Biological control of cassava green mites in Africa: impact of the predatory mite *Typhlodromalus aripo*

Cassava was attacked in the 1970's by the cassava green mite *Mononychellus tanajoa*, a pest of neotropical origin. This pest is currently object of an Africa-wide classical biological control program using *Typhlodromalus aripo*, a predatory mite introduced from Brazil, South-America. Our study aimed at analysing the impact of *T. aripo* on *M. tanajoa* densities. *Typhlodromalus aripo* inhabits the apex of cassava plants during the day and forages on cassava leaves at night. Population dynamics study over seven consecutive years in cassava fields in Benin, West-Africa, showed a drop in cassava green mite densities since the introduction of *T. aripo* and an ability of the predator to tolerate environmental conditions prevailing in West-Africa and to persist periods of green mite scarcity by the use of alternative food, *i.e.* pollen of maize, an important intercrop in cassava growing areas. Densities of *M. tanajoa* and *T. aripo* are linked and generally follow the rainfall pattern, showing two peaks per year. Our study showed that *T. aripo* is suitable for controlling *M. tanajoa*. However, one should not underestimate the role of endemic predatory mites in addition to the impact of the exotic predatory mites on cassava green mites.

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Cassava

Cassava, *Manihot esculenta* Crantz (Euphorbiaceae), is a woody semi-perennial shrub of 4-5 metre high, native to South-America and currently cultivated in most parts of the tropics (Poulter 1995) (figure 1). It has been introduced into Africa in the 16th century and has become a staple food for millions of people in sub-Saharan Africa (Nweke *et al*. 2002). Cassava is grown for its starchy roots, but its leaves are also consumed, as vegetables, in many parts of Africa. Cassava production is easily established, not requesting costly input. It can also thrive well on poor soils that are unsuitable for other food crops and can support harsh environmental conditions such as drought. All these advantages have made cassava a more and more attractive crop, especially to subsistence farmers in Africa.

An important constraint to cassava production is the combined effect of pests and diseases that can substantially reduce cassava yields. Among the pests, cassava green mite alone can cause serious reduction in cassava yield (Yaninek *et al*. 1990).

Cassava green mite

The cassava green mite, *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae), a neotropical spider mite (figure 2), has been accidentally introduced into Africa in the 1970's and has since then become a serious pest for cassava on the continent (Yaninek & Herren 1988). This mite resides and feeds on young leaves and green stems of cassava plants and increases its population density during the transition

Figure 1. Cassava field (a) and tuber (b). Photos: Alexis Onzo
Veld met cassaveplanten (a) en knol van de cassaveplant (b).

period between wet and dry seasons. At high population densities it reduces cassava yields by damaging the photosynthetically active leaf surface area of the plant (Yaninek *et al*. 1990). Root yield reduction can locally reach 80% (Yaninek & Hanna 2003).

Following its discovery, many control measures have been taken, including the use of chemicals and the breeding of resistant varieties (Hahn *et al*. 1989, Yaninek & Hanna 2003). However, none of them were appropriate, if not only due to their cost. The exotic nature of the pest coupled with the fact that cassava green mite is not a problem in its area of origin prompted scientists at the International Institute of Tropical Agriculture (IITA), in collaboration with many other institutions, to initiate a classical biological control program against this pest in 1984 (Yaninek & Herren 1988).

Biological control of *Mononychellus tanajoa* in Africa

Classical biological control aims at permanent control of a pest by the introduction and establishment of suitable natural enemies from the geographic origin of the pest for self-sustained maintenance of target pest populations below economically damaging levels (Eilenberg *et al*. 2001). Thus, because the pest (the cassava green mite) originates from the neotropics, several explorations have been conducted there to select natural enemies in the area of origin of the pest and to introduce them into Africa. A dozen of predatory mite species in the family Phytoseiidae have been selected in the neotropics and shipped to Africa for experimental releases via the quarantine facilities at the University of Amsterdam (Yaninek *et al*. 1993). Among them, two are established in many parts of Africa: *Typhlodromalus manihoti* Moraes and *Typhlodromalus aripo* DeLeon (Yaninek & Hanna 2003).

Figure 2. Cassava green mite, *Mononychellus tanajoa*, and its damage to the upper part of cassava plants. Photos: Alexis Onzo
Groene cassavemijten en de schade die deze mijt toebrengt aan de topbladeren van cassaveplanten.

Between these two exotic predator species, *T. aripo* is considered the most successful predator of cassava green mite due to its impact on the densities of the pest, its high capacity of dispersal (figure 3) and its persistence in cassava fields.

Typhlodromalus aripo

Typhlodromalus aripo is almost exclusively found in the apices of cassava plants (figure 4). The apex of cassava is an assemblage of young, non-expanded and generally hairy leaf primordia at the top of the plant; *T. aripo* seems to depend on this structure for its persistence in cassava fields. The apex of cassava plants function like those structures called domatia. Domatia are small invaginations (pits, pockets) or tufts of trichomes usually found at vein junctions on the undersides of leaves in many woody dicots (O'Dowd & Wilson 1989, Pemberton & Turner 1989, Walter 1992). Lundströem (1887) observed that these tiny structures sheltered mites and, consequently, proposed to call them 'acarodomatia' (*i.e.* mite houses) (O'Dowd 1994, Walter 1996). Acarodomatia are predominantly occupied by predatory mites of the families Tydeidae, Stigmaeidae and Phytoseiidae, but rarely by plant-parasitic (herbivorous) mites (O'Dowd & Wilson 1991, Wilson 1991, Walter 1996). As a consequence, plants with domatia are inhabited by a lower number of herbivorous mites (Agrawal 1997). When apices of cassava plants were cut off, very few *T. aripo* persisted on the plants and none of them could lay eggs, although prey was available (Bakker 1993). Thus, cassava apices – which Bakker (1993) described since then as extrafoliar domatia – not only provide shelter to *T. aripo* but also serve as oviposition sites for the predator. The predator reduces *M. tanajoa* densities not only in the apices but also in the upper part of cassava foliage (Bakker 1993, Onzo *et al*. 2003a).

Reducing pest densities – but how does this happen?

Field observations on cassava plants in Benin (West-Africa) show that *T. aripo* monopolises the apices of cassava plants during daytime, but forages on young cassava leaves during

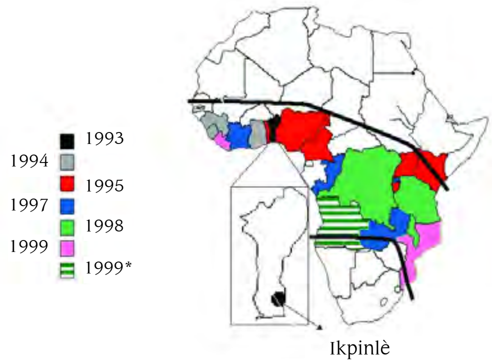

Figure 3. Introduction and distribution of *Typhlodromalus aripo* in Africa from 1993-1999. Ikpinlè, in Benin, was the first release site.
* Confirmation postponed due to the war in Angola
Introductie en verbreiding vanuit Ikpinlè, Benin, van de roofmijt Typhlodromalus aripo *in Afrika tussen 1993-1999.*
** Bevestiging uitgesteld tot na de oorlog in Angola*

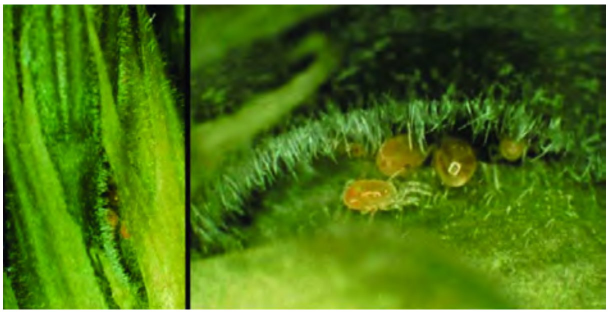

Figure 4. *Typhlodromalus aripo* inside the apex of cassava plant. Photos: Alexis Onzo
De roofmijt Typhlodromalus aripo *in de groeitop van een cassaveplant.*

night (figure 5). Furthermore, *T. aripo* elicits avoidance by within-plant vertical migration of mobile stages of the cassava green mite (Magalhães *et al*. 2002, Onzo *et al*. 2003b). Cassava plants therefore benefit from this apical domatia by acquiring protection for their photosynthetically most active young parts, because *T. aripo* protects primordial leaves in the apex, reduces the densities of cassava green mite on young leaves by feeding on the immobile stages, and causing mobile stages to move down to less profitable older leaves. As a consequence, within cassava plants, the highest cassava green mite densities have shifted from the first fully developed leaf (approximately leaf 4) to leaves 6-12, when *T. aripo* is present.

Studies on population dynamics in the same cassava fields within a growing season show that temporal trends in abundance of *M. tanajoa* and *T. aripo* are similar but with a slight delay in *T. aripo*'s responses to changes in *M. tanajoa* densities. For both predator and prey population trends follow the seasonal rainfall pattern (figure 6).

Long-term studies (seven years) at another site in Benin show that, after the release of *T. aripo*, cassava green mite densities dropped from *c*. 90 to *c*. 7 per leaf in about five months and *T. aripo* populations persisted in this field for the full seven years (figure 7). Time series analysis resulted into an annual model showing one absolute peak population size and one lower local peak for both *T. aripo* and the cassava green mite (figure 8). The pronounced herbivore peak coincided with a trough in rainfall intensity, whereas the lower local peak fell in a period of high rainfall. The pronounced peak in *T. aripo* densities occurred near the time when *M. tanajoa* densities reach a peak soon after the onset of the dry season (December). The lower local peak of *T. aripo* occurred during the rainy season (July), near the time when *M. tanajoa* densities reach a trough and maize pollen are available as an alternative food source for *T. aripo*. So, *T. aripo* populations persist in the field for more than seven years, limiting cassava green mite populations to levels that could be considered as control.

Before the introduction of *T. aripo*, field observations had shown that the indigenous predatory mites found on cassava – among which the most common are *Euseius fustis* (Pritchard & Baker) and *Typhlodromalus saltus* (Denmark & Matthysse) – were not able to control outbreaks of *M. tana-*

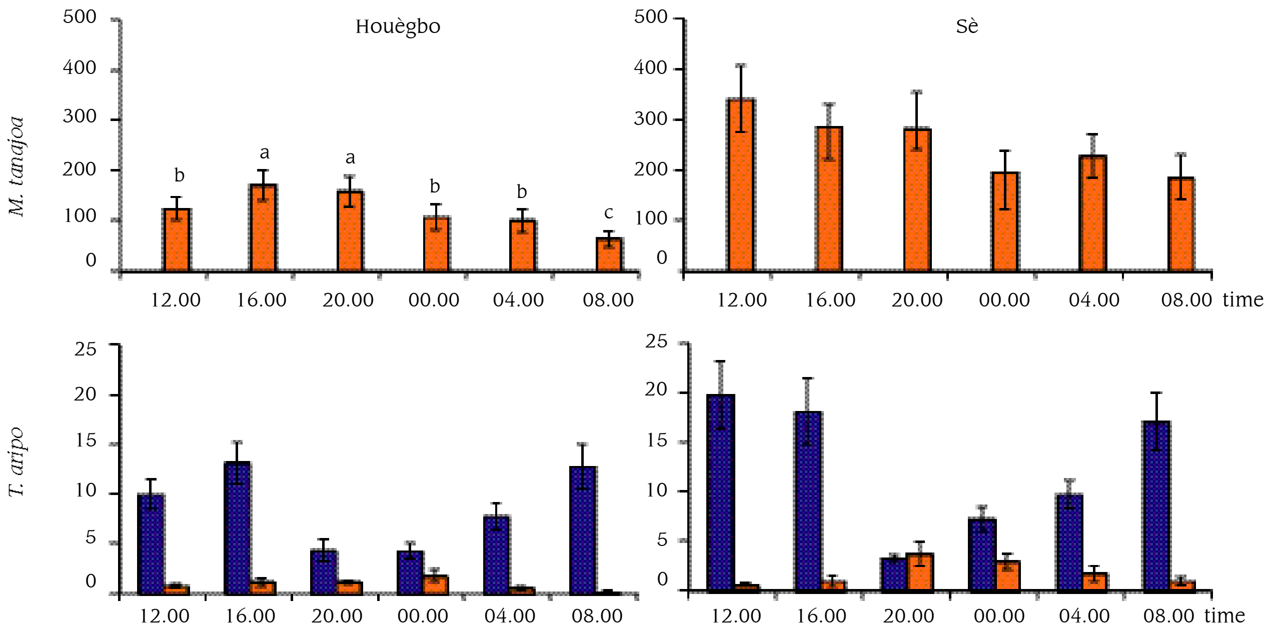

Figure 5. Mean number (± SE) of *M. tanajoa* (eggs + mobile stages) and *T. aripo* (mobile stages) found in the apex and on the even-numbered leaves among the top 20 leaves within cassava plants. Measurements were taken at four hour intervals during a 24 hour period, starting from 12:00 h. In Houègbo, samples were taken in August 1998, November 1998, January 1999 and May 1999, 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 ten leaves have been sampled, the number of *T. aripo* on the top 20 leaves was obtained by multiplying the number by two. For each plant part, bars with the same letter are not significantly different (PROC GLM; Student-Newman-Keuls multiple range test, SAS, 1999). Blue = apex, orange = leaves
Gemiddeld aantal groene cassavemijten M. tanajoa *(eieren + mobiele ontwikkelingsstadia; ± standaardfout) en roofmijten* T. aripo *(mobiele stadia) zoals gevonden in de groeitop en op de even nummers van de bovenste 20 bladeren in cassaveplanten (waarna dit aantal is vermenigvuldigd met twee). De waarnemingen zijn om de vier uur gemeten gedurende 24 uur vanaf 12:00 uur. Blauw = top, oranje = bladeren.*

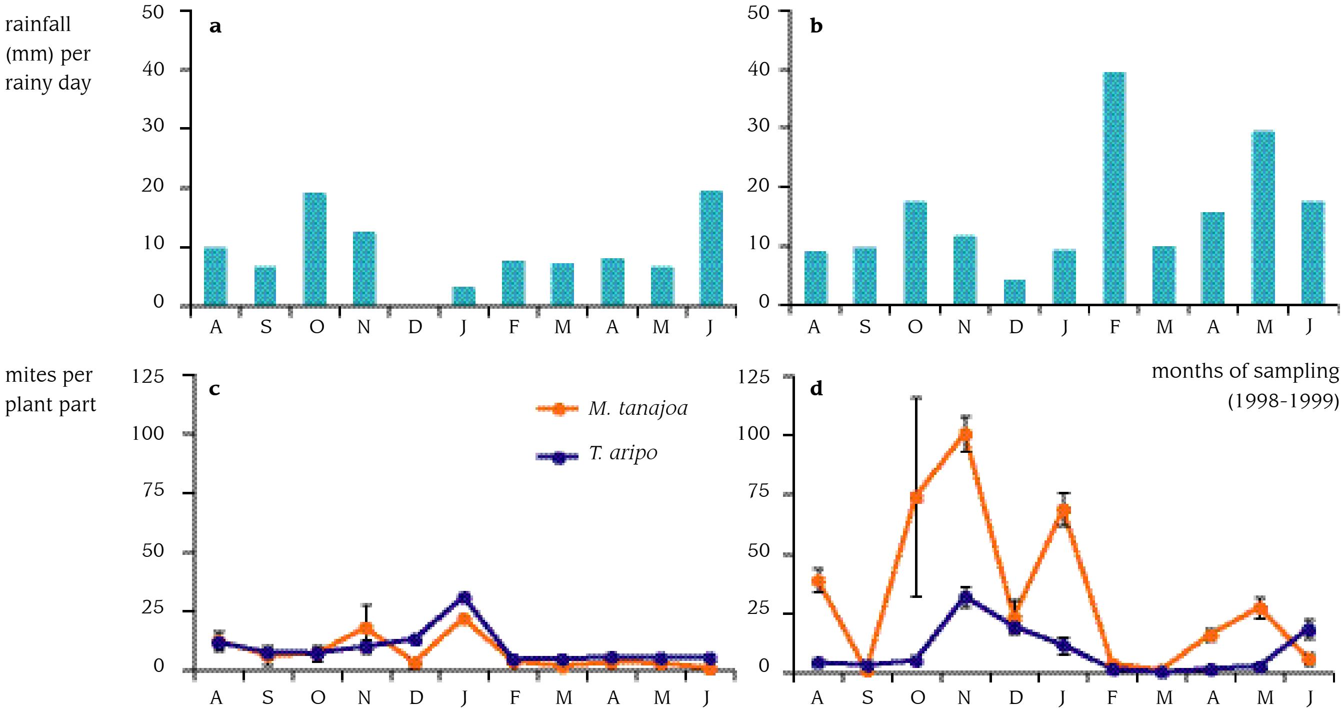

Figure 6. Rainfall pattern in the field sites at Houègbo (**a**) and Sè (**b**), Benin; seasonal pattern for all stages of *M. tanajoa* on first fully developed leaves (FDL) and mobile stages of *T. aripo* in the apex in the field at Houègbo (**c**) and Sè (**d**). Means ± standard errors are plotted.
*Regen in cassavevelden bij Houègbo (**a**) en Sè (**b**) in Benin; seizoensgebonden patroon van aantalsveranderingen in alle stadia van* M. tanajoa *en de mobiele stadia van* T. aripo *in cassavevelden bij Houègbo (**c**) en Sè (**d**), Benin. Gemiddelde ± standaardfout zijn gegeven.*

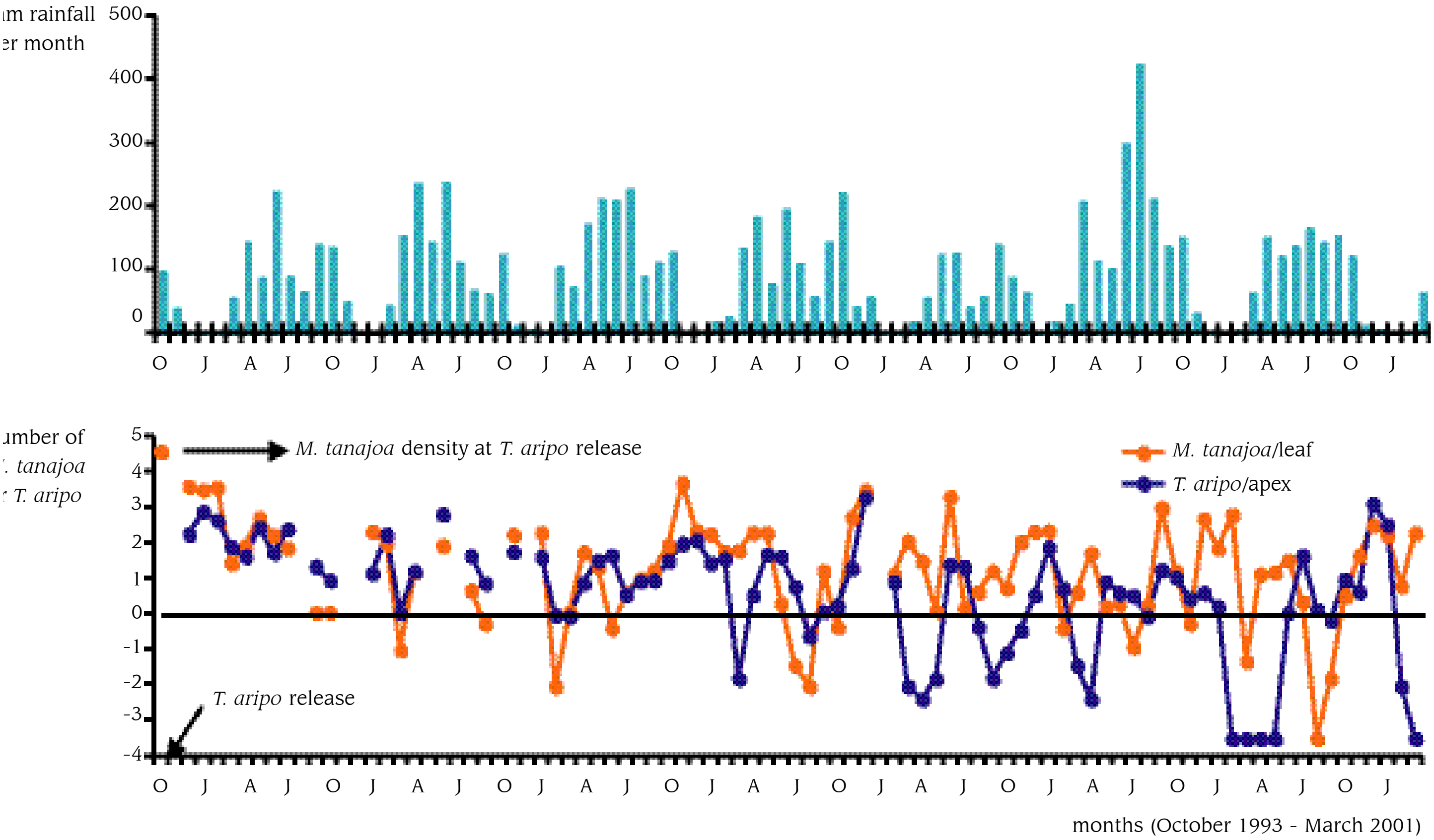

Figure 7. Rainfall and population trends of mobile stages of *M. tanajoa* and *T. aripo* in a cassava field at Ikpinlè, Benin.
Regenval en trends in de populatiegrootte van mobiele stadia van M. tanajoa *en* T. aripo *in een cassaveveld bij Ikpinlè, Benin.*

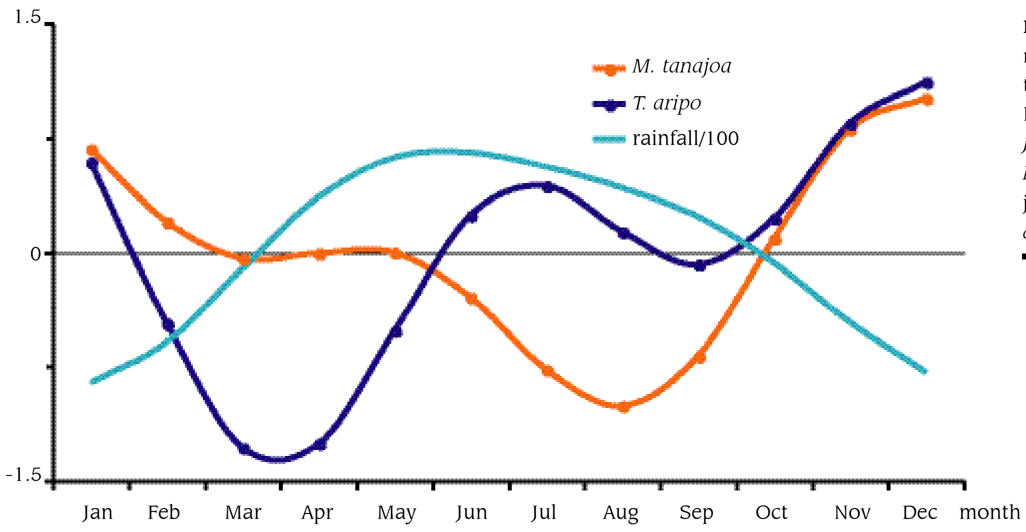

Figure 8. Per-year periods of rainfall (mm) and of log-population densities of *M. tanajoa* (per leaf) and *T. aripo* (per apex). *Jaarlijkse regen (mm) en dichtheden (log-schaal) van* M. tanajoa *en* T. aripo *(per groeitop van de cassaveplant).*

joa on their own (Yaninek & Herren 1988), but the magnitude of their impact on *M. tanajoa* suppression after the introduction of *T. aripo* and *T. manihoti* have not been rigorously tested under field conditions. It was also not known how these indigenous predators interact with the exotic species.

How does *T. aripo* interact with the other predatory mites?

Fields surveys conducted in the south-west of Benin show that the presence of an exotic or indigenous species of predatory mite in addition to *T. aripo* was associated with lower *M. tanajoa* densities. Moreover, *T. aripo* densities were usually positively affected by the presence of other predator species (Onzo *et al*. 2003a). The lack of negative effects of the predator species complex on biological control of cassava green mite is likely due to differential niche use by the various species, which reduces interference between *T. aripo* and the other predators. Indeed, *T. aripo* resides in the apex of cassava plants during the day and forages on leaves only at night; therefore, direct interactions with the other predators are reduced. Moreover, one predator species can benefit from the within-plant escape responses of *M. tanajoa* elicited by the other predator species (Magalhães *et al.* 2002, Onzo *et al.* 2003b): migration higher up in the plant in response to *T. manihoti* (or indigenous predator species) drives *M. tanajoa* upward towards the plant area occupied by *T. aripo*, whereas migration down the plant in response to *T. aripo* drives *M. tanajoa* downward towards the plant area occupied by *T. manihoti* and the indigenous predators.

Olfactometer experiments have also shown that *T. aripo* and *T. manihoti* avoid colonizing the same prey colonies (Gnanvossou *et al.* 2003ab). In the field, two predator species may avoid interference by moving to plants not occupied by their competitor (Janssen *et al.* 1995ab). Hence, complementarity of the two predator species is expected at the scale of a metapopulation in a cassava field, rather than at the scale of a single plant. These results show that indigenous phytoseiid species are more important in suppression of *M. tanajoa* populations in cassava fields than previously thought (Yaninek & Herren 1988) and provide additional evidence in support of the positive impact of complexes of natural enemy species on the success of biological control (*e.g.* Soluk 1993, Riechert & Lawrence 1997, Losey & Denno 1999). The phytoseiid species complex (whether exotic or indigenous) found in cassava fields in southern Benin (and other similar agroecologies in West-Africa) enhances rather than interferes with the biological control of *M. tanajoa*.

A full understanding of the interactions between host plants and natural enemies of herbivores, and of the interactions among natural enemy species, is expected to lead to designing more effective biological control strategies.

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Samenvatting
Biologische bestrijding van groene cassavemijten in Afrika: invloed van de roofmijt *Typhlodromalus aripo*

Cassave is een belangrijk voedingsgewas voor miljoenen mensen in Afrika ten zuiden van de Sahara. In de zeventiger jaren van de vorige eeuw trad *Mononychellus tanajoa*, de uit Zuid-Amerika afkomstige groene cassavemijt, voor het eerst op als plaag in Afrika. Deze plaag is nu onder controle door toedoen van een eveneens uit Zuid-Amerika overgebrachte roofmijt, *Typhlodromalus aripo.* Deze rover leeft overdag in de groeitop van cassaveplanten, maar komt 's nachts te voorschijn om op de bladeren te zoeken naar prooi. Na introductie van deze roofmijt waren de dichtheden van de groene cassavemijt op de eerste bladeren onder de groeitop lager dan ervoor. Daaropvolgende studies over meer dan zeven jaar in cassavevelden in Benin, West-Afrika, toonden een duidelijke daling van de aantallen groene cassavemijten na introductie van de roofmijt. Bovendien kon de roofmijt zich handhaven, zodat geen nieuwe introducties noodzakelijk waren. Een belangrijke factor die de kans op voortbestaan van de roofmijt vergroot is de beschikbaarheid van alternatief voer in het regenseizoen, als de groene cassavemijten schaars zijn. Dit alternatieve voer bestaat uit pollen van maïs, een gewas dat vaak in de buurt van cassavevelden te vinden is (als zogenaamd 'inter-crop'). Wij concluderen dat de exotische roofmijt *T. aripo* een geschikte natuurlijke vijand vormt voor de bestrijding van de (eveneens exotische) groene cassavemijt in cassavevelden in Afrika. Toch moet de rol van inheemse roofmijten niet veronachtzaamd worden. Zij spelen een belangrijke ondersteunende rol in het plaagbestrijdingssysteem.