Population dynamics of cassava green mite and its predator, Typhlodromalus aripo in Benin, West Africa
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Citation for published version (APA):
Onzo, A. (2003). Population dynamics of cassava green mite and its predator, Typhlodromalus aripo in Benin, West Africa Amsterdam: IBED, Universiteit van Amsterdam

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Download date: 07 Dec 2018
Interactions between two neotropical phytoseiid predators on cassava plants and consequences for biological control of a shared spider mite prey – a screenhouse evaluation

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The issue of introducing single or multiple natural enemy species for classical biological control has been an area of intense inquiry by ecologists and biological control practitioners. This is particularly relevant to classical biological control of cassava green mite *Mononychellus tanajoa* (Bondar) (Tetranychidae) in Africa, as this pest mite is shared by several natural enemies in the Neotropics (its area of origin), two of which have been introduced and established widely in Africa. We conducted two screenhouse experiments using the two neotropical phytoseiid predatory mites, *Typhlodromalus aripo* DeLeon and *Typhlodromalus manihoti* Moraes, to determine the effects of single and two-predator species on population dynamics of the two predators and on suppression of *M. tanajoa* populations. The two predators are thought to be complementary in their impact on their shared prey *M. tanajoa*, due to similarities in their preference for this prey and to differences in their spatial distribution and foraging activities on cassava. The two predator species were released alone or together at low and at high initial densities of *M. tanajoa*. In all cases, predator releases resulted in significant suppression of *M. tanajoa*, but the degree of suppression did not differ among single and two-species releases with one exception: at high initial density of *M. tanajoa*, releases of *T. aripo* alone had less impact than that of either *T. manihoti* alone or of the two species together. *Typhlodromalus aripo* also appeared to be inferior as a competitor of *T. manihoti*; at low initial density of *M. tanajoa*, the proportion of *T. aripo* in the two-predator release treatments gradually declined and was strikingly lower than in the single species release, probably due to intraguild predation on its larvae by *T. manihoti*. However, *T. aripo* persisted longer than *T. manihoti* after elimination of *M. tanajoa*. On the basis of this study under semi-natural conditions, it appears that either species is sufficient for controlling *M. tanajoa* populations, with *T. manihoti* being more efficient at high initial prey densities and *T. aripo* at low initial prey densities. At high prey density, *T. manihoti* increased to large numbers and outcompeted *T. aripo*. Relevance of these
findings to larger spatial scale and under natural conditions is discussed.

**Key words** Acari, Phytoseiidae, *Mononychellus tanajoa*, *Typhlodromalus arpo*, *Typhlodromalus manihoti*, cassava green mite, interspecific competition, intraguild predation

Most arthropod species are attacked by two or more natural enemy species (Briggs, 1993). Understanding the effects of multiple natural enemy species on prey/host populations is particularly important in biological control of agricultural pests. Most studies on natural enemy-prey interactions evaluate the effects of one natural enemy species on abundance of one prey species, in isolation from the effects of other predator species (Schaußberger and Walzer, 2001). Such simple communities are rare under natural conditions, where prey species are often attacked by two or more natural enemy species that can also interact directly or indirectly (through the shared prey) often resulting in pronounced effects on prey and natural enemy population dynamics. Multiple natural enemy species can cause interactions in populations and communities of predators and prey in many ways. For example, they may interfere through intraguild predation (Polis et al., 1989; Rosenheim, 2001), or they may reduce or increase predation risk for the prey (Sih et al., 1998), and this may increase or decrease the equilibrium level of the prey (Hochberg, 1996; Losey and Denno, 1998). With respect to long-term biological control, the question of using single vs. multiple natural enemy species, therefore, remains controversial (Kakehashi et al., 1984; Briggs, 1993; McEvoy and Goombs, 1999). The varied effects of using multiple predator species are reflected in the opinion of ecologists and biocontrol researchers; some favour the use of one natural enemy species (e.g., Myers, 1985; Spiller, 1986; Rosenheim et al., 1993), but others favor the use of multiple natural enemy species as long as they act in a complementary fashion (e.g., Heinz and Nelson, 1996; Ricchert and Lawrence, 1997; Losey and Denno, 1998).

The acarine predator-prey community comprised of cassava green mite, *Mononychellus tanajoa* (Bondar) (Acar: Tetranychidae) and two neotropical phytoseiid predators on cassava in Africa is a suitable system to determine the consequences of interactions among natural enemy species on suppression of populations of a shared pest and the persistence of such predator-prey systems. Three characteristics make this system ideal for testing the effects of one or two natural enemy species on a shared pest. First, *M. tanajoa* has numerous natural enemies in the Neotropics, its area of origin (Bellem et al., 1987; Morac et al., 1990), but in Africa, the main natural enemies are two predatory mite species *Typhlodromalus manihoti* Morac and *T. arpo* DeLeon, which were introduced into Africa from the Neotropics. Second, although both predator species can feed on a variety of food sources, their preferred prey is *M. tanajoa* (Bakker, 1993; Guanvossou et al., 2003b). Laboratory experiments also showed that adult females of one species could feed on larvae of the other species (R. Hanna and A. Onzo, unpublished data). The two predators are
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Therefore potential competitors through the shared prey, and through intraguild predation. Moreover, the two predator species may also act in a complementary fashion because they occupy different niches on the plant. *Typhlodromus manihoti* inhabits and forages on cassava leaves (Yaninek *et al.*, 1998; Bonato *et al.*, 1999), while *T. aripo* inhabits the apex of cassava plants but forages on cassava leaves during the night (Onzo *et al.*, 2003). The two predators may in this way 'sandwich' the pest population; with the two predator species attacking from both sides, the prey has less chance of escaping through within-plant movement, a phenomenon shown to occur in response to each of both predator species alone (Magalhães *et al.*, 2002; Onzo *et al.*, 2003). Third, as the two predator species can now be found together in cassava fields in some countries in Africa and efforts are continuing to introduce them into other countries (Yaninek *et al.*, 1998; Hanna and Toko, 2001; Yaninek and Hanna, 2003), there is an urgent need to determine the relative contribution of each predator species to biological control of *M. tanagro* in the short and long term.

The aim of the present study is to determine the effects of all these potential intraguild interactions between the two predator species on the dynamics of *M. tanagro* and the predators by (1) measuring the impact of each predator species on *M. tanagro* densities in single and combined predator species systems, (2) evaluating the impact of the presence of heterospecifics on the persistence of each predator species, and (3) evaluating the consequences of multiple natural enemy species on the persistence of the predator-prey system. To exclude the influence of enemies other than the two species of predatory mites and to enable quantitative assessment of the impact on their own populations as well as on those of the prey, the experiments were carried out on small groups of plants in a screenhouse. The outcome of these semi-field studies should serve as basis for investigating multi-species interactions at larger spatial scales in cassava fields and for evaluating the need for further introductions of natural enemies for the biological control of *M. tanagro* in Africa.

**MATERIAL AND METHODS**

**Experimental design**

Two experiments were conducted on potted cassava plants in a screenhouse to test the effects of single and two-predator species releases on *M. tanagro* populations. The screenhouse was 24 m long, 8.5 m wide and 5 m high, with the canopy in Teflon, and the sides covered with 32x32 Amber screen. The screenhouse was equipped on one side with an electric fan and on the opposite side with a window that automatically opens when the fan is turned-on. The fan was generally turned-on during the middle part of the day (*i.e.* from around 12:00 hours to 16:00 hours), to cool the screenhouse before inside temperature exceeded 38°C. In the first experiment predators were released at high initial *M. tanagro* densities while in the second experiment the predators were released at low
initial *M. tanajoa* densities. The two experiments were conducted at the Biological Control Centre for Africa, International Institute of Tropical Agriculture, located in Cotonou, Benin, from 10 May to 2 August 2000 and from 29 September to 9 December 2000, for the first and second experiments, respectively. Both experiments were identical in all other aspects, except for slight differences in temperature and humidity.

Cassava cuttings (20 cm long) of the variety 'Agric' were planted singly in plastic pots (14 cm diameter at the base, 20 cm at the top and 17.5 cm high), filled with c. 3.8 kg of topsoil collected from a field fallowed for more than four years. Potted plants were transferred to the greenhouse within 48 hours of planting and placed on 350x180x76 cm (LxWxH) iron benches that were arranged at 65 cm apart. Thirty plants (or 50% of the total number of plants in each of five treatments, for a total of two benches per treatment) were distributed evenly on top of each of the 10 benches. Treatments were randomly assigned to benches, which were kept apart to minimize among-treatment movements of predators and prey. Where needed, plants were thinned to one stem per cutting two weeks after planting. All plants were infested with *M. tanajoa* two weeks later (*i.e.* 4 weeks after planting) by placing 10 or 20 *M. tanajoa* adult females (for low or high initial prey densities experiments, respectively) on the youngest leaf of each cassava plant. Adult *M. tanajoa* females used in the experiments were collected from a culture that was initiated from field-collected mites maintained on potted cassava in a greenhouse for one to three weeks before they were used in the experiments. Temperature inside the greenhouse ranged from 23°C to 37°C with relative humidity varying between 42% and 85% for the first experiment, and 25°C to 38°C and relative humidity from 40% to 78% in the second experiment.

Each of the two experiments consisted of five treatments which were set up as follows: 1) release of 6 adult female *T. aripo*, 2) release of 6 adult female *T. manihoti*, 3) release of 3 adult female *T. aripo* plus 3 adult female *T. manihoti*; 4) release of 6 adult female *T. aripo* plus 6 adult female *T. manihoti*; and 5) a control that remained free of predatory mites. *Typhlodromalus aripo* used for the experiments was collected from farmer's fields the day before the release, while *T. manihoti* was also collected from farmers' fields but because of their low number in the field, they were first reared at ITA Benin Station for 8 weeks before being used. The appropriate number of predators for each plant in each treatment was aspirated into plastic microtubes that were then attached to the plants by means of a cotton thread. The micro-tubes were then opened on both sides to allow predators to move onto the cassava plants. Predators were released one week after infestation of plants with *M. tanajoa* in the low initial prey density experiment, and after two weeks in the high initial prey density experiment.

Five plants per treatment were selected for estimating *M. tanajoa* and predator abundance prior to predator release and at five-day intervals thereafter. Eggs and active stages (larvae, nymphs and adults) of *M. tanajoa* and predatory mites in the apex and on all the leaves from each plant were counted in the laboratory with the aid of a binocular
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Microscope. All active stages of predatory mites were collected and identified to species. Voucher specimens are kept at IITA's Biodiversity Centre in Ibadan, Benin.

Statistical analyses

Monoichiens (eggs + actives) and predatory mite (actives) densities were summed on a per plant basis. Averages and standard errors were calculated from the log-transformed sums per plant and plotted against sampling dates. A Mixed Model ANOVA (Proc Mixed, SAS Institute, 1999) with repeated statement (Littell et al., 2000) was used to determine the effect of treatment (i.e., predator release) and date of sampling on changes in population sizes of M. tanajoa, T. manihoti and T. aripo. In the Mixed Model, predator release and date were the fixed effect factors, while plant (nested within predator release) was the random effect factor, and plot (i.e. a group of plants with the same predator release) was the subject (repeated) factor. Treatment effects on prey and predator densities were compared pair-wise using pre-planned orthogonal contrasts. Within-date treatment effects on prey and predator densities were compared with ANOVA (PROC GLM, SAS Institute 1999) stratified by sampling date. Treatment pairs were compared with Student-Newman-Keuls (SNK) multiple range test, only where ANOVAs showed a significant treatment effect (P < 0.05). All statistical analyses were carried out for total densities of M. tanajoa (eggs + actives) and active stages of T. aripo and T. manihoti. Eggs of the two predator species were excluded from the analyses as it was not possible to separate eggs of the two predator species.

In the two predator species treatments, proportions of T. aripo were calculated for each sampling date and each treatment, to detect if the predator combination negatively affected any of the two predator species. Because population densities of T. aripo and T. manihoti might differ in the absence of heterospecifics, their densities in the single species treatments were pooled per sampling date, and proportions of T. aripo in this combined population were calculated. These fractions were used as expectations under the null hypothesis that the predator species did not affect each other. For each sampling date, this null hypothesis was tested against the alternative hypothesis that T. aripo and T. manihoti affect each other either directly (via interference or interspecific predation) or indirectly (via competition for food), or both.

Age structure of each predator species population was recorded per plant for both single and two-predator species and plotted against sampling dates. For each of the two series of experiments (predator-prey ratios 1:200 and 1:20), variation in the proportion of larvae was compared across all sampling dates and among treatments, as the larval stage is most susceptible to interspecific predation (Polis et al., 1989; Croft et al., 1996; Schausberger, 1997). These age structure data were used to check for gaps in age structure, which if present would indicate lack of reproduction, deaths by starvation, intraguild predation or all together.
Figure 1 Population trends of *M. tanajoa*, *T. aripo* and *T. manihoti* on plants in single and two-predator release treatments and on control plants (*M. tanajoa* only) in the low initial prey density experiment: (a) *M. tanajoa* (eggs + actives), (b) *T. aripo* (actives), and (c) *T. manihoti* (actives). For each sampling date, significantly different values (*P* < 0.05; ANOVA, with SNK mean separation; SAS Inst. 1999) are indicated with different letters. Data were log-transformed and averaged per plant.
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Table 1 Mixed Model repeated measures ANOVA of treatment and sampling date on densities of *Manicatella tanajoa*, *Tetramychus ario*, and *Tetramychus maniboti* in (a) the low initial prey density and (b) the high initial prey density experiments. *Tm* indicates *T. maniboti*, *Ta* indicates *T. ario*, and 'df' indicates numerator degrees of freedom.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>M. tanajoa</th>
<th>T. ario</th>
<th>T. maniboti</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td><strong>Low initial prey density</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Predators</td>
<td>4</td>
<td>44.42</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Date</td>
<td>7</td>
<td>7.30</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Predators*Date</td>
<td>28</td>
<td>3.94</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Control vs. Pred. release</td>
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<td>149.35</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>6Ta vs. 6Tm</td>
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<td>0.59</td>
<td>0.4508</td>
</tr>
<tr>
<td>6Ta vs. 6Ta+6Tm</td>
<td>1</td>
<td>0.78</td>
<td>0.3880</td>
</tr>
<tr>
<td>6Ta vs. 6Ta+6Tm</td>
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<td>17.02</td>
<td>0.0005</td>
</tr>
<tr>
<td>6Tm vs. 6Ta+6Tm</td>
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<td>2.77</td>
<td>0.1119</td>
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<tr>
<td>6Tm vs. 6Ta+6Tm</td>
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<td>24.29</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>6Ta+6Tm vs. 6Ta+6Tm</td>
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<td>10.66</td>
<td>0.0039</td>
</tr>
<tr>
<td><strong>High initial prey density</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predators</td>
<td>4</td>
<td>190.04</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Date</td>
<td>7</td>
<td>305.98</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Predators*Date</td>
<td>28</td>
<td>11.59</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

RESULTS

Cassava green mite dynamics

Densities of *M. tanajoa* differed among treatments in both high and low initial prey density experiments (Table 1a, b). The two predatory mites reduced *M. tanajoa* densities substantially compared with control treatments without predators (Figures 1a and 2a). There were also considerable differences in *M. tanajoa* abundance among predator treatments, and these differences were also affected by initial prey density.

The impact of single-predator species treatments on *M. tanajoa* differed in the two experiments: they had a similar negative impact on *M. tanajoa* densities in the low initial prey density experiment (Table 1a; Figure 1a), but differed substantially in their impact on *M. tanajoa* densities in the high initial prey density experiment (Table 1b; Figure 2a), where
Figure 2 Population trends of *M. tanajoa*, *T. aripo* and *T. manihoti* on plants in single and two-predator release treatments and on control plants (*M. tanajoa* only) in the high initial prey density experiment: (a) *M. tanajoa* (eggs + actives), (b) *T. aripo* (actives), and (c) *T. manihoti* (actives). For each sampling date, significantly different values (*P* < 0.05; ANOVA, with SNK mean separation; SAS Inst. 1999) are indicated with different letters. Data were log-transformed and averaged per plant.
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*T. maniboti* alone had a significantly greater impact on *M. tanajoa* densities compared with *T. aripo* alone. There were also considerable differences between single and two-predator species treatments, and this also depended on the predator species. In the experiments with high initial prey density, the two predator species treatments (3 or 6 of each species) had a significantly greater impact on *M. tanajoa* densities compared with treatments where only *T. aripo* was present (Figure 2a; Table 1b). In contrast, *M. tanajoa* densities were similar in the *T. maniboti* alone treatment and in the two-predator species treatments. In the experiments with low initial prey density, the mixed predator treatments only differed from the single-predator species treatments if the total number of predators added was double that of the single predator treatment, *i.e.* when 12 predators were added instead of 6 (Table 1a). There were also significant differences in impact on *M. tanajoa* densities when the two types of two-predator treatments are compared: the impact of adding 12 predators exceeds that of adding 6 (Table 1a, b).

**Predator dynamics**

Densities of predatory mites always increased soon after predator releases, and continued to increase after the onset of the decline in prey population. Densities of both predator species declined to near zero levels following the decline or complete disappearance of *M. tanajoa*.

Densities of *T. aripo* and *T. maniboti* in single-predator release treatments were always significantly higher than their densities in the two-predator release treatments (Figures 1b, c and 2b, c, Table 1a, b). These differences also hold even when initial numbers per predator species in the single and the two-predator species release treatments were equivalent, which strongly suggests that predator populations in mixed releases suffered from interspecific competition for prey and/or intraguild predation. Comparison of 6 vs. 12 predators treatments did not show significant differences in densities of either of the predator densities, irrespective of initial prey density (Table 1a, b).

To determine how the two species of predatory mites affected each other, the proportion of *T. aripo* was calculated for two-predator species treatments, separately for the two experiments (high and low initial prey density), and for three periods during these experiments: (1) the last two sampling dates, (2) the last five sampling dates, and (3) all sampling dates. These sampling periods corresponded to significant changes in prey densities, which could help in detecting effects of various interspecific interactions (competition or intraguild interaction) on each predator species. The results in Table 2 show that the fraction of *T. aripo* in the mixed predator population (3*T* + 3*M*, or 6*T* + 6*M*) is always lower than 0.5. During the last two sampling dates, the proportion of *T. aripo* in the high initial prey density experiment averaged 0.26 and less than 0.1 in the low initial prey density experiment, which were considerably lower than the proportion of *T. aripo* (c. 0.40) in the single species treatments (6*T* or 6*M*, Table 2; see Material and Methods). These results indicate that *T. aripo* suffers from interspecific competition or
intraguild predation because its share in the overall population in the mixed release treatments decreases toward the end of the experiment. Indeed, *T. aripo* disappeared in all mixed release treatments in the low initial prey density experiment.

Life stage composition of *T. aripo* and *T. maniboti* populations in the experiments initiated at high prey density (Figure 3) and at low prey density (Figure 4), shows that there are periods in which larvae and/or nymphs are absent. These periods occurred towards the end of the experiments, when prey densities were very low. This is most likely due to predators acquiring insufficient prey to reproduce. However, periods with adult predators and scarcity of larvae also occur at prey densities that are relatively high, as is the case for

### Table 2
Proportion of *T. aripo* (mean ± SE) in the two-predator species releases and expected proportion of *T. aripo* (mean ± SE) based on the single predator species treatments. *Tm* indicates *T. maniboti* and *Tt* indicates *T. aripo*. Ratio of *T. aripo* in single-species releases to the sum of *T. aripo* in single-species releases and *T. maniboti* in single-species releases

<table>
<thead>
<tr>
<th>Treatment</th>
<th>All 8 sampling days</th>
<th>Last 5 sampling days</th>
<th>Last 2 sampling days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Low initial prey density</td>
<td></td>
</tr>
<tr>
<td><em>Tt</em> + <em>Tm</em></td>
<td>0.271 ± 0.113</td>
<td>0.292 ± 0.184</td>
<td>0.100 ± 0.100</td>
</tr>
<tr>
<td><em>Tt</em> + 6<em>Tm</em></td>
<td>0.236 ± 0.065</td>
<td>0.124 ± 0.054</td>
<td>0.055 ± 0.055</td>
</tr>
<tr>
<td><em>Tt</em> or 6<em>Tm</em></td>
<td>0.378 ± 0.047</td>
<td>0.352 ± 0.058</td>
<td>0.400 ± 0.040</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High initial prey density</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tt</em> + <em>Tm</em></td>
<td>0.198 ± 0.041</td>
<td>0.226 ± 0.061</td>
<td>0.210 ± 0.050</td>
</tr>
<tr>
<td><em>Tt</em> + 6<em>Tm</em></td>
<td>0.308 ± 0.034</td>
<td>0.284 ± 0.027</td>
<td>0.320 ± 0.060</td>
</tr>
<tr>
<td><em>Tt</em> or 6<em>Tm</em></td>
<td>0.281 ± 0.046</td>
<td>0.350 ± 0.051</td>
<td>0.440 ± 0.060</td>
</tr>
</tbody>
</table>

### Table 3
Fraction of predator larvae (mean ± SE) per class of total prey (*M. lampra*) density per plant for a) *T. aripo* (*Tt*) and b) *T. maniboti* (*Tm*)

<table>
<thead>
<tr>
<th><em>M. lampra</em> density classes</th>
<th>Low initial prey density</th>
<th>High initial prey density</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Typhlodromalus aripo</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.100</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tt</em></td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>6 <em>Tt</em></td>
<td>1</td>
<td>0.120 ± 0.000</td>
</tr>
<tr>
<td>3 <em>Ta</em> + 3 <em>Tm</em></td>
<td>2</td>
<td>0.000 ± 0.000</td>
</tr>
<tr>
<td>6 <em>Ta</em></td>
<td>1</td>
<td>0.000 ± 0.000</td>
</tr>
<tr>
<td>10-10000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6 <em>Tt</em></td>
<td>7</td>
<td>0.090 ± 0.023</td>
</tr>
<tr>
<td>3 <em>Ta</em> + 3 <em>Tm</em></td>
<td>5</td>
<td>0.240 ± 0.192</td>
</tr>
<tr>
<td>6 <em>Ta</em> + 6 <em>Tm</em></td>
<td>6</td>
<td>0.010 ± 0.008</td>
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<tr>
<td><em>Typhlodromalus maniboti</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.100</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tt</em></td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>6 <em>Tt</em></td>
<td>1</td>
<td>0.109 ± 0.000</td>
</tr>
<tr>
<td>3 <em>Ta</em> + 3 <em>Tm</em></td>
<td>4</td>
<td>0.009 ± 0.000</td>
</tr>
<tr>
<td>6 <em>Ta</em> + 6 <em>Tm</em></td>
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<td>0.040 ± 0.010</td>
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<td>10-10000</td>
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<td>6 <em>Tt</em></td>
<td>8</td>
<td>0.205 ± 0.078</td>
</tr>
<tr>
<td>3 <em>Ta</em> + 3 <em>Tm</em></td>
<td>6</td>
<td>0.185 ± 0.086</td>
</tr>
<tr>
<td>6 <em>Ta</em> + 6 <em>Tm</em></td>
<td>4</td>
<td>0.146 ± 0.043</td>
</tr>
</tbody>
</table>
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T. aripo in the first 24 days of the two-predator treatments in the experiment initiated at low prey density (Figure 4). This scarcity of T. aripo larvae in the two-predator treatments contrasts with the presence of larvae in the single predator treatments for both predator species and for T. manihoti in the two-predator treatments. This strongly suggests that, at least at the population level, T. manihoti is an intraguild predator of T. aripo.

To determine the impact of prey density on fraction of larvae in T. aripo and T. manihoti populations, we grouped prey densities into two arbitrary density classes: (1) 0-10 prey per plant, (2) 10-10000 prey per plant. Within these prey density classes, the fraction of larvae in T. aripo and T. manihoti populations were calculated for each treatment; fraction of larvae was obtained by dividing the number of larvae of a predator species by the total number of the same predator species in the population (Table 3). This grouped analysis shows again that the fraction of T. aripo larvae at high prey density is strikingly low in the two-predator treatments (6 individuals per species), in both low and high initial prey density experiments. Moreover, it reveals that at low prey density the fraction of T. aripo larvae is higher than that of T. manihoti larvae; thus suggesting that T. aripo is able to survive longer than T. manihoti at low prey density.
Chapter 5

T. aripo and T. manihoti population sizes in single and two-predator species treatments in the experiments with low initial prey density

**DISCUSSION**

Our experiments showed that *T. manihoti* and *T. aripo* can suppress *M. tanajoa* densities and these results confirm field data presented elsewhere (Yaninek et al., 1998; Hanna and Toko, 2001; Onzo et al., 2003; Yaninek and Hanna, 2003). Under the physical and time scale conditions of our study, the combination of the two species did not lead to greater suppression of *M. tanajoa* densities compared with *T. manihoti* alone under both low and high initial prey densities, suggesting that the impact of the two-predator treatments is dominated by *T. manihoti*. This is likely due to the ability of *T. manihoti*, under screenhouse conditions, to out-compete *T. aripo* because of *T. manihoti*’s greater intrinsic growth rate [0.272 and 0.151 females/female/day for *T. manihoti* and *T. aripo* respectively (Gnanvossoo et al., 2003b)] and its greater level of predation on *T. aripo* larvae (see Croft et al., 1996; Walzer and Schausberger, 1999 for observations on other phytoseiid species). In the experiments initiated at high prey density, *T. aripo* alone had a lower impact on *M. tanajoa* densities than *T. manihoti* alone, or the two predator species together. Evidently, *T. aripo* cannot suppress local *M. tanajoa* populations to the same extent as *T. manihoti*. This conclusion, as derived from (local) population level phenomena, is confirmed by observations on behaviour and life history at the individual level. Predation rate and
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capacity for population increase are lower for T. aripo (Gunnarsson et al., 2003; Yaninek and Hanna, 2003) and both these traits are critically important for local prey population suppression, as argued by Janssen and Sabelis (1992) on the basis of a simple, yet quite realistic (see Pels, 2001) model of local predator-prey interaction.

We had expected, based on our previous research on within-plant distribution of the two predators (Onzo et al., 2003) and the response of M. tanajoa to predator odours (Magalhães et al., 2002), that the presence of T. aripo and T. maniboti on the same plant would result in greater suppression of M. tanajoa populations than the presence of either of the predators alone. Typhlodromalus aripo inhabits the apex during the day and forages on the upper leaves during the night, whereas T. maniboti frequents all strata (except the apex) of the cassava plant but is mostly found in the middle stratum. In this way, the two predator species occupy different niches and are therefore expected to complement each other in suppressing M. tanajoa population. This complementarity was not evident in our experiments, however, probably due to the small size of the plants in our experiments (c. 60 cm in length, as compared to more than 2 m in the field), which would have increased predator search efficiency and therefore prey suppression (O'Neil, 1989) and predator-predator encounters. Moreover, the smaller plants would have forced the two predator species to co-occur on the same leaves during the night, with obvious consequences for competition for prey and interference by intraguild predation. In addition, T. aripo in the screenhouse seems less restricted to the apex during daytime than in the field – 12.7% of T. aripo were found on leaves in the screenhouse during the day time compared to 0% in the field (Onzo et al., 2003) – which would have increased predator-predator encounters and exacerbated the negative effects of interspecific interactions (competition for prey and interspecific predation) between the two predators.

Our study reveals that the presence of T. aripo and T. maniboti together on cassava plants in a screenhouse did not add significantly to the suppression of M. tanajoa compared to the presence of T. maniboti alone. When the two predator species are together, inter-predator interactions negatively affected the population densities of both species, with a greater negative effect on T. aripo. Laboratory experiments conducted on cassava leaf disks with females of one species (either T. aripo or T. maniboti) and larvae (as prey) of the other species indicated that both predators feed equally in the other's larvae (6.7 ± 1.03 T. aripo larvae killed per female T. maniboti versus 7.07 ± 0.19 T. maniboti larvae killed per female T. aripo; t = 1.93, P = 0.089, n = 5; R. Hanna and A. Onzo, unpublished data). The apparent 'superiority' of T. maniboti observed on cassava plants in the screenhouse experiment (this study) most likely did not result from T. maniboti's greater intrinsic capacity to feed on juveniles of T. aripo, but probably from the numerical dominance of T. maniboti populations. Our data therefore suggest that under the conditions of our experiment the two predators did not act synergistically in suppressing M. tanajoa populations. At relatively high prey densities, T. maniboti alone reduced M. tanajoa to a greater extent than T. aripo alone, but at relatively low prey densities both predatory mites are equally efficient in
reducing *M. tanajoa* densities. Caution should be exercised, however, in extrapolating the outcome of our screenhouse experiments directly to expected outcome of predator interactions in the field. While conditions in our screenhouse were fairly similar to field conditions in terms of temperature and relative humidity, they differed from field conditions in three ways: (1) plant size (for plants in the field older than 2 months of age), (2) heterogeneity of predator and prey distribution and opportunities of prey/predator dispersal, and (3) the availability of alternative food for the predators.

Cassava plants in the field can be several times larger (depending on their age) than the plants in our screenhouse experiments (1-2 months old) and may offer more opportunity for co-existence of *T. aripo* and *T. manihoti* through niche segregation and partitioning of foraging periods (Gnanvossou *et al.*, 2003a; Onzo *et al.*, 2003). Larger cassava plants may also facilitate prey dispersal to avoid predation (Magalhães *et al.*, 2002), while prey dispersal could also have a stabilizing effect on predator-prey dynamics (Sabelis *et al.*, 1991). Spatial structure has been shown also to affect the persistence of predator-prey systems (Janssen *et al.*, 1997; Ellner *et al.*, 2001). We sought to establish a fairly homogenous environment in terms of plant size and prey/predator distribution, while restricting dispersal between treatments, together resulting in a simplified spatial structure which does not promote long term persistence of the predator/prey system. Moreover, the outcome of the interactions in our predator/prey system in the screenhouse may have been affected by the limited availability of alternative food sources such as maize pollen, which can be abundantly present and cassava during periods of maize flowering and can serve as an important food source for both *T. aripo* and *T. manihoti* during periods of low prey mite availability. Both *T. aripo* and *T. manihoti* feed on maize pollen, but only *T. aripo* reproduces on this diet (D. Gnanvossou, R. Hanna and S. Yanineck, unpublished data). The limited availability of maize pollen in our screenhouse experiment may have had a greater impact on *T. aripo* than on *T. manihoti* and may have exacerbated the negative effects of intraguild interactions on *T. aripo* and on the persistence of the system.

Acknowledgements

We are grateful to I. Zanno and B. Bovis for identifying the phytoseiid specimens. We also thank B. Eklou, J. Goulodji, D. Houmhagni, B. Adoum and A. Domingo for their valuable help while collecting and processing samples, D. Gnanvossou, G. Paras, C. Atcha-Ahoue and their team for their assistance in rearing the predatory mites. Thanks are due to S. Koré for his assistance in the statistical analyses, and to S. Magalhães and two anonymous reviewers for providing valuable comments on an earlier version of this manuscript. This research was supported with funds from ILTA core donors and two special projects funded by the Danish International Development Agency (DANIDA) and the International Fund for Agricultural Development (IFAD); and with funds provided to the University of Amsterdam by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).

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