <em>T. aripo</em></th>
<th>Among mobile <em>T. aripo</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>P</em> value</td>
<td><em>P</em> value</td>
<td><em>P</em> value</td>
<td><em>P</em> value</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Among blocks</td>
<td>Among plants</td>
<td>Among leaf node</td>
<td>Among blocks</td>
</tr>
<tr>
<td>Aug</td>
<td>Hou</td>
<td>0.0000</td>
<td>0.0864</td>
<td>0.9136</td>
<td>0.0000</td>
</tr>
<tr>
<td></td>
<td>Sè</td>
<td>0.0089</td>
<td>0.0851</td>
<td>0.9069</td>
<td>0.0139</td>
</tr>
<tr>
<td>Nov</td>
<td>Hou</td>
<td>0.1151</td>
<td>0.2894</td>
<td>0.5955</td>
<td>0.0953</td>
</tr>
<tr>
<td></td>
<td>Sè</td>
<td>0.0269</td>
<td>0.0130</td>
<td>0.9610</td>
<td>0.0302</td>
</tr>
<tr>
<td>Jan</td>
<td>Hou</td>
<td>0.0222</td>
<td>0.1701</td>
<td>0.3777</td>
<td>0.0582</td>
</tr>
<tr>
<td></td>
<td>Sè</td>
<td>0.0200</td>
<td>0.0879</td>
<td>0.8921</td>
<td>0.0292</td>
</tr>
<tr>
<td>May</td>
<td>Hou</td>
<td>0.0887</td>
<td>0.2991</td>
<td>0.6449</td>
<td>0.0510</td>
</tr>
<tr>
<td></td>
<td>Sè</td>
<td>0.0080</td>
<td>0.0146</td>
<td>0.9859</td>
<td>0.0224</td>
</tr>
</tbody>
</table>

for blocks df = 3; for plants df = 56; and for nodes, df = 75

* Hou = Houegbo

During periods of high rainfall, densities of *M. tanajoa* remained generally low. This pattern was especially observed in the field site at Houegbo. Fluctuations in *M. tanajoa* densities appeared to be more influenced by frequency of rainfall than total monthly rainfall. The coefficients of the regression between mean monthly *M. tanajoa* densities and rain data were $r^2 = 0.028$ (slope = 0.51, $P = 0.456$) for rainfall amounts and $r^2 = 0.24$ (slope = -3.91, $P = 0.02$) for rainfall frequency (i.e., number of days with rain).
Figure 1 Rainfall pattern in the field sites at Houègbo (a) and Sè (b); seasonal pattern for all stages of *M. tanajoa* on first fully developed leaves (FDL) and mobile stages of *T. aripo* in apex in the field site at Houègbo (c) and Sè (d). Means ± standard errors were plotted. Number on top of bar indicates number of days with rain during the month.

There were also significant differences in *T. aripo* densities between the two field sites (*P* < 0.001). Contrary to *M. tanajoa* densities, there are significantly more *T. aripo* in the field site at Houègbo than at Sè. In both field sites, fluctuations of *T. aripo* densities in the apices followed the same trend as *M. tanajoa* (Figure 1c, d). However, densities of the predatory mite were not correlated to rainfall pattern (*r*² = 0.13, slope = -0.35, *P* = 0.11 and *r*² = 0.07, slope = -0.69, *P* = 0.22, for monthly rainfall amount and number of days with rain, respectively). At Houègbo, average numbers of mobile stages ranged from 4.6 to 30.8 individuals per apex. The peak density was observed in January 1999 together with the second peak of *M. tanajoa*. At Sè and during the same period, predator numbers ranged from 0.23 to 31.95 individuals per apex. The highest *T. aripo* densities were observed in November 1998 when *M. tanajoa* densities were also highest, following a decline in rainfall intensity. However, a second peak in *T. aripo* density occurred in June 1999 as predator populations were increasing while prey density had dropped. During periods of abundant rainfall, predator densities remained low. Figure 1c, d shows that fluctuations in *T. aripo* and *M. tanajoa* numbers follow the predator–prey oscillations observed by Nachman (1981) and many others.
**Figure 2** Within-plant distribution of *M. tanajoa* on cassava plants; (a) at the Houègbô field site, and (b) at the Sè field site.

<table>
<thead>
<tr>
<th>Node position</th>
<th>August</th>
<th>November</th>
<th>January</th>
<th>May</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apex</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L16</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L20</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Number per node position
Table 2 Results of ANOVA (PROC GLM, SAS, 1999) on the within-plant distribution of *M. tanajoa* on cassava across leaf node. Means were separated using Student-Newman-Keuls multiple range test. In a column, means with the same letter are not significantly different (*p* < 0.05)

<table>
<thead>
<tr>
<th>Date</th>
<th>Leaf node</th>
<th>Houëgbô</th>
<th>Mobiles</th>
<th>Eggs + Mobiles</th>
<th>Sé</th>
<th>Mobiles</th>
<th>Eggs + Mobiles</th>
</tr>
</thead>
<tbody>
<tr>
<td>August</td>
<td>L2-L4</td>
<td>0.092b</td>
<td>1.22b</td>
<td>1.22a</td>
<td>1.57a</td>
<td>1.22b</td>
<td>1.57b</td>
</tr>
<tr>
<td></td>
<td>L6-L8</td>
<td>1.31a</td>
<td>1.67a</td>
<td>1.13a</td>
<td>1.39b</td>
<td>1.64a</td>
<td>2.05a</td>
</tr>
<tr>
<td></td>
<td>L10-L12</td>
<td>1.25a</td>
<td>1.52a</td>
<td>0.69b</td>
<td>0.87c</td>
<td>1.65a</td>
<td>2.06a</td>
</tr>
<tr>
<td></td>
<td>L14-L16</td>
<td>0.71c</td>
<td>0.87c</td>
<td>0.25c</td>
<td>0.28d</td>
<td>1.38b</td>
<td>1.72b</td>
</tr>
<tr>
<td></td>
<td>L18-L20</td>
<td>0.35d</td>
<td>0.45d</td>
<td>0.08d</td>
<td>0.09e</td>
<td></td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>L2-L4</td>
<td>0.28b</td>
<td>0.38b</td>
<td>0.52c</td>
<td>0.66c</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L6-L8</td>
<td>0.58a</td>
<td>0.80a</td>
<td>1.34b</td>
<td>1.73b</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L10-L12</td>
<td>0.77a</td>
<td>1.02a</td>
<td>1.64a</td>
<td>2.05a</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L14-L16</td>
<td>0.77a</td>
<td>1.04a</td>
<td>1.65a</td>
<td>2.06a</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L18-L20</td>
<td>0.58a</td>
<td>0.79a</td>
<td>1.38b</td>
<td>1.72b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>January</td>
<td>L2-L4</td>
<td>0.50c</td>
<td>0.72bc</td>
<td>1.22b</td>
<td>1.57b</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L6-L8</td>
<td>0.99a</td>
<td>1.28a</td>
<td>1.55a</td>
<td>1.88a</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L10-L12</td>
<td>1.00a</td>
<td>1.26a</td>
<td>1.33b</td>
<td>1.68a</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>L14-L16</td>
<td>0.73b</td>
<td>0.91b</td>
<td>1.01c</td>
<td>1.27c</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L18-L20</td>
<td>0.38c</td>
<td>0.49c</td>
<td>0.61d</td>
<td>0.76d</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>L2-L4</td>
<td>0.18b</td>
<td>0.24b</td>
<td>0.65c</td>
<td>0.78b</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L6-L8</td>
<td>0.45a</td>
<td>0.62a</td>
<td>1.44b</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L10-L12</td>
<td>0.51a</td>
<td>0.69a</td>
<td>1.62a</td>
<td>1.95a</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L14-L16</td>
<td>0.47a</td>
<td>0.62a</td>
<td>1.68a</td>
<td>1.97a</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L18-L20</td>
<td>0.16b</td>
<td>0.21b</td>
<td>1.55ab</td>
<td>1.82a</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Within-plant distribution of *M. tanajoa* and *T. aripo*

Figure 2 shows that within cassava plants, *M. tanajoa* densities increased from the apex down to lower leaves, reached a peak between nodes 6 and 12, then decreased towards the lower part of the foliage. Apart from August and November census data in Sé (Figure 2b), where the highest *M. tanajoa* densities were encountered on leaf 2-4 (August) and leaf 14 (November), peak densities of *M. tanajoa* (across all sampling dates) were found on leaf 6 to leaf 12, corresponding to strata 2 and 3 (Table 2). This distribution pattern remained the same when we considered eggs only or mobile stages only. Overall, leaf 2-4 and leaf 18-20 were statistically similar and harboured the lowest *M. tanajoa* densities, while leaf 14-16
harboured moderate mite densities.

Within-plant distribution of *T. aripo* revealed that 97.3% of mobile stages (and all eggs) of the predator were confined to the apices, as *T. aripo* resides in the apex during the day and forages on the foliage of cassava plants during night hours (Onzo et al., 2003).

**Aggregation indices**

Since *M. tanajoa* densities were similar and highest on leaf 6 up to leaf 12 (Table 2), the sampling unit for monitoring *M. tanajoa* populations in the field was chosen to be either of the nearest neighbour leaves in each of the two strata (*i.e.* leaf 8 and leaf 10). Mean *M. tanajoa* densities on these leaves were used in calculating Taylor's aggregation coefficients for between-plant distribution of *M. tanajoa*. Both of Taylor's *a* and *b* coefficients are required for developing the sampling plans.

Within-plant distribution of *T. aripo* was strongly concentrated in the apex; therefore, densities of the predator in the apex were used to calculate Taylor's parameters. Table 3 presents values of Taylor's parameters for both predator and prey. Overall, Taylor's coefficients are *a* = 3.22, *b* = 1.45 for *M. tanajoa*, and *a* = 4.44, *b* = 1.12 for *T. aripo*. For mobile *M. tanajoa* encountered on the first fully developed leaves, Taylor's coefficients were *a* = 2.86, *b* = 1.58. These aggregation coefficients indicated a clumped spatial distribution of *M. tanajoa* and *T. aripo* at both field sites as *b* values were larger than 1. However, the distribution of the predator was less aggregated than that of the prey, as the indices were lower for *T. aripo* than for *M. tanajoa*.

**Table 3** Taylor's aggregation indices for mobile stages of *M. tanajoa* on leaf 8-10 and *T. aripo* in apices of cassava plants

<table>
<thead>
<tr>
<th>Location</th>
<th>M. tanajoa</th>
<th></th>
<th></th>
<th></th>
<th>T. aripo</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Intercept ± SEM</td>
<td>Slope ± SEM</td>
<td><em>r</em>&lt;sup&gt;2&lt;/sup&gt;</td>
<td>n</td>
<td>Intercept ± SEM</td>
<td>Slope ± SEM</td>
</tr>
<tr>
<td>Houegbo</td>
<td>16</td>
<td>0.97 ± 0.35</td>
<td>1.62 ± 0.16</td>
<td>0.88</td>
<td>16</td>
<td>0.44 ± 0.47</td>
<td>1.31 ± 0.20</td>
</tr>
<tr>
<td>Sc</td>
<td>16</td>
<td>1.37 ± 0.84</td>
<td>1.33 ± 0.30</td>
<td>0.58</td>
<td>16</td>
<td>2.07 ± 0.30</td>
<td>1.14 ± 0.13</td>
</tr>
<tr>
<td>All</td>
<td>32</td>
<td>1.17 ± 0.34</td>
<td>1.45 ± 0.14</td>
<td>0.79</td>
<td>32</td>
<td>1.49 ± 0.38</td>
<td>1.12 ± 0.16</td>
</tr>
</tbody>
</table>

Intercepts are in **a**, coefficients are calculated with Proc Reg statement (SAS Inst., 1999). Back transformed **a**-values for Taylor's indices are as follows:

<table>
<thead>
<tr>
<th></th>
<th>for M. tanajoa</th>
<th>for T. aripo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Houegbo</td>
<td>2.64</td>
<td>1.55</td>
</tr>
<tr>
<td>Sc</td>
<td>3.94</td>
<td>7.92</td>
</tr>
<tr>
<td>All</td>
<td>3.22</td>
<td>4.44</td>
</tr>
</tbody>
</table>
Figure 3 Observed values and expected regression lines (Wilson and Room, 1983) relating, for both field sites together: (a) the proportion of infested cassava leaves (leaf 8-10) to mean numbers of *M. tanajoa* (mobile stages) on the same category of leaves, and (b) the proportion of infested cassava apices to mean numbers of *T. aripo* (mobile stages) per apex.

**Mean-incidence analysis (Wilson and Room model)**

Figure 3a shows the proportion of *M. tanajoa* infested leaves as a function of mean density \( \bar{x} \) of mobile stages of the herbivore on leaf 8 and 10, and the \( P(I) - x \) relationship calculated with equation (2) and the corresponding Taylor's parameters. Figure 3b shows the proportion of *T. aripo* infested apices as a function of mean density \( \bar{x} \) for mobile
stages of the predator per apex and the $P(I)$-x relationship calculated with equation (2) and the corresponding Taylor’s parameters. The regression of the expected $P(I)$ values against the observed values, resulted in a coefficient $r^2 = 0.59$ for $M. tanajoa$ which is also very near to the regression coefficient forced through the origin. For $T. aripo$ the regression coefficient was $r^2 = 0.53$, and $r^2 = 0.41$ when forced through the origin. The model indicated that the proportion of infested leaves become close to 90% when mean $M. tanajoa$ density reached 34 mobile stages per leaf. For $T. aripo$, it indicated that the proportion of predator-occupied apices become close to 90% when the mean $T. aripo$ density reached 13 mobile stages per apex.

Figure 4 Fluctuation of mean densities and percentages of mite-infested plants through sampling dates: (a) for $M. tanajoa$ on cassava leaf, and (b) for $T. aripo$ in apex of cassava plants
Temporal and spatial dynamics of an exotic predator and its herbivorous prey on cassava

![Graphs showing enumerative and binomial sampling plans for M. tanajoa in Africa.](image)

**Figure 5** Enumerative and binomial sampling plans for *M. tanajoa* in Africa

Plots of mean densities of *M. tanajoa* per leaf and percentages of *M. tanajoa*-infested plants against sampling periods (presented for the field site at Sè only) show that proportion of *M. tanajoa*-infested plants never reached unity even when densities of *M. tanajoa* were highest (Figure 4a). On the other hand, plots of mean densities of *T. aripo* per apex and percentages of *T. aripo*-infested plants (also for the field site at Sè; Figure 4b), show that the proportion of *T. aripo*-infested plants increases rapidly with relatively low mean *T. aripo* densities per apex.

**Sampling programs for *M. tanajoa* and *T. aripo***

Figure 2 shows that in the presence of the predator, the highest densities of *M. tanajoa* were found on leaves 6 to 12. Therefore, we recommend choosing either of leaves 8 to 10 as the sampling unit for *M. tanajoa*. For *T. aripo*, the apex should be chosen as the most
adequate sampling unit for assessing *T. aripo* populations in cassava fields, as 97.3% of the predators were found in the apices of cassava plants during the daylight hours. This sampling scheme is obviously developed for population monitoring during the daylight hours.

Enumerative sampling plans for *M. tanajoa* and *T. aripo* for two precision levels are presented in Figures 5a and 6a, respectively. For a mean density of 10 mobile stages of *M. tanajoa* on leaf 8-10, 450 and 200 cassava leaves are needed to achieve the precision levels of 0.2 and 0.3, respectively. For a mean density of 30 mobile stages of *M. tanajoa*, optimal sample sizes should be 65 and 30 leaves for the precision levels of 0.2 and 0.3, respectively. Sample size of 190 and 85 apices of cassava plants were recommended to estimate densities of *T. aripo* at the precision levels of 0.2 and 0.3, respectively, when mean density of the predator is 2.5 mobile stages per apex. With a mean density of one mobile *T. aripo* per apex, optimal sample sizes should be 426 and 190 apices for the precision levels of 0.2 and 0.3, respectively.

![Graph](image)

**Figure 6** Enumerative and binomial sampling plans for *T. aripo* in Africa
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The binomial sampling plans with the same precision levels are presented in Figure 5b for M. tanajoa and Figure 6b for T. aripo. For a mean M. tanajoa density of 10 mobile stages on leaf 8-10, the optimal sample sizes should be 11 and 8 leaves, respectively when precision levels of 0.2 and 0.3 were chosen. With a mean M. tanajoa density of 5 mobile stages on leaf 8-10, optimal sample sizes should be 31 and 23 leaves for precision levels of 0.2 and 0.3, respectively. For T. aripo, optimal sample size when mean density is 3 mobile stages per apex should be 180 and 95, respectively with precision levels of 0.2 and 0.3. With a mean T. aripo density of 5 mobile stages per apex, optimal sample sizes should be 42 and 23 apices of cassava plants for precision levels of 0.2 and 0.3 respectively.

DISCUSSION

Population dynamics and spatial distribution of M. tanajoa and T. aripo

Overall patterns of changes in population densities of M. tanajoa in cassava fields did not change after establishment of T. aripo as its population fluctuations followed seasonal rainfall patterns, similar to the period before T. aripo establishment in Benin. As shown in Figure 1, the highest densities of M. tanajoa occurred when rain intensity and frequency had dropped. A second but minor peak occurred soon after rains had resumed after the long dry season. These patterns are identical to those described by Yaminek et al. (1989a) in the absence of effective biological control agents. However, peak densities have decreased considerably as a result of the establishment of T. aripo, an effective predator of M. tanajoa. This reduction in peak density is also supported by long-term observations of M. tanajoa and T. aripo population dynamics in Benin (Hanna et al., in preparation). The data presented in the present study also clearly shows that the establishment of T. aripo has resulted in significant changes in within-plant distribution of M. tanajoa, as compared to earlier data (Yaminek et al., 1991). Indeed, a relative decrease in M. tanajoa densities was observed on upper leaves compared to leaves in the middle of the canopy. The most pronounced change in M. tanajoa distribution is the complete absence of this herbivorous plant from the apex of the cassava plant in the presence of T. aripo, as opposed to its abundant presence in the absence of T. aripo. The observed change in within-plant distribution of M. tanajoa is evidently caused by the presence of T. aripo which resides in the apex during daylight hours and limits its foraging bouts to young leaves in the upper strata of the canopy during night hours (Onzo et al., 2003). Likewise, through volatile infochemicals, M. tanajoa might avoid feeding and ovipositing in patches frequently visited by the predator (Magalhães et al., 2002; Onzo et al., 2003). Such behaviour was also reported for Tetrauchus urticae Koch (Tetranychid) and its predator Phytoseiulus persimilis Athias-Henriot (Phytoseiidae), on lima bean, Phaseolus lunatus L. (Grosal and Dicke, 1999; Pallini et al., 1999). Our results also show significant among-plant differences in M. tanajoa densities (Table 1). A noticeable reduction in the aggregation of M. tanajoa has also
occurred after introduction of the predator, as shown by our estimate of Taylor’s $b$
coefficient 1.45 and 1.58 on leaves 8 and 10 and the first fully developed leaf, respectively,
compared with the value of 1.69 for the first fully developed leaves reported by Yaninek et
al. (1991) in the absence of effective biological control agents. Reduced $M. tanajoa$
aggregation in the presence of predatory mites was also reported for $M. tanajoa$ in the
presence of Amblyseius limonicus Garman & McGregor, an effective predator of $M. tanajoa$
on cassava in Colombia (Braun et al., 1989). Other studies (e.g., Wilson et al., 1984) have
also reported differences in aggregation patterns for spider mites in the presence of
effective phytoseiid predators.

Neither rainfall intensity (monthly rainfall amount) or rainfall frequency (number of
days with rain) significantly affected densities of $T. aripo$ in the apex, while $M. tanajoa$
densities were negatively affected only by rainfall frequency. The relative lack of rainfall-
induced mortality of $T. aripo$ is most likely due to the shelter effect of the cassava apex, as
opposed to the lack of shelter for $M. tanajoa$ on cassava leaf surfaces which are mostly
glabrous and lack any form of domatia (R. Hanna, unpublished data). Fluctuations of $T.$
$aripo$ populations followed those of their prey $M. tanajoa$, as is common in many predator-
prey systems, peaking at the end of the rainy season or at the onset of the rainy season, in
response to increasing $M. tanajoa$ densities during those two seasonal changes in climate.
The cycles in $T. aripo$ and $M. tanajoa$ populations are extensively explained by Hanna et al.
(in preparation), using time series analysis (see Lingeman and van de Klashorst, 1992; van
de Klashorst et al., 1992; Janssen et al., 1997).

Taylor’s power law coefficients indicated that the distribution of $T. aripo$ is only
slightly clumped. The lower aggregation pattern of the predator compared with that of the
prey is also shown by the smaller $P(l)$ for $M. tanajoa$ than $T. aripo$ (Figure 3). The more
aggregated a species is, the smaller is the proportion of mite-occupied sampling units for a
given mean density (Wilson, 1982; Schulthess et al., 1991; Sétaoun et al., 2000). The lower
aggregation of $T. aripo$ could be explained by its high capacity of dispersal within and
among cassava fields (Yaninek and Hanna, 2003). The high proportion of $T. aripo$-infested
plants reached at relatively low $T. aripo$ densities (Figure 4b) supports this explanation.

The within-plant distribution of $T. aripo$ revealed that the predator is almost
exclusively confined to the apices, justifying the choice of the apex as a sampling unit for
monitoring the population of the predator in the field. However, this high concentration
of $T. aripo$ in the apices depended strictly on the time of the day when samples were taken.
It was shown in another study that within-plant distribution of $T. aripo$ follows a diurnal
pattern (Onzio et al., 2003). The predator concentrated in the apices only between 08:00
hours and 16:00 hours and moved to cassava leaves during night hours.

Sampling $M. tanajoa$ and $T. aripo$ in cassava fields
Within-plant distribution of $M. tanajoa$ (Figure 2) showed that the first fully developed leaf
(FDL) should no longer be considered the optimal sampling unit for estimating $M. tanajoa$
Temporal and spatial dynamics of an exotic predator and its herbivorous prey on cassava

densities, once *T. aripo* is established. The highest *M. tanajoa* densities are now found below the first fully developed leaf, necessitating the development of a new sampling strategy for *M. tanajoa* in Africa, at least for areas where *T. aripo* is established. In the presence of *T. aripo*, we recommend the selection of any leaf between leaf 8 and leaf 10. However, in circumstances when fewer leaves are found on cassava plants (e.g. dry season, diseased or too old cassava), the position of this sampling unit could be raised upward, not going beyond leaf 6. Because of the high number of sampling units required and the labour involved in an accurate and reliable mite count, enumerative sampling should be used only when mean *M. tanajoa* densities exceed 10 mobile stages per sampling unit, whereas binomial sampling should be used for *M. tanajoa* densities below 10 mobile stages per leaf, as above this value the percentage of infested plants becomes very close to 100%, which would lead to underestimation or overestimation of *M. tanajoa* densities with the binomial sampling.

The enumerative sampling plan proposed for *T. aripo* indicated that nearly 200 apices are needed to obtain a precision level of 0.2 when the mean density is about 2.5 mobile *T. aripo* per apex. In a cassava field, especially in a smallholder’s field, this number is too high since enumerative sampling of *T. aripo* would lead to extensive removal of apices, which is quite destructive in small fields. Enumerative sampling should not be used when mean density is lower than 5 mobile *T. aripo* per apex. The binomial sampling procedure, based on presence-absence of *T. aripo* in the apices, is practically relevant since it is a non-destructive sampling procedure, and it is cost efficient compared to the enumerative sampling procedure (Zalom et al., 1984; Schultess et al., 1989, Boavida et al., 1992). The binomial sampling procedure is particularly adequate for young cassava fields where density and frequency of the predator are still relatively low. Binomial sampling requires less equipment (just an optical glass binocular magnifier) and saves considerable time while conserving predator populations in the field. However, binomial sampling is not feasible at greater than 80% infestation levels because estimates above this level become inaccurate. To take advantage of both sampling methods, we suggest a rational combination of the enumerative and the binomial sampling plans while monitoring *T. aripo* populations in cassava fields. Binomial sampling should be used when densities are low and proportion of infested plants is less than 0.8. The enumerative sampling should be used when the mean density of the predator reaches 5 mobile stages per apex or when proportion of *T. aripo* infested plants exceeds 0.8.

Caution should be exercised when using any of these proposed sampling plans because they are developed on a cassava variety that is very suitable for the predator. In fact, it is now well known that plant (especially apical) characteristics are of great importance for the dynamics of *T. aripo* (Hanna et al., 2000), and that the abundance of *T. aripo* on the plant will determine the within-plant distribution and the aggregation pattern of *M. tanajoa*. Thus, the sampling rule developed here may not apply equally well for all cassava varieties. In addition, variation in climatic conditions between ecological zones
may introduce changes in the sampling plans as proposed here, therefore, corrections might turn out to be necessary.

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Chapter 2

Ercol. 10: 378-382.


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