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

In biological control programs involving the use of predators or parasitoids against herbivorous arthropods, plants are often considered as passive players in that their impact on predator-prey interactions is not made explicit in developing control strategies. However, successful biological control of herbivores in natural and managed systems generally implicitly integrates several plant defence strategies (Lewis et al., 1997; Cortesero et al., 2000). During the last two decades, ecologists have become fully convinced that plants can effectively defend themselves against herbivorous arthropods, either directly by limiting feeding by herbivores, or indirectly by promoting the effectiveness of natural enemies of the herbivores (Price et al., 1980; Sabelis et al., 1999). Direct defences include plant structures that reduce feeding by the herbivore, and secondary plant compounds that inhibit digestion, intoxicate or deter feeding by the herbivore (Dicke and Sabelis, 1988; Barret, 1994; Sabelis et al., 1999). The indirect strategy is based on a ‘mutualistic’ association between plants and the herbivores’ natural enemies, in which plants attract natural enemies through chemical lures, provide them with alternative food such as exudates, pollen or nectar, and/or develop shelters, called ‘domatia’, that protect natural enemies against harsh environmental conditions or relatively large hyperpredators (Dicke and Sabelis, 1988; Barret, 1994; Walter, 1996; Sabelis et al., 1999). 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 and Wilson, 1989; Pemberton and Turner, 1989; Walter, 1992). The importance of domatia in the ‘mutualistic’ association between plants and predatory mites has been suggested for the first time by Lundström in 1887. He observed that these tiny structures sheltered mites. Consequently, he proposed to call them ‘acarodomatia’ (i.e. mite houses) (Pemberton and Turner, 1989; O’Dowd, 1994; Walter, 1996). Leaf domatia associated with mites are widely distributed in both tropical and temperate habitats (O’Dowd and Wilson, 1989), on forest trees as well as on a number of crop plants (Pemberton and Turner, 1989; O’Dowd, 1994; Rosario, 1995).

Acarodomatia are predominantly occupied by predatory mites of the family Tydeidae, Stigmaeidae and Phytoseiidae (Figure 1c, d), but rarely by plant-parasitic (herbivorous) mites (O’Dowd and Wilson, 1991; Wilson, 1991; Walter 1996). Plants with leaf domatia are more likely to be inhabited by a predatory mite and generally have many more predators.
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per leaf compared with sympatric plants lacking these structures (Walter and O'Dowd, 1992b; Grostal and O'Dowd, 1994; Rosario, 1995; Walter, 1996). As a consequence, plants with domatia are inhabited by a lower number of herbivorous mites (Agrawal, 1997). Addition of artificial domatia has improved yield of cotton by almost 30 percent as a result of lower numbers of herbivores and a higher increase of predator numbers (Agrawal and Karban, 1997). Thus, predators in domatia help the plant to defend itself against herbivores and in turn, domatia protect predators from their arthropod natural enemies or abiotic stress (Walter and O'Dowd, 1992a; Norton et al., 2001). Indeed, inactive stages of predators, such as eggs and newly moulted mites, are certainly, better protected from intraguild predators and from desiccation when they are inside domatia. Several studies have demonstrated that predatory mites preferentially use domatia for oviposition (Pemberton and Turner, 1989; Walter and O'Dowd, 1992a,b; Faraji et al., 2002a) and (Faraji et al., 2002b). Grostal and O'Dowd (1994) found that domatia enhance reproduction by the predatory mite Metaseiulus occidentalis (Nesbitt), especially, at low relative humidity. Domatia are also suspected to promote aggregation of predatory mites in a newly colonized patch, through egg clustering (Faraji et al., 2002b). Overall, leaf domatia complement well the herbivore-induced chemical defence mechanisms of the plants in that the latter attract the predatory mites while the former protect them once on the plants. This combination should, likely, reinforce the defence strategy of the plants against herbivores (Grostal and O'Dowd, 1994).

In addition to host-plant traits, success in biological control is influenced by the relationships between the second and the third trophic levels and also within the third trophic level. Predator-prey interactions are a determinant for the persistence of the system. If predators decimate prey populations, they can have difficulties to persist unless they can feed on alternative food sources such as exudates or pollen (Toko et al., 1994; van...
Rijn et al., 1999, 2002), that maintain their population until prey densities rise again. Habitat complexity that creates refuges to the prey and the predator avoidance behaviour shown by certain prey species are suspected to improve the persistence of predator-prey interactions (Price et al., 1980).

Not to be underestimated is the impact of predator-predator interactions on control of the target pest populations. In many biological control programs, more than one natural enemy species are introduced and established on the same pest and in the same environment. They are therefore potential competitors and may interact directly during periods of prey scarcity (Schausberger, 1998). Direct interactions generally take the form of intraguild predation. Intraguild predation occurs when two species that share a host or prey (and therefore may compete) also engage in a trophic interaction with each other through parasitism or predation (Rosenheim et al., 1995). In this interaction, the species that feeds on the other is called 'intraguild predator' whereas the species on which the intraguild predator feeds is called the 'intraguild prey'. Intraguild predation can be symmetric, in which case, generally, adults of each species feed on younger stages of the other and vice-versa. It is asymmetric when one species always feeds on the other species that ultimately can be eliminated from the system (Polis et al., 1989). These types of predator-predator interactions (also termed 'interference') generally relieve prey from control and may lead to increase in prey populations. Indirect interactions between predator species occur when each species interacts with the other through the prey (i.e., exploitation competition). These types of predator-predator interactions for shared prey are favoured by segregation in preferred prey stage among the two predator species, differences in their foraging periods or a combination of both. One such example is the predator facilitation (or synergistic predation or additive predation) in which the presence of each predator species increases the efficiency of the other through niche segregation (Losey and Denno, 1998). Indeed, in its attempt to avoid one predator species, the prey species becomes available for other predator species. Predator facilitation is very beneficial for biological control (Chapter 6 of this thesis). The negative or otherwise positive effect of multiple predator species on pest populations is the main reason of the endless controversy among ecologists (Kakehashi et al., 1984) with respect to the use of one versus multiple natural enemy species in biological control of agricultural pests. In Africa, cassava, cassava green mite and predatory mites form a system in which predator-predator interactions are important and relevant for investigation.

Cassava, Manihot esculenta Crantz (Euphorbiaceae) is a woody semi-perennial shrub of 4 to 5 m high, native to South America. Over several centuries it has become cultivated in most parts of the tropics (Poulter, 1995). This plant is grown mainly for its starch stored in its roots. Cassava is a major source of calories for roughly two out of every five Africans (Nweke et al., 2002). Cassava plant does not have any foliar structures like acarodomatia. However, its apex (the growing point or tip) could play a role similar to that of leaf domatia (Bakker, 1993). The apex of cassava is an assemblage of young, non-expanded and
generally hairy leaf primordia at the top of the plant (Figure 1b, c). The size and shape of the apex vary with cassava cultivars and plant age (Hanna et al., 2000). High numbers of predatory mites have been observed in apices of cassava in Brazil and Colombia (Bakker, 1993) and also in Africa (Onzo et al., 2003).

Field observations have shown that, in absence of predators, the apices were often prone to attack by herbivores (Bakker, 1993; Onzo et al., 2003), whereas in presence of predators no herbivorous mites were encountered in the apices (Figure 2). Cassava plants (through the apices) and the predatory mites are therefore suggested to have established a mutualistic relationship similar to the plant-acarodoma-tia mutualisms. Based on this hypothesis, Bakker (1993) referred to the cassava apices as 'extrafloral domatia'. Field investigations revealed that the only one predatory mite species consistently found in the apices of cassava plants was Tiphlodromalus aripo De Leon (Acari: Phytoseiidae). This predator species is one of the species introduced from the Neotropics to Africa for the classical biological control of the cassava green mite, Mononychellus tangent (Bond) (Acari: Tetranychidae). Tiphlodromalus aripo is almost exclusively found in the apices of cassava plants (Figure 1) and its persistence in cassava fields seems to depend on this structure. When apices were cut off, very few T. aripo persisted on the cassava plants and none of them could lay eggs, although prey was available (Bakker, 1993). So, apices do not only provide shelter to T. aripo, but also serve as oviposition sites for the predator. However, the predator does not only reduce M. tangent densities in the apices but also in the upper part of cassava foliage (Bakker, 1993; Onzo et al., 2003).

The ‘apex-T. aripo system’ therefore, resembles a mutualistic association between this plant part and the predator. In the apex, the predator probably benefits from protection against harsh environmental conditions and intraguild predation. The plants can also provide alternative food to T. aripo in periods of low prey densities, such as during periods with intensive rainfall or severe drought. Indeed, cassava produces exudates (the extrafloral nectar) that can promote development of the predator. Moreover, the terminal position of the apex and its cavities allow the plant to trap air-borne pollen, such as those of maize, which is quite abundant during the rainy season and known to be highly nutritious to T. aripo. The predator can develop and oviposit well on this food source (Yannick and Hanna, 2003). The presence of the apex is also a key factor in the niche partitioning among T. aripo and the other leaf-inhabiting predatory mite species within the cassava plant. Niche segregation between competitors is one of the most important factors promoting coexistence of competing species (Losey and Denno, 1999), as it prevents direct contact between competing species, thereby reducing the possibilities of intraguild predation.

In West Africa, two common native phytoseid species, Luscus insitus (Pritchard and Baker) and Tiphlodromalus saltis (Denmark and Mun) occur on cassava plants (Yannick and Herren, 1998; Bruce-Oliver et al., 1996). The classical biological control program for cassava green mites as initiated by the International Institute of Tropical Agriculture, IITA,
in 1984 (Yaninek and Herren, 1988), should be credited for importing the exotic predatory mite species, Typhlodromalus maniboti Moraes and T. aripo from Latin America and establishing them in the cassava ecosystem in Africa. These exotic predator species now co-occur in cassava fields and/or on cassava plants and feed on the same prey species with the native species. On cassava, the two native species are exclusively found on leaves and were thought to have negligible impact on M. tanajoa populations (Yaninek and Herren, 1988; Bruce-Oliver et al., 1996). Therefore, T. aripo and T. maniboti are presently the most important natural enemies of M. tanajoa in Africa, given their persistence and impact on the pest mite (Yaninek et al., 1998; Hanna and Toko, 2001; Yaninek and Hanna, 2003). Typhlodromalus maniboti is one of the most common predatory mites associated with M. tanajoa in the Neotropics (Bellotti et al., 1987; Noronha and Moraes, 1989; Moraes et al., 1990; Bakker, 1993; Bonato et al., 1999) and inhabits exclusively the leaves (Bakker, 1993;
Bonato et al., 1999). This predator species is also well established in Africa (Yaninek et al., 1998) where it has a noticeable impact on M. tanajoa densities (Yaninek and Hanna, 2003). However, its establishment is limited to lowland humid regions, rain forests and transition forests ecozones with humid ambient conditions throughout the year (Yaninek et al., 1998).

Typhlodromalus aripo is the most successful biological control agent of the cassava green mite in Africa (Yaninek and Hanna, 2003). Subsequent to its establishment in cassava fields in West Africa, T. aripo has reduced M. tanajoa populations by two thirds, resulting in a 30% to 40% increase in cassava yield (Yaninek and Hanna, 2003). Typhlodromalus aripo is known to disperse at the rate of ca. 12 km during the first year following release, and up to 200 km during the second year following introduction (Yaninek and Hanna, 2003). This dispersal rate is much higher than expected from such a tiny and wingless arthropod. The notorious impact of T. aripo on M. tanajoa populations and its wide distribution in Africa made this predatory mite a unique example of a successful biological control of a mite pest on a field crop at a continent-wide scale (Yaninek and Hanna, 2003). Before being introduced to Africa, little was known about the biology and especially the foraging mode of T. aripo (Bakker, 1993). The success of T. aripo as a biological control agent justifies the increasing interest in identifying and understanding factors that promoted this success and what type of interactions this predator species might have introduced into the arthropod food web on cassava in Africa.

In some predator-prey systems, the effect of the predator on prey dynamics is noticeable for only a few generations, as the predators disappear when prey densities become low and fail to naturally colonize plants when prey densities increase. In such cases, supplemental natural enemy releases are required (McMurtry and Croft, 1997). This was likely the case with the predatory mite Neosculthius idaes (Denmark & Muma), which was established on M. tanajoa but went extinct less than two years after release (Yaninek et al., 1992), suggesting that this predator species failed to adapt to the cassava ecosystem in Africa. Such a natural enemy species does not meet the requirements of classical biological control (Murdoch and Briggs 1996; Thomas and Waage, 1996; Eilenberg et al., 2001), as it is not able to maintain prey or host populations at low densities over a long period and is unable to persist on cassava in Africa. To achieve long-term control of a pest, it is necessary for the natural enemy to survive the troughs in pest population densities and show adequate aggregative functional and numerical responses to any increase in pest densities. This natural enemy must, therefore, be able to cope with the climatic conditions prevailing in the area of its introduction. Among the climatic factors that influence species interactions, precipitation is the most important in terrestrial systems (Spiller and Schoener, 1995). Rainfall is known to induce mortality in M. tanajoa populations (Yaninek et al., 1989), and might, consequently, affect population dynamics of the predators directly or indirectly (i.e. by decreasing prey densities).
I studied the interactions among and within the three trophic levels in the acarine food web in the cassava ecosystem in West Africa. The studies were undertaken in open cassava fields and under semi-controlled conditions (screen-house). In the first part, I investigate the attributes of *T. aripo* that make this predator an effective control agent of the cassava green mite. I start by showing the seasonal fluctuations in the population densities of *M. tanajoa* and *T. aripo* in cassava fields within one host-plant generation to see how this predator responds to changes in prey densities under field conditions (Chapter 2). The predator-prey dynamics between *T. aripo* and *M. tanajoa* was also monitored on a long time scale in the field to assess the persistence of the system and to measure the adaptability of *T. aripo* to its new ecosystem (Chapter 3). Finally, I studied the foraging behaviour of *T. aripo* in open cassava fields (Chapter 4). In the second part of this thesis I present the predator-predator interactions in the cassava ecosystem and their impact on the biological control of the cassava green mite. I evaluated, through screenhouse experiments, the impact of combining the two most important predator species on the population dynamics of the prey and the persistence of the two predator species (Chapter 5). Subsequently, I show that under field conditions, a complex of natural enemies could influence and even complement the efficacy of *T. aripo* in controlling *M. tanajoa* (Chapter 6).

In Chapter 2 of this thesis, I present results of a study of the numerical response of *T. aripo* to fluctuations in *M. tanajoa* densities and characterize the distribution patterns of both the predator and the prey by monitoring their population dynamics in cassava fields during one crop cycle (planting-harvest). Changes in population density of both predator and prey follow the same trend, which was clearly dependent on rainfall pattern. Peak prey and predator densities were observed at the beginning and at the end of the rainy season. However, a slight delay was observed in the response of the predator to changes in prey populations. This time lag is normal from a biological point of view and suggests the presence of a numerical response of *T. aripo* to its prey. Positive numerical and functional responses are generally considered to be among the most important attributes of a good biological control agent (Hassell, 1966, 1978, 1980, 1985; Murdoch et al., 1985). Both *M. tanajoa* and *T. aripo* showed a clumped distribution pattern among-plants. However, *M. tanajoa* is less aggregated in presence of *T. aripo* than it was in absence of its enemies (Yaninek et al., 1991), and *T. aripo* is less aggregated than *M. tanajoa*. The contribution of apex (the extratoliar domatia) to the performance of *T. aripo* was also confirmed by the lower cassava green mite densities encountered on the upper leaves of the cassava plants compared to the within-plant distribution pattern observed before introduction of *T. aripo*. This observation has as immediate consequences for revising the sampling plan presently in use for evaluating population densities of *M. tanajoa* in cassava fields. This is because the first fully developed leaf is no more the adequate sampling unit for *M. tanajoa* when *T. aripo* is present in the system. The cassava leaf with the highest *M. tanajoa* densities has now shifted significantly lower in the foliage (between leaf 8 and leaf 10).
Once I had shown the predator-prey relationship between *T. aripo* and *M. tanajoa* during one crop cycle and the impact of the predator on the distribution patterns of *M. tanajoa*, it was of interest to determine the capacity of the predator to maintain pest populations at low levels over a relatively long period. Chapter 3 presents population dynamics of *T. aripo* and *M. tanajoa* over 7 consecutive years in cassava fields. In the area of observation, cassava is generally harvested 9 to 12 months after planting. However, there are always several adjacent cassava plots planted at different dates, but with the same cultivar. This allowed for the shift to a nearby plot when the one under observation was harvested. The results show a close association of *T. aripo* to cassava green mite and a high tolerance of the exotic predator to the environmental conditions in the study area. The outcome is long-term control of the pest since establishment of *T. aripo*, *M. tanajoa* densities never reached the levels before predator introduction. Population densities of *M. tanajoa* show one higher peak per year, which seems to be influenced by rainfall pattern and one lower (insignificant) peak. Population densities of *T. aripo* also show two peaks per year: one high peak followed by a lower but significant one. The annual model shows that the higher peaks for both *M. tanajoa* and *T. aripo* occur in December whereas the lower peak for *T. aripo* is observed in July. The higher peak of *T. aripo* coincides with the higher peak in *M. tanajoa* densities and occurs at the beginning of the dry season whereas the lower peak in *T. aripo* populations occurs during rainy season when *M. tanajoa* densities are generally low. This lower peak strongly suggests the existence of alternative food sources for the predator. Because in the observation site cassava is generally intercropped with maize, it is thought that when *M. tanajoa* densities were low during the rainy season, *T. aripo* fed on maize pollen. Indeed, maize pollen is generally abundant during the rainy season and *T. aripo* is known to develop and reproduce on a diet of maize pollen (Yaninek and Hanna, 2003). Moreover, the apex of cassava plants (especially hairy cultivars like the one used in this study) might trap pollen and make it available to *T. aripo*, as it resides inside the apex. After the seven years of this study, the population level of *M. tanajoa* has now stabilized whereas that of *T. aripo* continues to decline. However, because of the permanent availability of cassava plots of different age and the prey and predator’s ability to disperse, one should expect stability and persistence of this system of cassava, *M. tanajoa* and *T. aripo* (cf. Nachman, 1987, 2001). Indeed, the chance of simultaneous and permanent extinction of *T. aripo* from all cassava plots of this site is very low. It is, therefore, very unlikely that one might need to reintroduce the predator in this field site.

In Chapter 4 of this thesis, I analysed how *T. aripo* uses the extrafoliar domatia formed by the apices of cassava plants to control *M. tanajoa* populations in the apices and within the upper stratum of the cassava plants. I studied the foraging mode of the predator by carefully monitoring its within-plant movement in cassava fields every 4 hours within a day and in four different periods within the growing season. The results showed that *T. aripo* actively forages on young cassava leaves during the night and returns to the apices before the onset of the day. This foraging mode was found throughout the season and is
independent of prey densities. However, the distance covered by the predator while foraging for prey on the leaves and the number of predator that left the apex to forage on leaves were positively correlated with *M. tanajoa* densities on the upper leaves. All mobile stages of the predator were involved in this diurnal movement, but the females were more abundant among the migrants, probably due to their higher energy demands for egg production. Hiding in the apexes during the day is thought to protect the predator against harsh environmental conditions such as direct exposure to ultraviolet radiation, desiccation and against possible intraguild predation. This protection might be particularly important for inactive stages of the predator such as eggs and moulting stages (Pemberton and Turner, 1989) and for the juvenile stages, since larvae of *T. aripo* are potential prey for intraguild predators such as adult female *T. maniboti* (R. Hanna and A. Onzo, unpublished data). The apex of cassava may therefore be a key factor promoting the success of *T. aripo* in the biological control of *M. tanajoa*. This supports the observations by Bakker (1993) that *T. aripo* disappears from cassava plants from which apex has been removed.

The three chapters presented above showed that *T. aripo* is remarkably well adapted to its prey, to the host plant and tolerates the climatic conditions of its area of introduction. However, it is still an open question how *T. aripo* interacts with the other predatory mites present in the cassava system in Africa, especially with the exotic phytoseiid species *T. maniboti*. Therefore, I conducted two screenhouse experiments in which I monitored the persistence of *T. aripo* and *T. maniboti* in a single and two-species system at two initial predator:prey ratios (1:200 and 1:20, respectively). The results of these experiments are presented in Chapter 5 of this thesis and confirm the efficiency of the two exotic predator species in controlling cassava green mite; however, in the single species systems, *T. maniboti* was superior to *T. aripo* in reducing *M. tanajoa* densities. The combinations of both predator species did not lead to increased control exerted on *M. tanajoa* densities by *T. maniboti* when released alone. Moreover, the interactions between the two species seem negative for both *T. aripo* and *T. maniboti*; their population densities were clearly lower than in the single-species systems, strongly suggesting competition for food and possibly intraguild predation. These interspecific interactions affected *T. aripo* more than *T. maniboti*, especially when the initial predator:prey ratio was high (1:20). Except for *T. aripo*, which disappeared from the last samples in the combined treatments at high initial predator:prey ratio, both species persisted until the end of the experiments, even after prey depletion. This relatively long persistence may be explained by the larger than normal quantities of exudates (extrafloral nectar) produced by cassava plants in the screenhouse. This food source is known to sustain the development of both predatory mites but does not allow for oviposition (Bakker and Klein, 1992; Toko et al., 1994; Yaninek et al., 1998). However, results from screenhouse experiments were in contradiction with field observations where *T. aripo* persists longer than *T. maniboti* and seems to be associated more with *M. tanajoa* than *T. maniboti*. This contradiction may arise from factors in the field that differ from those in the screenhouse, such as climatic conditions, prey composition and abundance.
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habitat complexity and possibility for prey and predators to disperse.

To investigate this, I conducted five field surveys at critical periods of the growing season of cassava to assess the occurrence of all predatory mite species and their joint impact on M. tanajoa densities. The results of these surveys are presented in Chapter 6. They show that T. aripo and T. manibodi did co-occur in the same field with the indigenous predatory mite species. The co-occurrence of the two exotic predator species in cassava fields suggests that they overlap in their ecological requirements; therefore, they are potential competitors (Schausberger, 1998). However, the ecological range of T. aripo is wider than that of T. manibodi; the latter is restricted to a narrow range of ecological zones with particularly high relative humidity such as swamp areas and/or rainforest (Yaninek et al., 1998). The most important finding from these surveys was that, regardless of the status of the field (i.e. swamp or non-swamp), when T. aripo and T. manibodi co-occurred, M. tanajoa densities were lower and T. aripo densities were higher than in fields where T. manibodi was absent, suggesting a complementary action of the two exotic predatory mites on M. tanajoa. Moreover, in presence as well as absence of T. manibodi, occurrence of T. saltus or E. justis in cassava fields generally contributed to lower M. tanajoa densities and higher T. aripo densities. This suggests predation facilitation between T. aripo and the other (leaf-inhabiting) predatory mite species. Results from path analyses showed that T. aripo was assisted, in controlling M. tanajoa populations, by T. manibodi, E. justis and T. saltus and that their contribution varied depending on environmental conditions. For instance, during the wet season, the indigenous predator species T. saltus and E. justis were surprisingly the most important biological agents of M. tanajoa, and during the dry season, their effects on reducing M. tanajoa densities were also important. That T. saltus and E. justis play an important role in controlling M. tanajoa in cassava fields has been underestimated (Yaninek and Herren, 1988; Bruce-Oliver et al., 1996). The availability of alternative food sources such as exudates (Bakker, 1993) and pollen, together with the possibility for predatory mites to disperse within and between fields (Sabelis and Dieke, 1985; Sabelis et al., 1991; McMurtry and Croft, 1997; Peis and Sabelis, 1999) are factors that may promote the coexistence of T. aripo and the other members of the predator guild within cassava fields. Our results provide additional evidence in support of the positive impact of complexes of natural enemy species on the success of biological control (e.g., Charnov et al., 1976; Soluk and Collins, 1988; Soluk, 1993; Morris, 1996; Richeert and Lawrence, 1997; Losey and Denno, 1999).

In summary, this thesis elucidated how T. aripo contributed to the control of the cassava green mite in Africa. The use of the plant apex as a refuge by T. aripo plays an important role in the success of this predator. The predator avoidance behaviour shown by M. tanajoa and availability of alternative food sources has certainly contributed to the persistence of the predator-prey system on cassava. The overlap in the ecological requirements of T. aripo and the other predator species (including T. manibodi), their niche partitioning within
cassava plants and differences in their foraging periods are factors that promote their co-occurrence, which is advantageous for the control of the pest. However, detailed studies are still required to explore the relevant interactions within this food web of plants, herbivorous mites and predatory mites. I have the following recommendations:

1. As shown in this thesis, plant (especially apical) characteristics are of great importance for *T. aripo* and thereby also for *M. tanajoa*, both with respect to their dynamics and distribution within the plant. Thus, the sampling rule developed in this thesis may not apply equally well for all cassava varieties and under every climatic conditions. It is therefore necessary to test the applicability of the proposed sampling plans on other cassava cultivars and/or in different ecological zones (such as eastern or southern Africa) where climatic conditions are significantly different from those observed in West Africa.

2. The thesis provides information on the diurnal use of refuge by *T. aripo* but provides only correlative information on the movement of the predator out of the apex, in relation to prey density and location on the plant. Field manipulations of prey densities are then necessary to test the hypotheses on searching behaviour of *T. aripo* that might explain the observed spatial correlations. Moreover, it would be relevant to determine exactly how apical characteristics influence searching behaviour of *T. aripo* and how they vary among cassava cultivars and wild types. An even more exciting possibility to be explored is to study whether and how apical plant characteristics change upon actual attack by *M. tanajoa* (induced morphological changes in the apex that promote the performance of *T. aripo*).

3. The thesis advocates the importance of indigenous phytoseiid in the biological control of *M. tanajoa*, however, interactions among indigenous and exotic predatory mites needs detailed studies. This should be addressed through manipulative field (as well as laboratory) experiments with exclusion and/or addition of both indigenous and exotic predator species.

4. The time series analysis presented in this thesis was done without any pre-occupied idea of the underlying mechanism. With the understanding provided (in this thesis) on the dynamics of both *M. tanajoa* and *T. aripo*, it is now possible to define one or more mechanistic models specific to this predator-prey system and determine their relative fit to the long-term population time series (see Ellner et al., 1997, 1998; Kendall et al., 1999). Such a model-guided time series analysis should lead to a better identification of the mechanisms underlying predator-prey-plant dynamics and possibly also to better forecasts.

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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REFERENCES


General introduction and summary


Chapter 1


General introduction and summary


Chapter I


