

Of Mites and Men

**Agro-ecological factors affecting the neotropical predatory mite
Typhlodromalus aripo DeLeon and its potential to control the
cassava green mite in the mid-altitudes of Cameroon**

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General introduction

Cassava in Africa

Cassava (*Manihot esculenta* Crantz, 1766; Euphorbiaceae) is a perennial shrub originating from Latin America, most probably from the Amazon region (Hillocks 2002). The starchy tubers are among the most important staple foods of the world – today, it is the fourth-most important source of nutritive energy in the tropics (Alves 2002). Cassava was brought from Brazil to the West Coast of Africa by the Portuguese in the 16th century (Jones 1959) in the context of their trade triangle between Europe, Latin America and Africa. Today, it is grown in the so-called cassava belt of Africa, i.e. everywhere between the two Tropics where annual rainfall is at least 500 mm (Figure 1). In Africa, cassava production has been increasing at annual growth rates of 3 to 4 % for several decades, more due to increases in area under cultivation than due to increases in yield (Hillocks 2002). In Africa, cassava is mostly grown as a food security crop by poor farmer who can not afford inputs such as inorganic fertilizers or pesticides. Cassava is grown and appreciated for its ability to withstand drought, pests and diseases, and acid, infertile soils (Hillocks 2002; Howeler 2002).

Cassava in northwest Cameroon

Cassava reached today's North-West Province (NWP) of Cameroon from the coastal areas only between 1918 and 1920, as a consequence of the influenza pandemic, which had caused labour shortage and had hampered the timely planting and harvesting of traditional crops like yams (Ohadike 1981; Warnier 1984). Mainly produced for home consumption in the beginning, cassava became one of the most important staple food crops of the area around the mid-20th century. Today, cassava is also a source of income. Its processed products, in particular gari¹ and waterfufu², are very popular with the urban population because they are easier to prepare and can be kept longer than other staple crops of the area. In the NWP, as everywhere in Cameroon, cassava is produced by small scale farmers (Simeu Kamdem 1996).

¹ Processed (grated, fermented and roasted in palm oil) cassava tubers. The dry yellowish granules are ready for consumption after mixing with water.

² Processed (fermented, pounded and sieved) cassava tubers. The white paste can be kept up to four weeks. It is eaten with leafy vegetables.

Preliminary studies have shown that it is rather labour than land availability which limits cassava farming since cassava can be grown on marginal soils. How much area can be grown to cassava, when the planting can be done, how much care (weeding) can be given to the crop, and which quantity can be processed into gari largely depends on labour availability, i.e., on the family situation, on the health state of the farmer, and the possibility to hire labour. In the humid savannas of Cameroon (to which the NWP belongs), 80 % of the farmers who are growing cassava also plant it as a sole crop (for commercial purposes). Only 20 % grow it exclusively as an intercrop (for home consumption). Neither manure nor fertilizer nor direct plant protection measures are applied. The average planting density of 20800 plants per hectare is twice as high as recommended (Okeleye et al. 2001). Harvesting is done continuously, and in small quantities. Farmers only harvest what they can process within a few days. Large quantities are only harvested when big sums of money are needed. Processing is done at home or in community infrastructures. Gari is a predominant source of income, but plays an important role in home consumption, too. Bags of gari are sent to the children staying in the boarding schools during the term since food is not provided by the school.

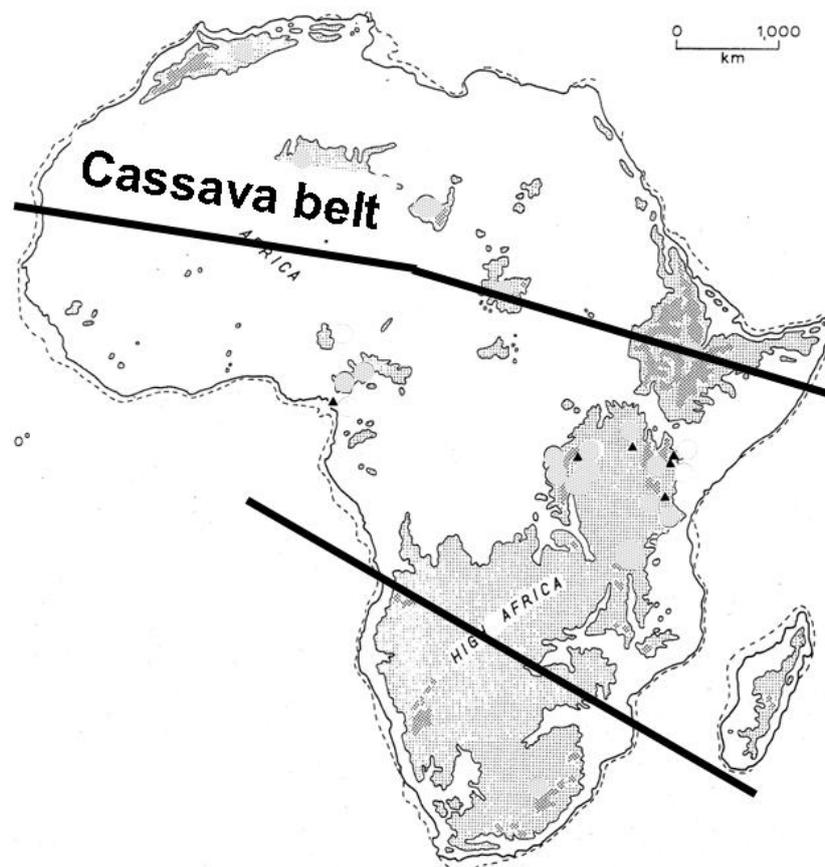


Figure 1. Cassava growing area in Africa. Hatched areas indicate land above 1000 m asl. Map adapted from Taylor (1996).

The inhabitants of the NWP live predominantly in rural areas. Agriculture is characterized by units of family households, mostly growing maize, beans, cassava, yam, cocoyam, fruits and vegetables. Small livestock has a certain importance for household consumption and as a cash reserve (Federer and Bachmann 1994). The area is densely populated, as it is also typical for other sub-humid tropical highlands of Africa. The high population growth causes an increasing pressure on land. The arable land, traditionally between 1100 and 1700 meters above sea level (m asl), has been extended up to 2200 m asl and fallow periods are being reduced, which consequently leads to a decrease in soil fertility (Prinz and Rauch 1987; Federer 1995). This trend promoted the production of cassava since this crop can be grown on soils which are too depleted for the successful production of other staple crops (Prudencio and Al Hassan 1994; Bakia et al. 1999; Hillocks 2002).

The target pest and its antagonists

In 1971, the cassava green mite *Mononychellus tanajoa* (Bondar, 1938) (Acari: Tetranychidae), a neotropical spider mite, was discovered on cassava in Uganda (Lyon 1973) where it was accidentally introduced on cassava cuttings imported from South America (Yaninek and Herren 1988). *M. tanajoa* has since spread over the whole cassava belt of Africa (Yaninek 1988) where it causes estimated yield losses of 30 to 50 % (Markham and Robertson 1987; Yaninek and Herren 1988; Yaninek et al. 1998). The International Institute of Tropical Agriculture (IITA) initiated a project in 1983 to develop control measures against *M. tanajoa* including biological control, host-plant resistance and cultural practices (Herren and Bennett 1984). A complex of indigenous natural enemies was found on cassava, but it was not considered sufficiently effective to control the pest (Nyiira and Mutinga 1977). Initial efforts were made with the introduction and release of 10 phytoseiid predator species from Colombia (Yaninek et al. 1993). The first phytoseiid predators that were effective had been found in 1988 in Brazil and released in the cassava belt of Africa, namely *Neoseiulus idaeus* Denmark and Muma, 1973 (Yaninek et al. 1991) and *Amblydromalus* (syn. *Typhlodromalus*) *manihoti* (Moraes, 1994) (Yaninek et al. 1998). In 1993, *Typhlodromalus aripo* DeLeon, 1967 (Yaninek and Hanna 2003; Hanna et al. 2005) followed. Today, *T. aripo* is established in 20 countries of sub-Saharan Africa (Hanna and Toko 2003). In fields in West Africa where *T. aripo* is present, *M. tanajoa* populations are 16 to 60 % lower than in nearby fields without *T. aripo* (Hanna and Toko 2003; Yaninek and Hanna 2003). Though *T. aripo* is less voracious and develops more slowly than *T. manihoti* and *N. idaeus*, it is more successful in the long run

than the other two phytoseiids in terms of establishment, persistence and spread: *T. aripo* is very efficient in locating its prey (Magalhaes et al. 2003; Gnanvossou et al. 2001), but it does not overexploit it. *T. aripo* is able to survive and develop also on alternative food, such as cassava extrafloral exudates, and maize pollen (Yaninek and Hanna 2003; Gnanvossou et al. 2005). *T. aripo* inhabits the apex of the cassava plant and is better protected from climatic extremes than other leaf dwelling phytoseiids (Onzo et al. 2003; Yaninek and Hanna 2003).

***Typhlodromalus aripo* in northwest Cameroon**

Unpublished data recorded in 1994 in the NWP of Cameroon by the Ecologically Sustainable Cassava Plant Protection project (ESCaPP) (Yaninek et al. 1994) showed moderate to high *M. tanajoa* abundance and moderate to severe damage symptoms. *T. aripo* (*Pir* strain, originating from the Bahia State of Brazil) had been released in the NWP in 1997 through the ESCaPP project and could still be found in one of the five release fields in November 1999 and March 2000, though it was far less abundant than in western and southern Cameroon (Hanna et al., unpublished data) and in Benin (Hanna et al. 2005).

To improve the livelihood of the small farmers in the NWP, the Rural Training Centre (RTC) Fonta started in 1969 as a non-governmental agricultural school with extension activities. Since 1997, RTC Fonta and the Swiss College of Agriculture (SCA) in Zollikofen, Switzerland, have been jointly conducting an applied research project on soil fertility, plant health and selection and dissemination of new genetic material of staple food crops. It is in this context that it was decided to follow up the *T. aripo* releases of 1997, and to make another attempt to settle the predatory mites in the NWP, using a more controlled approach than during the ESCaPP releases. At the outset, the following possible causes for the low establishment of *T. aripo* after the first releases were suspected: (1) In the NWP, the predatory mite's climatic requirements might not be met, e.g. temperature during a certain time of the year may be too low or humidity may be insufficient for proliferation. (2) The poor establishment of *T. aripo* might be partly explained by the fact that *T. aripo* prefers cassava cultivars with hairy apices (Hanna et al. 2000) which are not common in the NWP. (3) There were reports (Fon, personal communication) that release fields may have been affected by bush fires in adjacent fallow land in the dry season. (4) Finally, the practice reported from the NWP to clip the apices and top leaves of the cassava plant to prepare traditional dishes, preferably during the dry season, could hamper establishment of *T. aripo*. It was apparent that the agro-ecological requirements of *T. aripo*, and the seasonal dynamics of pest and predator, needed further studies if we want to know the predator's potential to control the pest mite *M.*

tanajoa in mid-altitude northwest Cameroon. Interacting with farmers was considered very important in identifying strategies and developing options to settle *T. aripo* since the key for successful establishment seemed to be habitat management. Initial ideas in this direction included: vegetation management, growing mixtures of cassava varieties preferred by farmers and predators, adaptation of cassava harvesting practices and creation of predator reservoirs managed by farmers. In the course of this study, it became apparent that climatic reasons and corresponding pest and predator dynamics are largely responsible for poor establishment (cause 1), while suitable cassava cultivars and habitat management can only marginally offset or mitigate these limiting conditions (cause 2). Therefore, the remaining possible causes 3 and 4 were not further investigated.

The ecological setting/context of the study

Most of the NWP of Cameroon lies within a sub-humid, mid-altitude climate, characterized by a unimodal rainfall distribution with eight humid months (March through October) and an average annual precipitation of 2300 millimeters. Mean annual temperatures at Fonta (near the provincial capital Bamenda) on 1294 m asl are 21 °C with the coolest months in July and August (20 °C) and the hottest month in March (23 °C). Mean annual relative humidity (RH) is 78 %. The driest month is February with 55 % RH and the most humid month is August with 91 % RH (own data; mean of the years 2002 to 2004). Soil properties are very heterogeneous, the younger volcanic soils being more fertile than the older and heavily weathered soils (Prinz and Rauch 1987).

The hilly area with valleys at 600 m asl and mountain peaks at 2500 to 3000 m asl is largely covered with a Guineo-Congolian mosaic of lowland to mid-altitude forest and secondary grassland, and afro-montane vegetation (forest, shrub land, and primary grassland above the timberline) (White 1983). Savanna as well as most of the forest of the area is of secondary nature (Letouzey 1968): Human activities such as slash-and-burn agriculture, population increase and movements and the introduction of brasswork and the respective use of firewood are assumed to be the cause for the deforestation and conversion to the Grassfields as we know the area today (Warnier 1984). It can be assumed that under the present climatic conditions, the vegetation would transform back to forest if anthropogenic influence stopped (Letouzey 1968).

Objectives and outline of the thesis

The objective of this thesis was to explore the potential of the predatory mite *T. aripo* as an agent to control the pest mite *M. tanajoa* in the mid-altitudes of the NWP of Cameroon. Options to make *T. aripo* effective in *M. tanajoa* control were to be tested.

As a first step, we explored the potential for a successful long-term establishment of *T. aripo* in the mid-altitudes of the NWP of Cameroon (**Chapter 2**). After the experience of ESCaPP with the *Pir* strain, we considered an additional attempt of working with *T. aripo* promising because: (1) Another strain of *T. aripo* (*Bam* strain), collected in the Minas Gerais State of Brazil showed life table data (Negloh 2000) which let assume a better adaptation to the climatic conditions of the NWP than the previously used *Pir* strain. (2) Meanwhile, evidence had been growing that cassava plants with hairy apices are preferred by *T. aripo* (Hanna et al. 2000). We supposed that planting hairy cassava cultivars at the release sites increases the chance for a successful establishment. As no data on *M. tanajoa* dynamics existed for the mid-altitudes with unimodal rainfall pattern, the population cycle of the pest mite was also studied. In two subsequent years, two strains of *T. aripo* (*Bam*, *Pir*) were released in villages of the mid- and low-altitudes. The fields were monitored monthly for 16 months and 12 months, respectively.

Based on the life table data of Negloh (2000), we looked more closely into the potential of the newly imported *T. aripo* strain from Minas Gerais (**Chapter 3**). The objective of this study was to determine with a greenhouse population-level experiment the short-term dynamics of the *Bam* (from Minas Gerais) and the *Pir* (from Bahia) strains of *T. aripo* and their effects on *M. tanajoa* populations, parallel to the field evaluations of the two strains done in **Chapter 2**.

In the studies described in **Chapter 2** it became evident that *T. aripo* dynamics are strongly affected by the dry season. Thus, the overall objective of the work reported in **Chapter 4** was to identify options to prolong the predators' presence into the dry season and to promote its fast recolonization of cassava to increase predation on *M. tanajoa*. The hypotheses were: (i) Habitat type has an impact on *T. aripo*'s dry season presence; (ii) *T. aripo*'s disappearance in the dry season and its reappearance in the beginning of the rainy season are depending on relative humidity in the habitat; (iii) morphological features and the physiological state of the host plant are able to mitigate adverse climatic conditions in the habitat, and therewith have an effect on *T. aripo*'s dry season presence on the plant. We selected a village with a high diversity of habitats and released predators on sites in grassland hills, in multiple cropping

areas and in riparian forests. Since the degree of cassava apex pubescence is known to have an effect on *T. aripo* presence, we planted cassava genotypes with hairy, semi-hairy and glabrous apices in each habitat type. To support field results, we conducted a growth chamber experiment including three levels of relative humidity (33 %, 55 % and 85 %) and four levels of substrates simulating host-plant morphological and physiological characteristics (hairy apices, glabrous apices, cassava leaves, empty mini-Petri dishes).

In the mid-altitudes of the NWP of Cameroon, as in some other mid-altitude areas and drier lowland savannas of sub-Saharan Africa which are characterized by long (\geq five months) dry seasons, *T. aripo* disappears from its habitat in the cassava apex during the dry seasons and reappears after the onset of rains. It is not known, however, where and how the predator survives during the dry season. In the research reported in **Chapter 5**, we conducted a field enclosure experiment of cassava plants with the objectives to determine if (i) *T. aripo* recolonizes the cassava plant from the surrounding vegetation, if (ii) it survives in the soil or leaf litter below the cassava plant, and if (iii) it survives at very low densities in the apex. Because the mode of survival is expected to have an effect on the rates of recolonization, we compared the timing of the predator's reappearance in the cassava apex between the different enclosure treatments. During a vegetation survey conducted in the frame of the research reported in this chapter, two new phytoseiid species were found. They are described in the **Appendix**.

During the work with *T. aripo* it became clear that cassava cultivars will play an important role in the control of *M. tanajoa*. Either cassava cultivars with hairy apices will be needed to foster the establishment of *T. aripo* or resistant or tolerant cassava cultivars have to be developed as an alternative option to control *M. tanajoa* if *T. aripo* fails to establish. The question arose how RTC Fonta, being a key actor in this venture, should best manage their cassava variety selection and dissemination scheme to make new varieties available to farmers. Thus, the objective of the work reported in **Chapter 6** was to find the most effective way of cassava variety selection in the agro-ecologically diverse environment of the NWP of Cameroon. By means of a formal on-farm variety trial, farmer-designed variety trials, field visits, semi-structured farmer interviews and an assessment of farmers' ability to differentiate between new varieties, we explored to which extent decentralized and participatory cassava variety selection are useful, and how much we can build on farmers' own experimentation and expertise.

In **Chapter 7**, a general discussion with conclusions emerging from this thesis work is presented. This chapter focuses on the practical implications of the results and experiences and on the proposed way forward in *M. tanajoa* control in the mid-altitude of northwest Cameroon.

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TWO

Seasonality and persistence of two strains of the neotropical phytoseiid mite *Typhlodromalus aripo* and their potential to control the cassava green mite in the mid-altitudes of Cameroon

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ABSTRACT

In 1993, *Typhlodromalus aripo* DeLeon, an exotic predatory mite from Brazil, was released in Africa for the first time to control the cassava green mite *Mononychellus tanajoa* (Bondar). It has now successfully established in 20 countries of sub-Saharan Africa. It never established well in the mid-altitude areas of the North-West Province of Cameroon, however. This study documents another attempt to launch *T. aripo* in this area, using a strain which is supposedly better adapted to the cooler climate, and using cassava varieties which are known to be suitable host plants. As no data on *M. tanajoa* dynamics exist for the mid-altitudes areas with unimodal rainfall pattern, the pest mite was also studied. In two subsequent years, two strains of *T. aripo* (*Bam*, *Pir*) were released at sites of the mid- (1100 – 1300 meters above sea level) and lower (600 – 850 meters above sea level) altitudes. The fields were monitored monthly for 16 months and 12 months, respectively. We found that *M. tanajoa* populations had their peak in the end of the dry season, which is in contrast to other regions in Africa where they peak shortly after the onset of the dry season. The predator's presence dropped to very low levels in the dry season, and recovered only four to eight weeks after the rains had started again. Despite this asynchrony of predator and prey, *T. aripo* was able to persist in both altitudes for one year or more, most probably because of its ability to develop on alternative food. A control effect of *T. aripo* on the pest mite could not be found. The great challenge for *T. aripo*'s long-term persistence was the survival of the crop harvest. As it did not spread to neighbouring fields in the mid-altitudes, it was not able to persist beyond one cropping cycle. It did spread and survive for more than one cropping cycle in the lower areas, though. The *Pir* strain had an advantage over the *Bam* strain in the first three months after release. On a longer term, the altitude effect was more important for the predators' presence than the strain effect, the lower altitudes being more favourable than the mid-altitudes. Effectiveness of *T. aripo* to control *M. tanajoa* in mid-altitude areas is doubtful, because of the asynchrony of predator and pest mite population cycles, and because of the predator's difficulties to spread on its own.

Key words. Biological Control, spider mites, phytoseiids, release, *Manihot esculenta*

INTRODUCTION

Classical biological control is the utilization of exotic species as natural enemies, and their establishment in a new habitat, to reduce the damage caused by pest organisms (DeBach and Rosen 1991). The main targets for classical biological control are pests which have invaded – or were accidentally imported – from another place, sometimes from another continent. The earliest spectacular success in classical biological control dates back to the end of the 19th century, when the Australian ladybird beetle *Rodolia cardinalis* (Muslant, 1850) (Coleoptera: Coccinellidae) was introduced in Californian citrus orchards to control the cottony cushion scale *Icerya purchasi* Maskell, 1876 (Hemiptera: Margarodidae) (Greathead 2003). Modern classical biocontrol became possible through fast air shipments which led to an empiric trial-and-error approach, but not much effort was made to determine an optimal introduction strategy in advance. It was cheaper to send many species and to see which ones established, than to follow a predictive approach and to carefully evaluate and select a few species for a targeted introduction (Ehler 1990). Today, classical biological control has proven its effectiveness in a wide range of crops and pests all over the world, and it is a well established approach to control insect and weed pests. Fitness and adaptability, high searching capacity, sufficient power to increase (relative to that of the prey), host specificity and host preference, synchronization with the host and its habitat, density-dependent performance, detection and responsiveness to the condition of the host, and good competitive ability are attributes of successful natural enemies (Huffacker et al. 1977 in: Ehler 1990). Experience shows that the origin of the control agent is crucial for later establishment and control success (Hoy 1976; Greathead 2003). To find natural enemies originating from similar ecoclimatic conditions is one of the concerns and challenges in classical biological control. The concept of climate matching helps to evaluate, if a biocontrol agent has a chance to establish and spread in a new locality (Worner 1988; Phillips and Baird 1996; Day and McAndrew 2002; Iline 2004). Size and number of releases are important (Greathead 1986), as well as alternative food sources (Cullen and Snowball 1979) and alternative habitats (Vargo et al. 1993). The ability of dispersal and overwintering (Pickett and Pitcairn 1999), and macro-predation (van Klinken et al. 2003) are other critical issues. Also, host plants can affect natural enemies directly or indirectly through multitrophic interactions (Bottrell et al. 1998). Many of these issues also affected the releases achievements of the study presented in this paper.

In 1971, the cassava green mite *Mononychellus tanajoa* (Bondar, 1938) (Acari: Tetranychidae), a neotropical spider mite, was discovered on cassava in Uganda (Lyon 1973), where it was accidentally introduced on cassava cuttings imported from South America

(Yaninek and Herren 1988). *M. tanajoa* has since spread over the whole cassava belt of Africa (Yaninek 1988), where it causes estimated yield losses of 30 to 50 % (Markham and Robertson 1987; Yaninek and Herren 1988; Yaninek et al. 1998). The International Institute of Tropical Agriculture (IITA) initiated a project in 1983 to develop control measures against *M. tanajoa* including biological control, host-plant resistance and cultural practices (Herren and Bennett 1984). A complex of indigenous natural enemies was found on cassava, but it was not considered sufficiently effective to control the pest (Nyiira and Mutinga 1977). Initial efforts were made with the introduction and release of 10 phytoseiid predator species from Colombia (Yaninek et al. 1993). The first phytoseiid predators that were effective, were found in 1988 in Brazil and released in the cassava belt of Africa: *Neoseiulus idaeus* Denmark and Muma, 1973 (Yaninek et al. 1991) and *Amblydromalus* (syn. *Typhlodromalus*) *manihoti* (Moraes, 1994) (Yaninek et al. 1998). In 1993, *Typhlodromalus aripo* DeLeon, 1967 (*Pir* strain, originating from the Bahia State of Brazil) (Yaninek and Hanna 2003; Hanna et al. 2005) followed. Today, *T. aripo* is established in 20 countries of sub-Saharan Africa (Hanna and Toko 2003). In fields in West Africa where *T. aripo* is present, *M. tanajoa* populations are 16 to 60 % lower than in nearby fields without *T. aripo* (Hanna and Toko 2003; Yaninek and Hanna 2003). Though *T. aripo* is less voracious and develops more slowly than *T. manihoti* and *N. idaeus*, it is more successful in the long run than the other two phytoseiids in terms of establishment, persistence and spread: *T. aripo* is very efficient in locating its prey (Magalhaes et al. 2003; Gnanvossou et al. 2001), but it does not overexploit it. *T. aripo* is able to survive and develop also on alternative food, such as cassava extrafloral exudates, and maize pollen (Yaninek and Hanna 2003; Gnanvossou et al. 2005). *T. aripo* inhabits the apex of the cassava plant and is better protected from climatic extremes than other leaf dwelling phytoseiids (Onzo et al. 2003; Yaninek and Hanna 2003).

Unpublished data recorded in 1994 in the North-West Province (NWP) of Cameroon by the Ecologically Sustainable Cassava Plant Protection project (ESCaPP) (Yaninek et al. 1994) showed moderate to high *M. tanajoa* abundance and moderate to severe symptoms. *T. aripo* was released in the NWP in 1997 through the ESCaPP project and was still found in one of the five release fields in November 1999 and March 2000, though it was far less abundant than in western and southern Cameroon (Hanna et al. unpublished data), and in Benin (Hanna et al. 2005). Next to unfavourable climatic conditions, *T. aripo* abundance seems to be affected by the prevalence of cassava cultivars with hairy apices (Hanna et al. 2000).

The objective of this work is to study the dynamics of *M. tanajoa* in a unimodal rainfall pattern in the mid-altitudes. Respective work has been done for areas with a bi-modal rainfall pattern in the lowlands of Benin by Hanna et al. (2005) and in the mid-altitudes of Kenya by Skovgard et al. (1993). We also wanted to explore the potential for a successful long-term establishment of *T. aripo* in the mid-altitudes, and to identify the necessary cues. Another attempt to work with *T. aripo* was considered promising because: (1) Another strain of *T. aripo* (*Bam* strain), collected in the Minas Gerais State of Brazil showed life table data (Negloh 2000) which let assume a better adaptation to the climatic conditions of the NWP than the previously used *Pir* strain. (2) The releases were done on cassava varieties with hairy apices which were purposefully selected for their suitability to host *T. aripo*.

MATERIAL AND METHODS

Selection of release sites. Two predator release experiments were conducted in the North-West Province of Cameroon in 2002/2003 and 2003/2004 cassava growing cycles with the objective of comparing the establishment, seasonality and persistence of lowland and mid-altitude strains of *T. aripo*. For the 2002/2003 experiment, a total of 12 sites were selected, of which nine sites were in the mid-altitudes (between 1100 and 1300 meters above sea level (masl)), and three sites were in the lower altitudes (between 600 and 850 m asl). One cassava field was established at each site in June 2002. At both altitudes, each site was randomly assigned to one of three treatments: release of *T. aripo Bam* strain; release of *T. aripo Pir* strain; no predator release as a control (see Figure 1 for the location of the release sites, and Table 1 for their coordinates, altitudes, and ecoclimatic details). Two release sites, one where the *Bam* strain had been released and one where the *Pir* strain had been released, were later excluded from the study, as the plants had been destroyed either by livestock or bushfire. The two cultivars TMS 91/02327 and TMS 91/0234 which are good host plants for *T. aripo* (Zundel, unpublished data), were planted in equal proportions next to each other at each site. A field was 20 x 16 meters, and the net plot was planted with 144 plants (72 plants per variety), at a planting distance of 1 x 1 meter. Release sites were spaced a minimum of two kilometers apart to minimize between-site colonization by the *T. aripo* strains during the experiments.

A slightly different approach was taken for site selection in the 2003/2004 experiment. The same three treatments (*Bam* strain, *Pir* strain, no predator release as a control) were randomly assigned to three villages, in both of the two altitudes (lower altitude, mid-altitude).

In each of the total six villages, we had four trial sites with one field each. The two cassava varieties TMS 92/0326 and TME1, which showed to be even more suitable to *T. aripo* than the two varieties used in the previous experiment, were used in the 2003/2004 experiment. Planting arrangement within fields and minimum distance between fields was the same as in the 2002/2003 experiment.

Table 1. Overview of release sites, release years, ecoclimatic details, *Typhlodromalus aripo* strains (*Bam*, *Pir*) released, and *T. aripo* persistence.

Village	Year	Coordinates	Alt. (m asl)	Mean T (°C) of hottest month (Mar 04)	Mean RH (%) of driest month (Feb 04)	Sr.	Recovery period (months)
Bambui	2002	N 06°00'13'' E 10°13'09''	1254	-	-	<i>Bam</i>	1
Bamessing	2002	N 05°59'40'' E 10°21'03''	1266	24.9	31	<i>Bam</i>	3
Guneku	2002	N 06°01'34'' E 09°58'12''	1281	-	-	<i>Pir</i>	3
Babanki	2002	N 06°05'58'' E 10°13'45''	1133	22.8	42	<i>Pir</i>	3
Matrufon	2002	N 05°58'26'' E 10°05'46''	1251	21.9	63	<i>Bam</i>	14
Mile 20	2002	N 06°07'50'' E 10°07'44''	832	23.6	61	<i>Bam</i>	25
Mile 24	2002	N 06°08'56'' E 10°05'29''	637	24.5	62	<i>Pir</i>	25
Mankon	2003	N 05°59'04'' E 10°06'42''	1233	21.4	62	<i>Bam</i>	12
Chomba	2003	N 05°53'56'' E 10°06'11''	1267	21.0	60	<i>Pir</i>	12
Mile 20	2003	N 06°07'45'' E 10°07'27''	819	23.6	61	<i>Bam</i>	12
Mile 24	2003	N 06°08'51'' E 10°05'29''	613	24.5	62	<i>Pir</i>	12

Alt. = altitude; m asl = meters above sea level; T = temperature; RH = relative humidity; Sr. = strain.

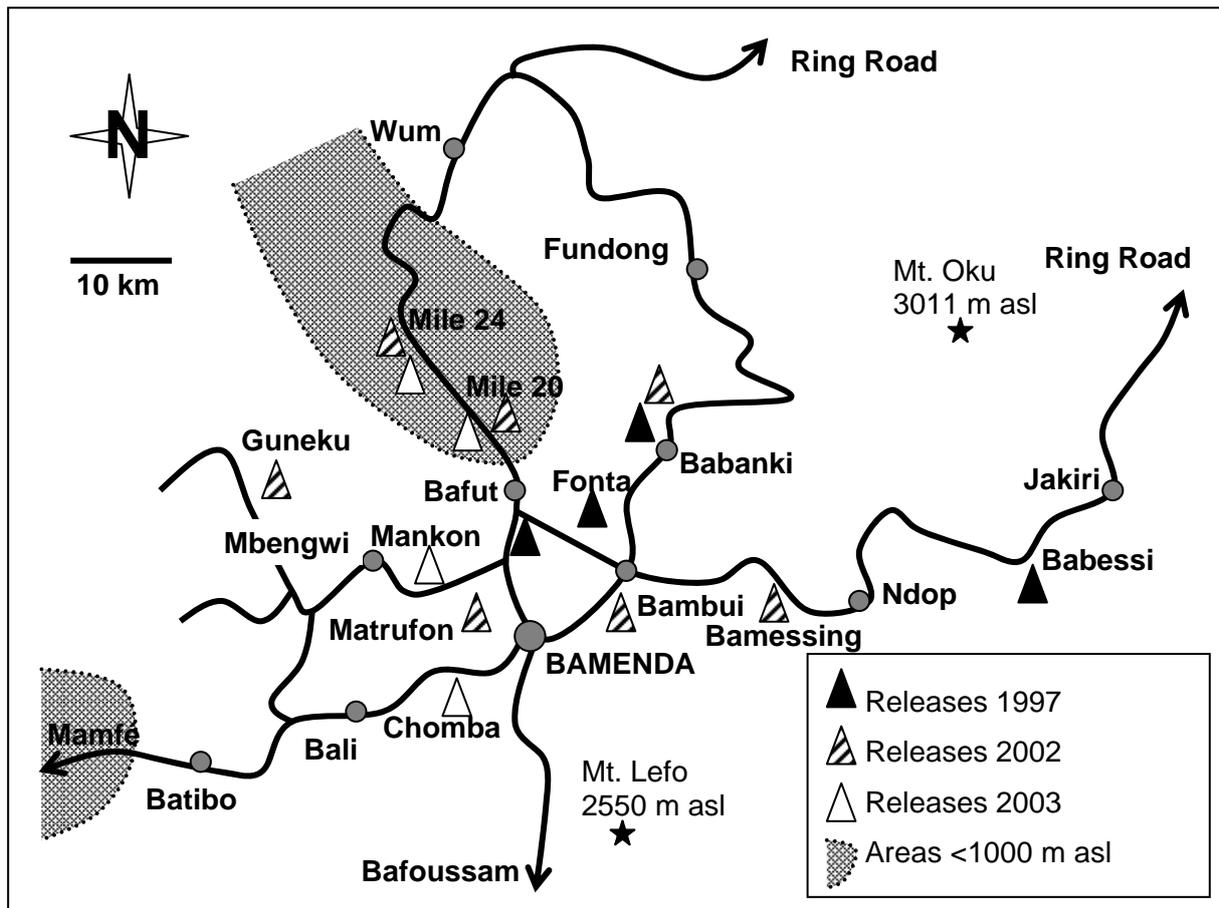


Figure 1. Map of *Typhlodromalus aripo* releases from 1997 to 2003 in the North-West Province of Cameroon.

Source of predatory mites. The predator populations used in the experiments were provided by the International Institute of Tropical Agriculture, Biological Control Centre for Africa located in Cotonou, Republic of Benin. The *Bam* strain has been maintained in the laboratory on detached cassava leaves at 25 ± 1 °C and 80 ± 10 % relative humidity since 1997. The predators were multiplied in semi-natural rearing facilities in a screenhouse prior to packing and shipping to Cameroon. The *Pir* strain was collected in cassava fields near Cotonou, where it had been present since 1994. In preparation for shipping, the predators were aspirated into disposable seven centimeters long plastic pipette tips, each tip containing 30 female predators. The pipette tip was sealed with parafilm at one end while the other end was covered with mite-proof gauze (Mégevand 1997). The predators were then transported to Cameroon in a styrofoam box containing cooling elements. At the time when the predators were released (maximum of 96 h after packing), mortality in the tips was 20 to 30 %. The two strains of *T. aripo* were released at each of their respective target fields on randomly pre-selected and

labelled sample plants, by attaching the tips containing the predators with scotch band to the stem close to the apex.

Mite and weather monitoring. In 2002, a monthly inspection of the fields and surrounding areas between planting and release indicated that *T. aripo* was absent from all the sample plants and the surrounding fields. In the pre-release inspection of 2003, *T. aripo* was found in surrounding fields of the release fields in the lower altitudes, but not in the release fields, and not in the mid-altitudes. Sample plants, 10 and eight respectively for the 2002/2003 and 2003/2004 experiments, were randomly selected from the 72 plants of each variety in a field and tagged for subsequent sampling. For the 2002 release, sampling of the release field was done until harvest in January 2004. We continued to monitor in monthly intervals – through May 2004 – for *T. aripo* presence (on 30 randomly selected plants) in the immediate vicinity (within 100 meters) of the harvested field. For the 2003 release, sampling was done in the release fields until one year after release (i.e., until October 2004). In both release experiments, sampling consisted of monitoring the presence/absence of *T. aripo* in the cassava apices with 4x head lenses in a non-destructive manner and of monitoring the densities (only mobile stages) of *M. tanajoa*.

In addition to mite monitoring, we collected climatic data from a weather station located at RTC Fonta (1294 m asl). A self-contained logger (HOBO H8 Pro from Onset Computer Corporation) recorded temperature with an internal sensor (accuracy: +/- 0.2 °C) and relative humidity (accuracy: +/- 3%) in 12-minute intervals. Rainfall was measured with a rain gauge at the same site. The Fonta climatic data were supplemented with temperature/humidity loggers which were installed in selected release sites as from 4 January 2004 onwards (see Table 1).

Data analysis. We were interested in testing for the effects of strain and altitude on establishment and persistence of *T. aripo* over the entire cassava crop cycle, and over specific seasonal periods which are known to have a substantial effect on *T. aripo* field dynamics. *T. aripo* presence was the dependent variable in the general linear model (GLM) repeated measures analyses (NCSS 2000), and altitude and predator strain were the between-subject factors. Site was the subject variable and time (i.e., sampling months) was the within-subject factor. The control treatment (no predator release) was excluded from the analysis. In preliminary analyses, the variety effect was not significant in the studies of 2002 and 2003 and therefore the data from each field were pooled across varieties. Box's M test for equality

of between-group covariance matrices could not be performed because we had more levels of the within-subject factor (i.e., sample months of the time factor) than subjects per group (i.e., sites per treatment). For the dependent variable (*T. aripo*, expressed in proportion of plants infested in a field), arcsine-transformation was applied. In a first test, the data of the two experiments of 2002 and 2003 were combined and analyzed in view of potential effects of the factors altitude, strain and year, and their interactions. The number of replicates (sites) of each treatment was unbalanced. In a second test, the experiments of each year were analyzed separately. In the 2003 release, we had four sites as replicates for each treatment, and we studied the potential effects of altitude and strain, and their interaction. In the 2002 release, we had an unbalanced number of release sites as replicates. Because we had only one replicate for each of the treatments in the lower altitudes, we pooled the data across strains to analyse altitude effects, and we pooled the data across altitude to look at strain effects. The division into different time periods was done as follows: As we know from other studies (Zundel et al., manuscripts in preparation), *T. aripo* presence is strongly affected by the climatic seasonality, i.e., by rainy and dry season. Therefore we looked at the whole experimental period of 16 months in the 2002 experiment, at the complete seasonal cycle of 12 months in both experiments, at the first dry season after release (October/November to February) in both experiments, at the rainy season (March to October) in both experiments, and at the second dry season (November to January) in the 2002 release.

The question whether predator release had an effect on *M. tanajoa* densities, was also addressed. For this purpose, the same GLM repeated measures analyses as for *T. aripo* presence was run, with altitude and predator release (the two strain treatments were pooled) as between-subject factors, site as subject variable, and time (i.e., sampling months) as within-subject factor. In preliminary analyses, the variety effect was not significant in either study and therefore the data from each field were pooled across varieties. The dependent variables were transformed to $\log_{10}(x + 1)$ for *M. tanajoa* (expressed in number of mobile mites per leaf averaged over all plants within a field to reduce the heterogeneity of error variance). The procedure regarding the analysis of the two experiments was similar to the procedure used for *T. aripo* presence analysis. However, the seasonal periods which were analyzed separately, had been defined differently, because, in our study area, *M. tanajoa* populations peak in the transition from dry to rainy season. We therefore looked at the whole experimental period of 16 months in the 2002 experiment, at the complete seasonal cycle of 12 months in both experiments and in the combined analysis, and at the peak period of the pest mite (defined as: months with > 10 mobiles on the first fully developed leaf in any of the treatments; in the

combined analysis: January to June; in the 2002 experiment: January to June; in the 2003 experiment: January to April). In addition to the repeated measures GLM, we analyzed the means of *M. tanajoa* densities during the peak period with altitude and predator release as the independent variables, and with *T. aripo* presence as a covariate.

RESULTS

Population dynamics of *T. aripo*. After the release in September 2002, the predator's populations developed as follows (Figure 2): In the mid-altitudes, the *Bam* strain remained on 47 to 63 % of the sample plants for three months. In January 2003, the population broke down sharply, and the predators disappeared in February 2003. They were back in the apices on 2 % of the sample plants in March 2003. In July and August 2003, they reached a peak of 15 % of the sample plants. In September 2003, the densities began to decrease, and in December, the *Bam* strain had disappeared from all sample plants. The *Pir* strain, in the same altitude, remained on a level of 55 to 70 % of the sample plants for three months after the release. The predators of this strain had disappeared from all sample plants in January 2003, and did not return during the time period of the experiment. In the lower altitudes, the *Bam* strain had to be released a second time, because rodents had severely damaged the field after the first release. Consequently, the predators reached a level of 22 % of the sample plants in December 2002. They disappeared from the sample plants in February 2003, reappeared in May 2003, and reached a peak of 72 % in July. The *Bam* strain underwent a temporary breakdown in September 2003, when colonized plants dropped to 6 % of all sample plants. The predators recovered fast, though, and reached a second peak in December 2003, with 94 % of the sample plants colonized. In January 2004, the population had reduced to 31 % of the sample plants. The *Pir* strain in the lower altitudes maintained a level of 67 to 100 % of sample plants colonized for four months after the release. They disappeared from the sample plants in a sharp decline between January and February 2003, and reappeared only in June 2003. The *Pir* population reached a peak level of 67 to 100 % of plants colonized from August to December 2003. The predators of this strain had disappeared in January 2004 from all sample plants.

In the release 2003 (Figure 2), in the mid-altitudes, the *Bam* strain remained on 94 to 100 % of the sample plants in the two months after the release. Densities declined to 9 % in April 2004, immediately recovered, and peaked in July 2004 with 22 % of the sample plants colonized. After that, densities fell to a level of 0 to 3 % of the sample plants in September and October 2004. The *Pir* strain, in the mid-altitudes, maintained a level of 94 to 100 % of

the sample plants until three months after the release. The predator population broke down to a minimum of 6 % of plants colonized in April 2004, recovered immediately, and reached a peak of 28 % of the sample plants colonized in June and July 2004. After that, densities descended to a level of 5 to 8 % of the sample plants in September and October 2004. In the lower altitudes, the *Bam* strain began at a density of 78 to 91 % of the sample plants colonized. The following decline reduced the predator's presence to 3 % of the sample plants in February 2004. The populations recovered instantly and peaked in July 2004 with 67 % of the sample plants colonized. They remained on a high level until October 2004, not dropping below 50 % of the sample plants inhabited. The *Pir* strain kept a level of 91 to 100 % of the sample plants colonized during the first three months after the release. Then, it declined to a minimum in April 2004 with a density of 9 % of the sample plants having the predators. After a short recovery phase, the population peaked in June 2004 being present on 74 % of the sample plants. Until October 2004, the population did not go below 45 % of the sample plants.

Factors affecting the presence of *T. aripo*. In the GLM repeated measures analysis of the combined experiments of 2002 and 2003, in the time period of 12 months, we found that *T. aripo* presence was higher in the lower altitudes than in the mid-altitudes (Table 2). If split into two climatic seasons, we found that, in the dry season, the *Pir* strain performed better than the *Bam* strain, and in the rainy season, the lower altitudes were more favourable to *T. aripo* presence than the mid-altitudes. An interaction between altitude and strain did not occur at any time. Site and time of sampling had an effect in all three time periods analyzed. The year of the experiment made a difference over the 12-months period and in the dry season, but not in the rainy season. Interactions between altitude and sampling time were significant in all three time periods. Interactions between strain and sampling time, and year and sampling time, were important only in the 12-months period. In the experiment of 2003 alone, we found the same picture as in the analysis of the combined experiments – except that it was not the interaction between altitude and sampling time which was significant in the dry season, but the interaction between strain and sampling time. In the experiment of 2002, over the whole cassava cropping cycle of 16 months, in the rainy season and in the second dry season, the lower altitudes were the more suitable area for *T. aripo* presence. The strain effect was not significant in any time period analyzed. Site and sampling time effects, and the interaction between altitude and sampling time, were significant in all time periods (Table 3).

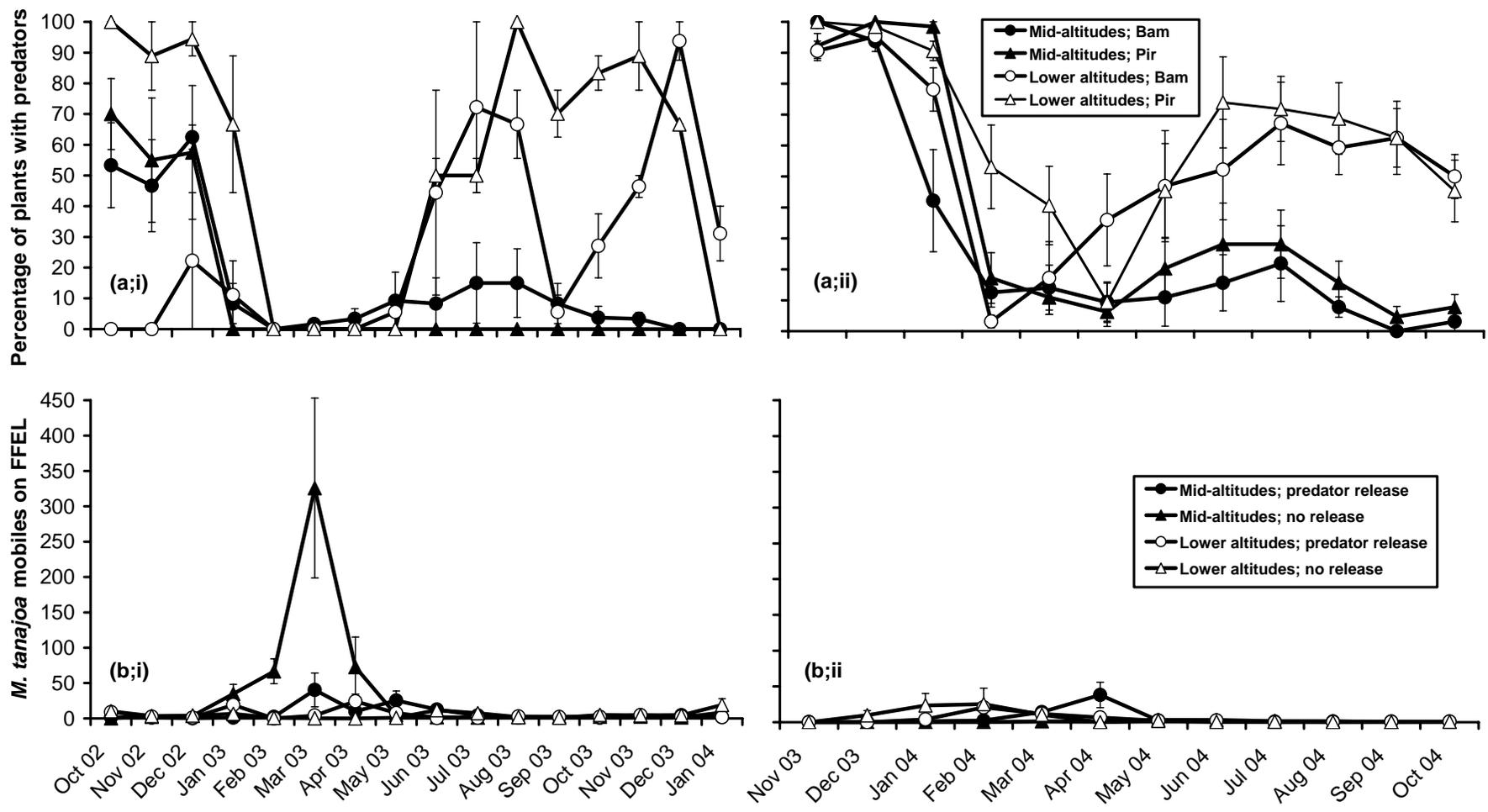


Figure 2. Seasonal dynamics of two *Typhlodromalus aripo* strains (*Bam*, *Pir*) (a) and *Mononychellus tanajoa* (b) in two altitudes (mid-altitudes: 1100 to 1300 meters above sea level; lower altitudes: 600 to 800 meters above sea level) of the NWP, Cameroon, with releases in October 2002 (i) and in October 2003 (ii). *T. aripo* abundance is expressed as mean percentage of plants with predators. *M. tanajoa* data points are mean numbers of mobile *M. tanajoa* on the first fully expanded leaf (FFEL). Vertical bars are standard errors of the means.

Table 2. Results of repeated measures analyses on *Typhlodromalus aripo* presence depending on altitude and strain, in the combined release experiments of 2002 and 2003, and in the 2003 experiment alone, over various time periods.

Source of variation	Releases 2002/2003 combined				Release 2003			
	DF	SS	F-Ratio	p-value	DF	SS	F-Ratio	p-value
<i>12 months</i>								
Altitude	1	6.46	8.24	0.0117	1	6.63	7.94	0.0155
Strain	1	0.78	0.99	0.3346	1	0.87	1.04	0.3283
Altitude*Strain	1	0.73	0.93	0.3513	1	0.00	0.00	0.9699
Site	15	11.75	12.73	<0.0001	12	10.02	12.02	<0.0001
Time	11	20.21	29.86	<0.0001	11	30.38	39.76	<0.0001
Altitude*Time	11	5.50	8.13	<0.0001	11	4.09	5.35	<0.0001
Strain*Time	11	1.26	1.86	0.0479	11	1.57	2.05	0.0280
Altitude*Strain*Time	11	0.79	1.17	0.3143	11	1.48	1.94	0.0397
Year	1	5.39	6.88	0.0192				
Altitude*Year	1	0.00	0.01	0.9385				
Strain*Year	1	0.00	0.00	0.9452				
Altitude*Strain*Year	1	0.67	0.85	0.3713				
Time*Year	11	3.24	4.80	<0.0001				
Altitude*Time*Year	11	0.78	1.15	0.3255				
Strain*Time*Year	11	1.25	1.84	0.0513				
Altitude*Strain*Time*Year	11	1.07	1.58	0.1077				
<i>Dry season</i>								
Altitude	1	0.12	0.65	0.4313	1	0.07	0.52	0.4845
Strain	1	1.39	7.51	0.0152	1	1.05	7.88	0.0158
Altitude*Strain	1	0.57	3.07	0.0999	1	0.02	0.19	0.6673
Site	15	2.79	3.71	0.0004	12	1.59	2.36	0.0232
Time	3	9.16	61.10	<0.0001	3	12.51	74.07	<0.0001
Altitude*Time	3	0.46	3.05	0.0385	3	0.11	0.64	0.5937
Strain*Time	3	0.15	0.84	0.4816	3	0.69	4.07	0.0137
Altitude*Strain*Time	3	0.30	1.97	0.1327	3	1.16	6.88	0.0009
Year	1	6.05	32.61	<0.0001				
Altitude*Year	1	0.00	0.04	0.8453				
Strain*Year	1	0.02	0.13	0.7202				
Altitude*Strain*Year	1	0.35	1.91	0.1876				
Time*Year	3	0.39	2.61	0.0636				
Altitude*Time*Year	3	0.19	1.27	0.2954				
Strain*Time*Year	3	0.77	5.12	0.0040				
Altitude*Strain*Time*Year	3	0.60	3.99	0.0137				

Table 2. (Continuation)

Source of variation	Releases 2002/2003 combined				Release 2003			
	DF	SS	F-Ratio	p-value	DF	SS	F-Ratio	p-value
<i>Rainy season</i>								
Altitude	1	8.31	11.45	0.0041	1	8.80	10.80	0.0065
Strain	1	5.56	0.08	0.7857	1	0.17	0.21	0.6527
Altitude*Strain	1	0.25	0.35	0.5624	1	0.00	0.01	0.9391
Site	15	10.89	12.79	<0.0001	12	9.78	11.83	<0.0001
Time	7	4.43	11.14	<0.0001	7	3.00	6.22	<0.0001
Altitude*Time	7	3.22	8.11	<0.0001	7	1.74	3.60	0.0019
Strain*Time	7	0.41	1.03	0.4143	7	0.53	1.09	0.3740
Altitude*Strain*Time	7	0.38	0.96	0.4667	7	0.29	0.60	0.7508
Year	1	1.18	1.62	0.2218				
Altitude*Year	1	0.02	0.03	0.8648				
Strain*Year	1	0.03	0.05	0.8267				
Altitude*Strain*Year	1	0.33	0.46	0.5088				
Time*Year	7	0.80	2.03	0.0582				
Altitude*Time*Year	7	0.56	1.41	0.2079				
Strain*Time*Year	7	0.41	1.04	0.4096				
Altitude*Strain*Time*Year	7	0.44	1.11	0.3653				

DF = degrees of freedom; SS = sum of squares; p = error probability.

Persistence of *T. aripo*. On the release sites of 2002, two years after the first release, *T. aripo* was only found in Mile 20 and Mile 24 (lower altitude) and in Babessi (mid-altitude; Table 1), where it had been present before our experiment started. In the mid-altitudes, it survived the dry season only in Matrufon, but it did not persist beyond one cassava cropping cycle. In the mid-altitudes, *T. aripo* was not found in any of the monthly follow-up surveys in the immediate vicinity of the harvested fields, whereas, in the lower altitudes, it was found in neighbouring fields.

Table 3. Results of repeated measures analyses on *Typhlodromalus aripo* presence depending on altitude, or on strain, in the release experiment of 2002, over various time periods.

Source of variation	Altitude effect				Strain effect			
	DF	SS	F-Ratio	p-value	DF	SS	F-Ratio	p-value
<i>16 months</i>								
Altitude	1	4.28	8.20	0.0353	Not applicable			
Strain	Not applicable				1	0.10	0.08	0.7935
Site	5	2.61	11.29	<0.0001	5	6.36	13.31	<0.0001
Time	15	8.31	11.96	<0.0001	15	8.71	6.08	<0.0001
Altitude*Time	15	4.00	5.75	<0.0001	Not applicable			
Strain*Time	Not applicable				15	0.93	0.65	0.8230
<i>12 months</i>								
Altitude	1	1.75	2.91	0.1486	Not applicable			
Strain	Not applicable				1	0.09	0.11	0.7548
Site	5	3.01	14.06	<0.0001	5	4.24	10.19	<0.0001
Time	11	7.68	16.32	<0.0001	11	8.15	8.89	<0.0001
Altitude*Time	11	2.54	5.40	<0.0001	Not applicable			
Strain*Time	Not applicable				11	0.81	0.89	0.5516
<i>1st dry season</i>								
Altitude	1	0.30	0.48	0.5199	Not applicable			
Strain	Not applicable				1	0.46	0.99	0.3657
Site	5	3.13	383.84	<0.0001	5	2.35	9.02	0.0002
Time	4	4.08	625.03	<0.0001	4	4.36	20.94	<0.0001
Altitude*Time	4	0.60	91.93	<0.0001	Not applicable			
Strain*Time	Not applicable				4	0.24	1.14	0.3704
<i>Rainy season</i>								
Altitude	1	2.37	7.56	0.0403	Not applicable			
Strain	Not applicable				1	0.01	0.02	0.9033
Site	5	1.57	14.00	<0.0001	5	3.93	10.94	<0.0001
Time	7	2.57	16.39	<0.0001	7	1.30	2.59	0.0293
Altitude*Time	7	1.92	12.27	<0.0001	Not applicable			
Strain*Time	Not applicable				7	0.20	0.39	0.9018
<i>2nd dry season</i>								
Altitude	1	2.65	203.99	<0.0001	Not applicable			
Strain	Not applicable				1	0.00	0.00	0.9871
Site	5	0.06	0.35	0.8731	5	2.71	6.39	0.0065
Time	2	0.61	8.20	0.0078	2	0.30	1.79	0.2165
Altitude*Time	2	0.55	7.30	0.0111	Not applicable			
Strain*Time	Not applicable				2	0.07	0.43	0.6644

DF = degrees of freedom; SS = sum of squares; p = error probability.

Population dynamics of *M. tanajoa*. The dynamics of *M. tanajoa* populations for the duration of the field experiments of 2002 and 2003 are shown in Figure 2. In the study beginning in October 2002, in the fields of the mid-altitudes where either strain of *T. aripo* had been released, *M. tanajoa* densities were low (0 to 2 mobiles of the first fully developed leaf) until February 2003. Populations had a first peak in March 2003, with 40 mobiles per leaf. In April 2003, the population collapsed to 10 mobiles per leaf. A second peak occurred in May 2003, at 25 mobiles per leaf. In July 2003, the population had collapsed to the level of 1 to 5 mobiles per leaf. On the fields of the same altitude without predator release, *M. tanajoa* levels remained low (0 to 4 mobiles of the first fully developed leaf) until December 2002. After that, the populations of the pest mite took off and reached a peak in March 2004, with 326 mobiles per leaf. The populations were back to a low level of 1 to 8 mobile mites per leaf in March 2003, where they remained until the end of the study in January 2004. In the lower altitudes, in the fields where *T. aripo* had been released before, *M. tanajoa* densities were low from October to December 2002 (1 to 9 mobiles on a leaf). They rose to a first peak in January 2003 (19 mobiles per leaf), but dropped again to 0 and 4 mobiles per leaf in February and March 2003, respectively. The pest mite had a second peak in April 2003 (24 mobiles per leaf) before it collapsed again to a level between 0 and 5 mobiles per leaf. In the fields of the lower altitudes where the predators had not been released, the pest populations were between 0 and 10 mobiles per leaf over the whole time period of the study, except for two small peaks in June 2003 (12 mobiles per leaf) and in January 2004 (19 mobiles per leaf).

In the study after *T. aripo* release in October 2003, *M. tanajoa* dynamics developed as follows: In the mid-altitude fields with predator addition, the pest mite was present in low densities of 0 to 2 mobiles per leaf until February 2004. It reached its peak in April 2004, with 28 mobiles on a leaf. It was back on low levels between 1 and 2 mobiles per leaf as from May 2004 onwards. In the fields where the predators had not been added, the pest mite population never exceeded 3 mobiles per leaf. In the lower altitudes, in the fields where *T. aripo* had been released, *M. tanajoa* levels were low from November 2003 to January 2004 (0 to 4 mobiles per leaf). A peak occurred in February 2004 (21 mobiles per leaf), before densities went down to low levels as from May 2004 onwards (0 to 2 mobiles on a leaf). Where no predators had been released, we had low *M. tanajoa* densities in November 2003 (0 mobiles per leaf). After that they reached their peak in February 2004 (25 mobiles per leaf). From April 2004 until the end of the study in October 2004, the pest mites were present with densities between 0 and 2 mobiles per leaf.

Factors affecting the presence of *M. tanajoa*. In the GLM repeated measures analysis of the combined experiments of 2002 and 2003 (Table 4), none of the main effects (altitude, predator release) were significant in any of the time periods analyzed. A lot of the variance in the data was explained by the site effect (over 12 months, and in the peak period of the pest mite) and the sampling time effect (over 12 months). In all time periods analyzed, many differences could be attributed to the differences between the two years. *T. aripo* presence as a covariate did not contribute to explaining the differences in *M. tanajoa* densities. The analysis of the 2003 release alone provided the same results. In the 2002 experiment alone (Table 5), no significance was found in the main effects. The site effect (over 16 months, over 12 months and over the peak period of the pest mite) and the sampling time effect (over 16 months and over 12 months) explained most of the variability in the data. The interaction between release and sampling time was significant over 12 months and over the peak period of *M. tanajoa*. *T. aripo* presence as a covariate did not contribute to explaining the differences in pest mite densities.

Table 4. Results of repeated measures analyses on *Mononychellus tanajoa* densities depending on altitude and predator release in the combined release experiments of 2002 and 2003, and in the 2003 experiment alone, over various time periods.

Source of variation	Releases 2002/2003 combined				Releases 2003			
	DF	SS	F-Ratio	p-value	DF	SS	F-Ratio	p-value
<i>12 months</i>								
Altitude	1	0.11	0.41	0.5269	1	0.20	1.16	0.2962
Release	1	0.21	0.76	0.3931	1	4.26	0.24	0.6272
Altitude*Release	1	0.27	1.00	0.3278	1	0.12	0.69	0.4178
Site	24	6.58	3.78	<0.0001	18	3.14	2.88	0.0002
Time	11	5.90	7.39	<0.0001	11	4.06	6.11	<0.0001
Altitude*Time	11	2.65	3.31	0.0003	11	3.55	5.34	<0.0001
Release*Time	11	2.62	3.28	0.0003	11	1.81	2.72	0.0027
Altitude*Release*Time	11	1.81	2.27	0.0118	11	0.77	1.15	0.3216
Year	1	3.65	13.29	0.0013				
Altitude*Year	1	0.70	2.54	0.1240				
Release*Year	1	0.46	1.71	0.2036				
Altitude*Release*Year	1	0.82	3.00	0.0960				
Time*Year	11	0.59	0.75	0.6903			Not applicable	
Altitude*Time*Year	11	5.47	6.85	<0.0001				
Release*Time*Year	11	1.82	2.28	0.0112				
Altitude*Release*Time*Year	11	4.22	5.28	<0.0001				
<i>M. tanajoa</i> peak period								
Altitude	1	0.70	1.73	0.2007	1	1.27	3.74	0.0689
Release	1	3.44	0.09	0.7728	1	0.36	1.07	0.3156
Altitude*Release	1	0.71	1.77	0.1960	1	0.47	1.40	0.2526
Site	24	9.69	3.57	<0.0001	18	6.11	3.59	0.0001
Time	5	1.04	1.84	0.1110	3	0.51	1.78	0.1618
Altitude*Time	5	1.77	3.13	0.0108	3	2.04	7.21	0.0004
Release*Time	5	2.439	4.31	0.0012	3	1.27	4.49	0.0069
Altitude*Release*Time	5	1.16	2.05	0.0770	3	0.13	0.47	0.7046
Year	1	2.29	5.67	0.0255				
Altitude*Year	1	2.70	6.68	0.0163				
Release*Year	1	0.48	1.19	0.2868				
Altitude*Release*Year	1	1.65	4.10	0.0542				
Time*Year	5	0.45	0.80	0.5509			Not applicable	
Altitude*Time*Year	5	3.20	5.65	0.0001				
Release*Time*Year	5	1.71	3.02	0.0134				
Altitude*Release*Time*Year	5	3.12	5.52	0.0001				

DF = degrees of freedom; SS = sum of squares; p = error probability.

Table 5. Results of repeated measures analyses on *Mononychellus tanajoa* densities depending on altitude, or strains, in the release experiment of 2002, over various time periods.

Source of variation	Strains pooled				Altitudes pooled			
	DF	SS	F-Ratio	p-value	DF	SS	F-Ratio	p-value
<i>16 months</i>								
Altitude	1	0.00	0.01	0.9130	Not applicable			
Release	Not applicable				1	1.00	2.05	0.1902
Site	8	4.83	4.09	0.0003	8	3.91	3.44	0.0014
Time	15	3.87	1.75	0.0511	15	7.22	3.40	0.0001
Altitude*Time	15	3.37	1.52	0.1090	Not applicable			
Release*Time	Not applicable				15	4.04	1.90	0.0296
<i>12 months</i>								
Altitude	1	0.11	0.17	0.6925	Not applicable			
Release	Not applicable				1	0.96	1.80	0.2160
Site	8	5.06	3.47	0.0017	8	4.27	3.07	0.0044
Time	11	3.71	1.85	0.0577	11	6.90	3.61	0.0003
Altitude*Time	11	3.04	1.52	0.1411	Not applicable			
Release*Time	Not applicable				11	3.70	1.93	0.0463
<i>M. tanajoa peak period</i>								
Altitude	1	1.08	1.33	0.2829	Not applicable			
Release	Not applicable				1	0.99	1.19	0.3072
Site	8	6.53	2.65	0.0207	8	6.64	3.18	0.0074
Time	5	1.01	0.65	0.6607	5	1.61	1.23	0.3127
Altitude*Time	5	1.70	1.10	0.3763	Not applicable			
Release*Time	Not applicable				5	3.48	2.66	0.0371

DF = degrees of freedom; SS = sum of squares; p = error probability.

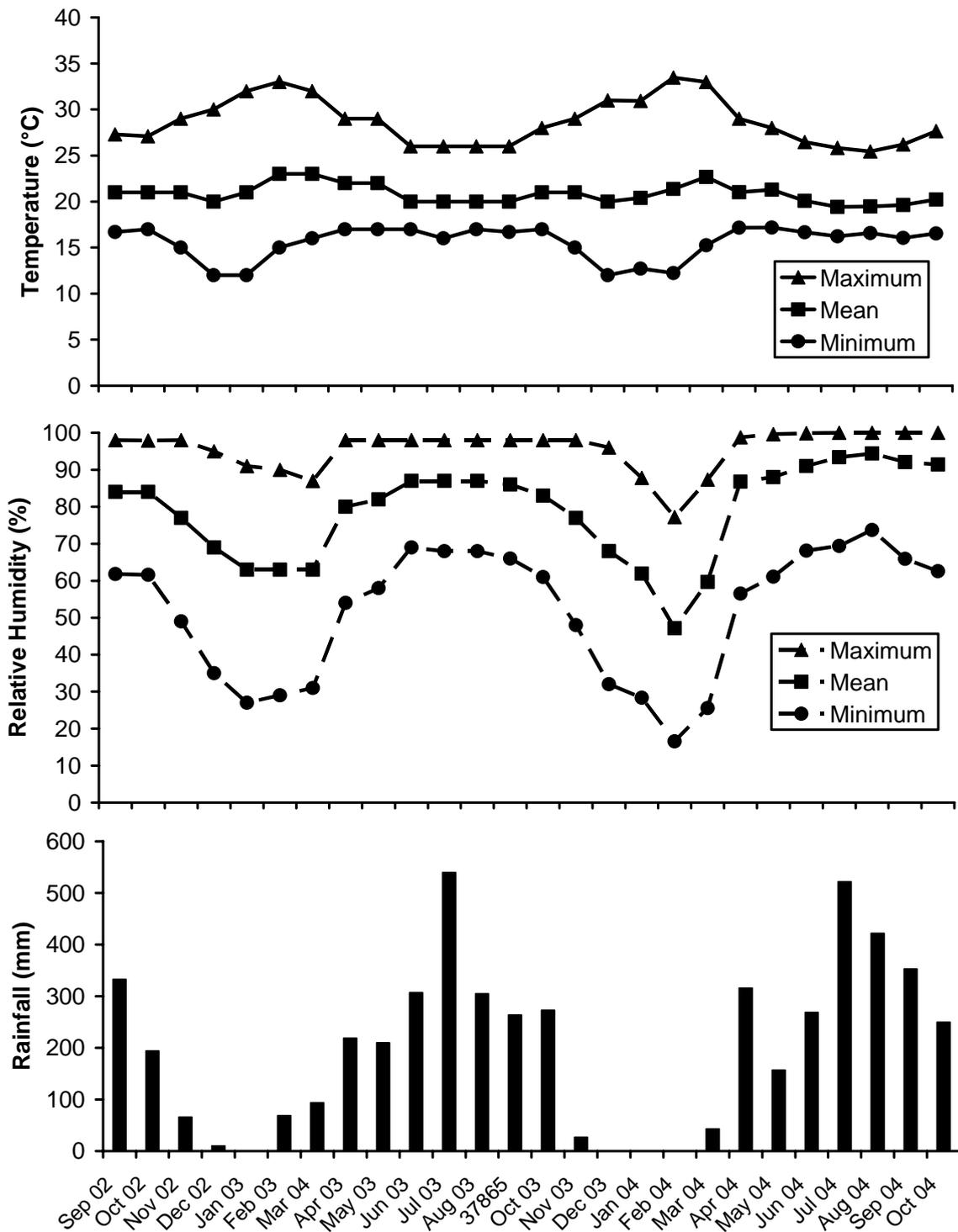


Figure 3. Rainfall, temperature and relative humidity data for the mid-altitudes of the NWP, Cameroon, from September 2002 to October 2004 at RTC Fonta (1294 meters above sea level).

DISCUSSION

***T. aripo* dynamics.** Data from the two release experiments showed that in the dry season, it was the strain effect which affected the presence of *T. aripo* most, the *Pir* strain being more suitable than the *Bam* strain on both altitudes under consideration. In the rainy season, and over the whole seasonal cycle of 12 months, it was altitude which made a difference in the predator's presence, the lower altitudes being more favourable than the mid-altitudes. Three distinct specifications need to be made to these findings: (1) Since the two release studies were not run longer than 16 and 12 months, it is not possible to tell the dry season apart from "the period immediately after release", and the rainy season from "the situation on a longer term". In the second dry season of the 2002 experiment, it was indeed altitude, which had a significant effect on *T. aripo*'s presence, and not strain. This fact supports the hypothesis that importance of strain and altitude are related to short-term and long-term requirements, rather than to dry season and rainy season requirements. (2) It is assumed that the altitude effect is mostly a temperature effect, the lower altitudes being warmer than the mid-altitudes. This is why, based on the life table studies over a wide range of temperatures (Negloh 2000), we expected the *Bam* strain to be more viable than the *Pir* strain in both altitudes. The opposite was the case in the first four months of the release experiment of 2003, though. An explanation might be that in the field, relative humidity, next to temperature, also played a crucial role in *T. aripo* presence, and that the *Pir* strain was able to cope better with these conditions than the *Bam* strain. Tolerance to low humidity levels was not included in the life table study of Negloh (2000). (3) Conclusions about differences in strain performance must be treated with care: First, part of the poor performance of the *Bam* strain in the dry season of the first experiment must be attributed to the fact that this field had to be re-planted after serious damage caused by rodents. Second, it is noteworthy that in the first experiment, the *Bam* strain survived the dry season in one out of three release sites in the mid-altitude areas, whereas the *Pir* strain did not survive in any of the two release sites in the mid-altitudes.

In the mid-altitudes of northwest Cameroon, over the two years of our study, the dynamics of the exotic predatory mite *T. aripo* and its likewise exotic prey were asynchronous. In the mid dry season, when prey densities started to increase, *T. aripo* populations reached their lowest levels, and they recovered only in the full rainy season, when *M. tanajoa* densities had dropped. Overlap of the two species' prevalences was limited to short periods of time, and to small populations. This is a different situation compared to the regions where *T. aripo* is well established today. In Benin, where the temporal trends of *M. tanajoa* and *T. aripo* are more immediately related to the rainfall pattern, their cycles are

synchronous (Hanna et al. 2005; Onzo et al. 2005). Although less well synchronized, prey and predator dynamics still meet in Brazil (Magalhaes et al. 2003).

The *T. aripo* cycle (Figure 2) in the mid-altitudes of Cameroon was equally driven by abiotic (ambient relative humidity and temperature) as by biotic factors (availability of suitable habitats and diets). The decrease in the middle of the dry season was due to dry ambient conditions rather than to food limitations. Prey density was low, but alternative foods were probably available. For instance, exudates production of cassava plants was higher in the dry than in the rainy season (Zundel, unpublished data). From Gnanvossou et al. (2005), we know that *T. aripo* is able to survive, develop and oviposit on a maize pollen diet. Magalhaes et al. (2003) found that *T. aripo* is able to perform better than other phytoseiids (i.e., *A. manihoti*), if prey densities are low. However, in the early rainy season, when ambient relative humidity had reached more favourable levels again, *T. aripo* populations did not respond immediately. One reason may be that fresh apices which offer a suitable habitat were rare at this time (for the relationship between population density and habitat area see Matter 2000). Cassava plants needed to develop new apices first. The low temperatures typical for the mid-altitudes which may have delayed *T. aripo* population growth could be an additional cause. Predator densities increased constantly until the middle of the rainy season. As *T. aripo* was well protected in the apex and therefore remained mainly unaffected by rain (Onzo et al. 2005), ambient relative humidity was favourable, and, once prey had entirely disappeared, flowering maize provided pollen as a valuable alternative food (Zundel, unpublished data). Later in the rainy season, in the 2002 experiment, we found predator populations developing in heterogeneous ways. In some sites, densities were continuously high, in others they went through a temporary breakdown in September and October 2003, before they increased again in November and December 2003 (Figure 2). It may have been food scarcity/availability that determined the population level at that time. In some areas, off-season maize was coming to pollen production by then, in others, food may have reached critical levels, as exudates production was low, and the wild grasses started flowering only towards the end of the rainy season. It is remarkable that, despite the fact that *T. aripo* missed its prey, it was able to survive a year or longer, in both altitudes, provided that the average ambient relative humidity did not drop below 50 % in the dry season (Table 1).

The greatest challenge for *T. aripo*'s long-term persistence was the survival of the end of the cassava cropping cycle. Plant senescence led to small and flowering apices in most of the varieties and *T. aripo* presence became weak. If the predators were not able to spread to younger cassava in other fields, the remaining population was removed by crop harvest. The

ability to spread is not only important for an area-wide pest control – first of all it is a prerequisite for the long-term persistence of the exotic predator. This may be the reason why *T. aripo* had well established in the lower areas of the NWP, where it spread fast, whereas in none of the mid-altitude release sites *T. aripo* persisted beyond one cropping cycle. Almost no spread to neighbouring fields was found there. In the lower altitude sites, high *T. aripo* abundance was also found in the control field by June 2003.

***M. tanajoa* dynamics.** Neither of the two main factors tested (altitude, predator release) in the two trials showed an effect on *M. tanajoa* densities, in none of the time periods under consideration. Instead, we found a high variability between the sites, strong seasonal dynamics and large differences between the two experiments of 2002 and 2003. These three sources of variance are discussed in the following:

High *M. tanajoa* densities have proved to occur irregular in space. The same is also reported by Toko et al. (1996). In retrospect, we doubt if our trial design was adequate to detect control effects of a predatory mite on *M. tanajoa*. Many more trial fields are required to overcome the large site effects in an agro-ecologically diverse environment like the mid-altitudes of Cameroon: Because it was practically impossible to have proper control fields, (i.e., fields adjacent to release fields that remained free of predators), we established the control fields at least two kilometers away from the release fields. As a consequence, they were likely to be quite different in terms of ecological conditions, and hence were not proper controls. The only way to achieve proper control fields would be to establish the release and the control fields close together, and to chemically exclude the predators, which was not practically feasible in our case. *M. tanajoa* densities were lower in the lower altitudes than in the mid-altitudes, and lower than we would expect in relation to the prevailing temperatures, in particular in the release of 2002. This gives rise to the notion that *T. aripo* actually did control the pest mite in the lower altitudes, as it was well established there, but that we were not able to detect this effect because the predators had invaded the control fields. At a first glance, the high peak of 326 mobiles per leaf in the experiment of 2002 in the mid-altitude fields where *T. aripo* had not been released, also points to a strong control effect of the predators. However, here too, *T. aripo* had invaded one (Baba 1) of the two control fields in the mid-altitudes. What we observed here was not a control effect, but the fact that, in the mid-altitudes, high *M. tanajoa* densities can be reached despite the predator's presence. This is why the previously suspected control effect did not show up in the analysis with *T. aripo* as a covariate.

Seasonal population dynamics of *M. tanajoa* in the mid-altitudes of Cameroon turned out to be different from those in other African regions: i.e., from the lowlands of Benin (Hanna et al. 2005; Onzo et al. 2005) but also from the mid-altitudes of Kenya (Skovgard et al. 1993) and Uganda (Hanna et al., unpublished data). In these regions, *M. tanajoa* is having the conspicuous peak shortly after the onset of the dry season, and a second peak at the beginning of the rainy season, while in our studies, it only had one (2003) and two peaks close together (2002) in the transition period from the dry to the rainy season. Several authors (Yaninek et al. 1989a; Yaninek et al. 1989b; Onzo et al. 2005; Hanna et al. 2005) reported that limited availability of fresh plant growth (during the main part of the dry season) and heavy rainfall (in the middle of the rainy season) are the factors keeping the pest populations low. Temperature is seen as a dominant factor for the *M. tanajoa* population growth rate. Annual average temperature in Benin is 25 to 27 °C, and 23 to 24 °C in the mid-altitudes of Kenya. In this light, our NWP data are consistent with the other findings cited above: Basically, populations started to grow in the beginning of the dry season. Due to the low average temperature (21 °C in the mid-altitudes; 23 °C in the lower altitudes) (Table 1; Figure 3), however, development was very slow. Yaninek et al. (1989a) show that, at 20 °C, the egg-to-adult period takes 1.4 times longer than at 24 °C, and 1.7 times longer than at 27 °C. At 20 °C, females lay only 40 % and 25 % of the number of eggs per day which they lay at 24 °C and 27 °C, respectively. It takes a population 1.8 times longer to double its number at 20 °C than at 24 °C, and 2.6 times longer than at 27 °C. That is most probably why, in the NWP, elevated *M. tanajoa* densities were found only towards the end of the dry season (i.e., as from February onwards). New plant growth usually starts in April, a few weeks after the rains have come back. Due to low temperatures, the first and the second peak observed in the literature cited above fell together. The rule of Yaninek et al. (1987) that we have two *M. tanajoa* population peaks in areas where the dry season is discrete and lasts longer than three months needs to be revised by adding the condition that temperature is high enough for *M. tanajoa* to build up within three months.

The differences in number of peaks (2002: mostly two; 2003: only one), in peak length (2002 release: from January to June 2003; 2003 release: from January to April 2004) and in peak densities (Figure 2) between the two experimental years might be due to the fact that other cassava varieties were used, that the sites were located in different places, and that possible climate differences occurred between the two years.

CONCLUSIONS

Based on data of Zundel et al. (manuscript in preparation), we know that varieties with hairy apices are able to promote *T. aripo*'s presence better than glabrous varieties, particularly under difficult conditions, as in the dry season. However, even favourable varieties were not able to sustain the predator's persistence beyond one cropping cycle. Therefore, *T. aripo*'s presence in the mid-altitudes would require continuous human intervention. The predators would need to be actively transferred to newly planted fields. To have enough predators available, rearing fields would need to be maintained. Natural habitats which could take over this role are looked at in another study of Zundel et al. (manuscript in preparation). The climate data in Table 1 suggest warm habitats with an average ambient relative humidity not below 50 % in February. However, since no control effect of *T. aripo* on the pest mite could be found, and in view of the asynchronous cycle of predator and prey, the potential for an efficient pest control through *T. aripo* is limited, exploitable perhaps in the lower altitude range of northwest Cameroon, but not justifying any specific efforts to sustain the predator in the mid-altitudes.

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THREE

Population dynamics of two strains of the neotropical phytoseiid mite *Typhlodromalus aripo* and their impact on the cassava green mite in a screenhouse experiment in the mid-altitudes of Cameroon

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ABSTRACT

Similarity of climatic conditions in the area of origin of a control agent and in the area where it is introduced is crucial for the successful establishment of a natural enemy. We evaluated in a screenhouse experiment the impact of two Brazilian strains of the predatory mite *Typhlodromalus aripo* DeLeon on its prey mite the tetranychid *Mononychellus tanajoa* (Bondar). One strain originated from a lowland dry area (Piritiba) in Bahia State, whereas the second strain originated from a cooler area (Bambui) in Minas Gerais State. Earlier laboratory life table studies had shown that the Bambui (*Bam* strain) strain was more adapted (based on intrinsic rate of increase) than the Piritiba (*Pir* strain), particularly at temperatures ranging from 17 to 25 °C. We determined with a screenhouse population-level experiment the short term dynamics of the *Bam* and *Pir* strains of *T. aripo* and their effects on *M. tanajoa* populations on potted cassava plants. The *T. aripo* populations used in the experiment were collected from two fields in the mid-altitudes, where they had been reproducing for several generations. Mean temperature in the screenhouse during the experiment was 21 °C, and relative humidity was 87 %. *T. aripo* numbers decreased from a mean over all treatments of 4.0 ± 0.0 (mean \pm standard error) individuals per plant at the date of release to 1.5 ± 0.15 individuals per plant at the end of the four-week observation period. Over the whole experimental period, the population density of the *Pir* strain was higher than that of the *Bam* strain ($p = 0.0133$). The most likely reason for the deviation of the screenhouse results from the life table results is that the *Pir* strain has a greater capacity to adapt to the new environment than the *Bam* strain, in particular to dry conditions, which have not been tested in the life table study. Similar results have been found in field releases where, during the dry season, the *Pir* strain performed better than the *Bam* strain. However, neither of the two strains showed a significant impact on *M. tanajoa* populations. The results showed that *M. tanajoa* numbers increased from a mean over all treatments of 46.0 ± 2.0 individuals per plant to a mean over all treatments of 512.0 ± 135.0 individuals per plant four weeks later. We suspect that *T. aripo* populations in the screenhouse were too small to have an effect on the rapidly increasing *M. tanajoa* populations. Thus, the screenhouse experiment conducted was not suitable to make any conclusions about *T. aripo* population dynamics and its control effect on *M. tanajoa* in the field.

Key words. Biological Control, *Mononychellus tanajoa*, spider mites, *Manihot esculenta*

INTRODUCTION

Decades of experience in classical biological control show that the climatic conditions in the area of origin of the control agent are of crucial importance for its later establishment and success in controlling the target pest in a new area (Hoy et al. 1976; Stiling 1993; Greathead 2003). Thus, finding natural enemies from areas with climatic conditions similar to those prevailing in the target area has become one of the major concerns and challenges in classical biological control programs. If an ecotype of a biocontrol species has proven to be successful in a given area, Goldson et al. (1997) see a potential in targeting another ecotype of the same species in another environment with a different climate. And indeed, strains of the same species can, although they can not be differentiated morphologically, manifest significantly different climatic adaptations and different respective behaviour (Lee and Elliott 1998; Yoder and Hoy 1998). In phytoseiid mites, Bakker et al. (1993) found that the inter-strain differences in saturation deficit tolerance are sometimes larger than interspecific differences.

Typhlodromalus aripo DeLeon, 1967 (Acari: Phytoseiidae) (*Pir* strain) was collected from Piritiba, Bahia State, Brazil (11°43'36'' S // 40°34'00'' W; elevation: 572 meters above sea level (masl)). In this area, mean annual temperature is 26 °C, mean annual relative humidity (RH) is 55 %, annual rainfall is 1050 millimeters, and the dry season lasts seven months. *T. aripo* was shipped to Africa and released for the first time in 1993. It spread fast and had a strong impact on the tetranychid mite *Mononychellus tanajoa* (Bondar, 1938), the most important cassava pest at that time. Today, *T. aripo* is established in 20 countries of sub-Saharan Africa (Hanna and Toko 2003). In fields in West Africa where *T. aripo* is present, *M. tanajoa* populations were found to be 16 to 60 % lower than in nearby fields without *T. aripo* (Hanna and Toko 2003, Yaninek and Hanna 2003). In contrast to that, however, *T. aripo* has been slow in colonizing and establishing in mid-altitude regions. This is particularly the case in latitudes above 4° North and South where temperatures are cooler and relative humidity in the dry season is lower than in the low altitudes and in areas closer to the equator (Mebelo et al. 2001; Mebelo et al. 2003; Zundel et al., manuscript in preparation). These experiences led to another expedition to Brazil to collect *T. aripo* from a location with cooler temperatures.

The *Bam* strain of *T. aripo* was collected from the vicinity of Bambuí in Minas Gerais State (20°00'32'' S // 48°58'20'' W; elevation 720 m asl). In this area, mean annual temperature is 21 °C, mean annual relative humidity is 74 %, annual rainfall is 1426 millimeters, and the dry season lasts four months (Mebelo 1999). The predators were brought to the International Institute of Tropical Agriculture (IITA) in Cotonou, Benin, and reared in the laboratory at 25 ± 1 °C and 80 ± 10 % RH. Life table studies showed that this strain had

the higher intrinsic rate of increase (r_m) at a temperature range of 17 to 25 °C compared with populations of the *Pir* strain – yet at 30 °C, the latter had a significantly higher r_m than the *Bam* strain (Negloh 2000).

The objective of this study was to determine with a greenhouse population-level experiment the short term dynamics of the *Bam* and *Pir* strains of *T. aripo* and their effects on *M. tanajoa* populations on potted cassava plants, in parallel to field evaluations of the two strains.

MATERIAL AND METHODS

The experiment was conducted in June and July 2004 in the North-West Province (NWP) of Cameroon, at the Rural Training Centre (RTC) Fonta, at 1294 m asl, with mean annual temperatures of 21 °C and mean annual RH of 78 %.

The two strains of *T. aripo* used in the experiment were initially collected from their respective locations (Piritiba and Bambui, Brazil) and shipped to IITA after undergoing quarantine certification at the University of Amsterdam, the Netherlands. They were subsequently maintained in the laboratory at 25 ± 1 °C and 80 ± 10 % RH. The *Pir* and *Bam* strains were released in Cameroon in October 2003, coming from populations collected from cassava fields in southern Benin (*Pir* strain) and laboratory populations (*Bam* strain). The latter was multiplied on cassava plants in a greenhouse for at least two generations before shipping to Cameroon. The *Pir* and *Bam* strains were released at Chomba ($5^{\circ}53'56''$ N // $10^{\circ}06'11''$ E; 1267 m asl) and Fonta ($6^{\circ}02'59''$ N // $10^{\circ}12'18''$ E; 1294 m asl), respectively. After several generations (36 and 39 weeks, respectively) in the field, the two strains were collected from their release locations and maintained on detached cassava leaves at 11 °C for one day before the start of the greenhouse experiment. Adult *M. tanajoa* females were collected from the field immediately before they were used in the experiment.

The experiment was conducted in a greenhouse (8 x 6 x 2.5 meters) from 14 April to 13 July 2004 on potted cassava plants and consisted of four treatments arranged in a randomized complete block design with four replicate blocks. The greenhouse was covered with amber screen of 32 x 32 micrometers mesh size with a UV-resistant, transparent white polyethylene cover mounted at 1.5 meters above the structure. Mature 20-centimeters long cuttings of the cultivar TME1 were collected from a multiplication field in Fonta and planted in groups of four in pots of 15 liters (25 centimeters in diameter, 30 centimeters high) filled with topsoil from the RTC Fonta station nursery next to the greenhouse. Pots were arranged

in groups of four, consisting of one replicate, on wooden benches of 100 x 70 x 76 centimeters (L x W x H) with a spacing of 1 meter between the benches. The total of 16 plants (four plants in four pots) of a group represented one replicate of a treatment. Six weeks after planting, each plant was infested with 15 mobiles of *M. tanajoa*. Three weeks after *M. tanajoa* had been added (i.e., nine weeks after planting) the following treatments were established: (a) release *T. aripo Bam* alone; (b) *T. aripo Pir* alone; (c) *T. aripo Bam* + *T. aripo Pir*; and (d) a control that remained free of predatory mites. Four adult *T. aripo* females were added to the respective solitary strain treatments, while two adult females of each strain were added to the mixed predator treatment. The appropriate number of predators for each plant in each treatment was placed on the first fully expanded leaf of each cassava plant using a camel-hair brush. The plants were trimmed to one stem and five leaves the day before predator release. The removed leaves were then placed back on the plant to minimize the loss of *M. tanajoa*. Mean temperature inside the greenhouse was 21 °C (minimum: 16 °C; maximum: 31 °C), and mean relative humidity was 87 % (minimum: 45 %; maximum 98 %).

Three plants per replicate (for a total of 12 plants per treatment) were sampled weekly. Plant stems were removed at the base from the cutting and placed in a plastic pot for conducting the *M. tanajoa* and *T. aripo* census. A non-destructive baseline count with 4 x head lenses, on the day of and just prior to *T. aripo* release gave an equal, but low *M. tanajoa* establishment. On the subsequent sampling dates, eggs and active stages (larvae, nymphs and adults) of *M. tanajoa* and predatory mites on all the leaves from each plant were counted in the laboratory with the aid of a binocular microscope. The apices of the sample plants were removed and placed individually in vials containing 75 % alcohol. *T. aripo* eggs and active stages (larvae, nymphs and adults) were subsequently counted under a dissecting microscope at IITA in Cotonou.

Data analysis. *Mononychellus tanajoa* (eggs and actives) and *T. aripo* (actives) densities were summed up for each plant. For the use in data summary and statistical analyses, treatment means were then calculated for each replicate and sampling date.

A Mixed Model ANOVA (PROC MIXED; SAS Institute 2003) with repeated statement (Littell et al. 2000) was used to determine the effect of treatment and date of sampling on changes in population sizes of *M. tanajoa* and *T. aripo*. In the mixed model, treatment, date and interaction between treatment and date were the fixed effect factors, while replicate was the random effect factor, and replicate nested in treatment was the subject (repeated) factor. Density of *T. aripo* was used as covariate in the analysis of *M. tanajoa*

count data, whereas density of *M. tanajoa* was used as covariate in the analysis of *T. aripo* count data. Treatment effects on prey and predator densities were compared pairwise using pre-planned orthogonal contrasts. Within-date treatment effects on prey and predator densities were determined with ANOVA (PROC GLM; SAS Institute 2003) stratified by sampling date. Treatments were compared with Student-Newman-Keuls (SNK) multiple range test, only where ANOVA showed a significant treatment effect ($p < 0.05$).

All statistical analyses were carried out on log-transformed values of total densities of *M. tanajoa* (eggs and actives) and active stages of *T. aripo* found in the apex of cassava plants, where *T. aripo* is usually found during the day. All eggs were excluded from the analyses since it was not possible to determine their identity.

RESULTS

Typhlodromalus aripo densities of the *Pir* strain reached 5.0 ± 0.45 (mean \pm SE) individuals per plant two weeks after release, and decreased to 2.1 ± 0.57 individuals per plant four weeks after release. Predator population of the *Bam* strain continuously decreased to 1.3 ± 0.59 individuals per plant four weeks after release. The mixed strain population *Pir* + *Bam* remained on the initial level (4.1 ± 0.76 individuals per plant) until two weeks after release. Afterwards, they decreased to 1.7 ± 0.41 individuals per plant (Figure 1). The mixed model repeated measures ANOVA and the treatment contrasts performed showed that, over the course of the experiment, densities of *T. aripo* in the *Pir* strain treatment was higher than in the *Bam* treatment, but they were not different from the densities in the mixed *Pir* and *Bam* treatment (Table 1). There were also no differences in *T. aripo* densities between *Pir* strain only and the mixed *Pir* + *Bam* treatment. *M. tanajoa* densities used as covariates did not contribute to the explanation of *T. aripo* variance. Within-sampling dates, the results of the ANOVA (PROC GLM) did not show any differences in *T. aripo* densities among the predator treatments ($p > 0.05$).

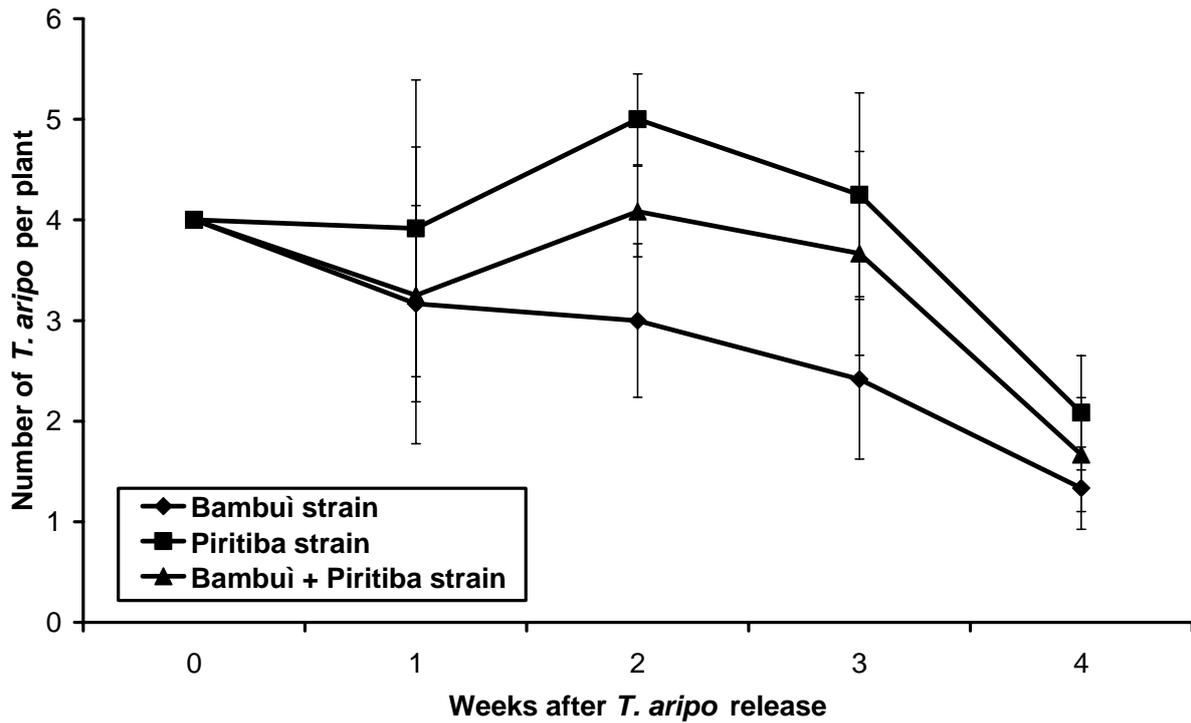


Figure 1. Population trends of *Typhlodromalus aripo* for three predator treatments. Data points are means on a per plant basis. Vertical bars are standard errors of the means.

Table 1. Mixed Model repeated measures ANOVA of treatment and sampling date on densities of *Mononychellus tanajoa* (with *T. aripo* densities as covariate), and *Typhlodromalus aripo* (with *M. tanajoa* densities as covariate).

Source of variation	<i>Mononychellus tanajoa</i>			<i>Typhlodromalus aripo</i>		
	df	F	p-value	df	F	p-value
Treatments	3	0.53	0.6646	3	37.66	<0.0001
Week	3	4.88	0.0030	3	7.84	<0.0001
Treatments*Week	9	1.05	0.4074	9	1.65	0.1084
<i>T. aripo</i> densities (covariate)	1	2.88	0.0921	-	-	-
<i>M. tanajoa</i> densities (covariate)	-	-	-	1	1.26	0.2643
<u>Contrasts</u>						
Control vs <i>Ta</i>	1	0.64	0.4266	-	-	-
Control vs <i>Ta Bam</i>	1	1.03	0.3123	-	-	-
Control vs <i>Ta Pir</i>	1	0.72	0.3991	-	-	-
Control vs <i>Ta Bam + Ta Pir</i>	1	1.03	0.3123	-	-	-
<i>Ta Bam</i> vs <i>Ta P</i>	1	0.01	0.9087	1	6.30	0.0133
<i>Ta Bam</i> vs <i>Ta MG + Ta P</i>	1	0.75	0.3877	1	2.47	0.1187
<i>Ta Pir</i> vs <i>Ta MG + Ta Pir</i>	1	0.57	0.4520	1	0.87	0.3528

Ta = *T. aripo*; *Bam* = Bambuí strain; *Pir* = Piritiba strain; df = numerator degrees of freedom; F = F-value; p = error probability; the denominator degree of freedom equals 131.

Mononychellus tanajoa populations were relatively low (46 ± 2 individuals per plant) at the date of *T. aripo* release, and increased to 512 ± 135 (mean of all treatments) individuals per plant over the subsequent four weeks of observation (Figure 2). The results from the mixed model ANOVA did not show any differences between the four treatments, probably because of the high variance of *M. tanajoa* numbers in the treatments. *T. aripo* densities, when used as a covariate, did not explain this variation (Table 1). Moreover, the analyses of within-date treatment effects on prey densities did not show any among-treatments differences for any of the five sampling dates ($p > 0.05$).

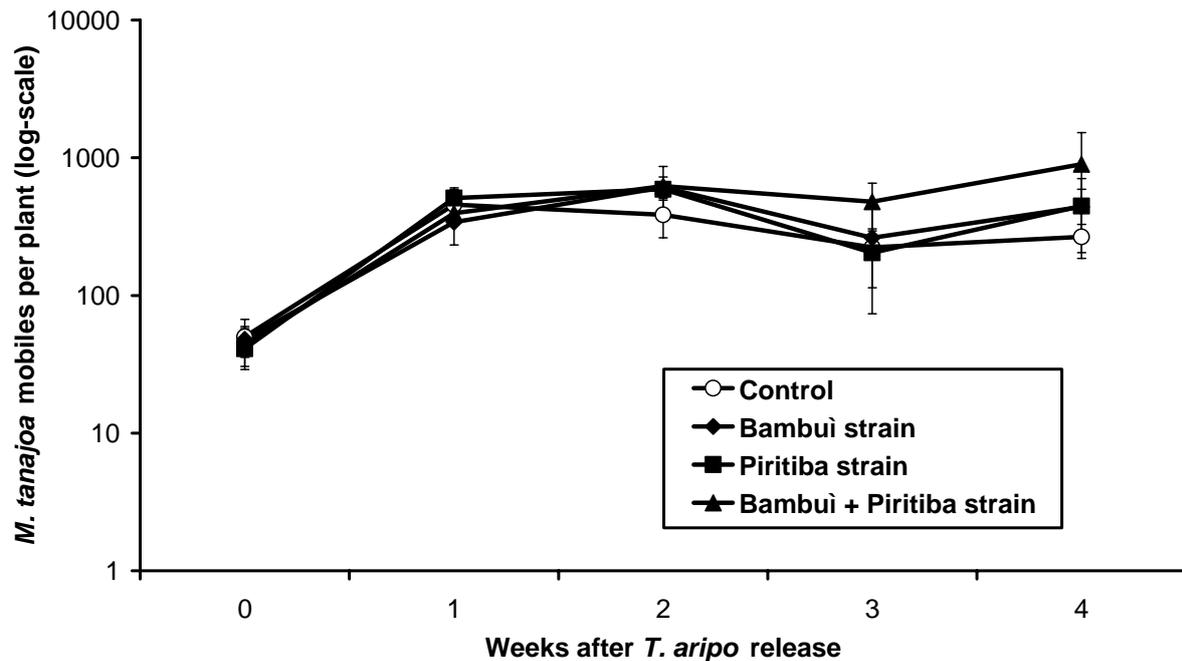


Figure 2. Population trends of *Mononychellus tanajoa* for the three *Typhlodromalus aripo* treatments and the control. Data points are means on a per plant basis. Vertical bars are standard errors of the means.

DISCUSSION

In this study we wanted to compare the ability of two *T. aripo* strains – originating from two climatically different regions in Brazil – to suppress the target prey *M. tanajoa* under screenhouse conditions in the NWP of Cameroon, where the climate is characterized by unimodal rainfall and a dry season of four months, 21 °C mean annual temperature and 78 % RH. The experiment was conducted during the rainy season when conditions were favourable for the development of *T. aripo* populations. The statistical analysis shows that the overall population density of the *T. aripo* *Pir* strain is higher than that of the *Bam* strain. A similar effect could be found in the mid-altitudes of the NWP under field conditions (Zundel et al., manuscript in preparation). However, these results contrast with the results from laboratory life table studies conducted at IITA Cotonou, where in the temperature range of 17 to 25 °C, the *Bam* strain performed better than the *Pir* strain. This temperature range includes the annual mean temperature of the Fonta area and the mean temperature during the screenhouse experiment (both 21 °C). There are three possible explanations for the discrepancy between the screenhouse and the life table results: One is that the life table study has been conducted under conditions with 70 to 90 % RH, whereas, during the time of the screenhouse

experiment, ambient RH dropped to 45 % during the day. Mebelo (1999) found in a lab experiment that 67 % RH is the LRH_{50} (equivalent to LD_{50}) for *T. aripo* (*Bam* strain) egg hatch. At 21 days during the experimental period, RH dropped below LRH_{50} . We therefore hypothesize that the *Bam* strain, though better adapted to lower temperatures, had difficulties to persist on the lower RH level prevailing during the screenhouse experiment in the mid-altitudes. An experiment determining LRH_{50} for a laboratory population of the *Pir* strain would be useful in this regard. Another explanation is that the *Pir* strain had been able to adapt better to the field conditions in the mid-altitudes than the *Bam* strain since the time of released. A second life table study using field populations from the mid-altitudes in Cameroon is necessary to elicit if and how life table parameters of the two strains shifted over the range of temperatures tested. We suggest that, at the level of 20 °C, a relative humidity treatment of 67 % be added to this experiment, to test if relative humidity may have contributed to the difference between *Pir* and *Bam* strain performance in the screenhouse experiment. The third explanation is given further below.

The most unusual part of the results is that none of the predator treatments has induced a significant reduction in *M. tanajoa* densities compared with the control. This is contrary to the results of a screenhouse experiment of Onzo et al. (2004) in Cotonou, where *T. aripo* showed a strong impact on *M. tanajoa*. The lack of a control effect on *M. tanajoa* in the present study has to be attributed to the fact that *T. aripo* was not able to keep up with the fast increase of *M. tanajoa* populations: Whereas the predator-to-prey ratio was 1 : 20 on average in the experiment of Onzo et al. (2004) it was 1 : 257 on average in the present study. Under the temperatures similar to the Cotonou experiment (30 °C) the r_m is considerably higher for *M. tanajoa* (0.28; Yaninek et al. 1989) than for *T. aripo* (*Bam* strain: 0.18; *Pir* strain: 0.20; Negloh 2000). Still, the predatory mites manage to control the pest mite. Under temperature conditions similar to Fonta (20 °C), the r_m 's of the pest mite (0.10; Yaninek et al. 1989) and the predatory mite (*Bam* strain: 0.12; *Pir* strain: 0.09; Negloh 2000) are almost the same, and we would expect the same population increases for predatory mite and pest mite. This was not the case, though. While *M. tanajoa* populations were growing fast, *T. aripo* populations slightly decreased. This is the opposite of the trends observed in the field at the same time (Zundel et al., manuscript in preparation), where *M. tanajoa* populations collapsed (most probably because they were washed off the plants by the rain), and *T. aripo* populations increased. We hypothesize that the small diameters of the cassava apices (where *T. aripo* stays) were the factor limiting *T. aripo* population growth in the screenhouse – affecting the *Bam* strain more than the *Pir* strain (third possible explanation for the higher presence of the

Pir strain compared to the Bam strain). During this time of the year, cassava plants in the field are growing fast, and apices are large (4 to 10 millimeters, depending on the cultivar). In the greenhouse, though, plant growth was slow and apex diameters remained the same (3 to 4 millimeters) throughout the experiment. Thus, the greenhouse experiment conducted was not suitable to make any conclusions about *T. aripo* population dynamics and its control effect on *M. tanajoa* in the field.

CONCLUSIONS

On the basis of the greenhouse experiment described here, we can not advocate *T. aripo* Bam strain as the better alternative to *T. aripo* *Pir* strain to control *M. tanajoa*. If it is not possible to establish *T. aripo* *Pir* in the mid-altitudes by other means (i.e., by using preferred cassava varieties as host plants, and/or by establishing *T. aripo* pools under favourable conditions), alternatives for *M. tanajoa* control should be considered. This could either be the promotion of *M. tanajoa* resistant cassava cultivars or the use of another biocontrol agent.

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FOUR

Habitat and host-plant genotype effects on seasonal dynamics of a neotropical predatory mite on cassava in the mid-altitudes of Cameroon

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ABSTRACT

In the mid-altitudes of Cameroon, the neotropical mite *Typhlodromalus aripo* DeLeon (Acari: Phytoseiidae), a predator of the cassava green mite *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae), is severely affected by the four months of the dry season. Similar dynamics of *T. aripo* are known from other seasonally dry areas in Africa. The overall objective of this study was to identify options to prolong the predators' presence into the dry season to increase their predation on *M. tanajoa*. In particular, we wanted to investigate the potential benefit of reservoir habitats for the fast recolonization of less favourable sites after the dry season, and the role which cassava cultivars could play in the predators' dry season persistence. The hypotheses were: (i) Habitat type has an impact on *T. aripo*'s dry season presence; (ii) *T. aripo*'s disappearance in the dry season and its reappearance in the beginning of the rainy season are depending on relative humidity in the habitat; (iii) morphological features and the physiological state of the host plant are able to mitigate adverse climatic conditions in the habitat, and therewith have an effect on *T. aripo*'s dry season presence on the plant. We selected a village with a high diversity of habitats and released predators on sites in grassland hills, in multiple cropping areas and in riparian forests. Since the degree of cassava apex pubescence is known to have an effect on *T. aripo* presence, we planted cassava genotypes with hairy, semi-hairy and glabrous apices in each habitat type. To support field results, we conducted a growth chamber experiment including three levels of relative humidity (33 %, 55 % and 85 %) and four levels of substrates simulating host-plant morphological and physiological characteristics (hairy apices, glabrous apices, cassava leaves, empty mini-Petri dishes).

We found that grassland hill sites were drier and hotter than the multiple cropping areas and riparian forest sites. *T. aripo* disappeared earlier and came back later in grassland hill and riparian forest sites, as compared to the multiple cropping areas. A discriminant analysis and subsequent time series analysis over grassland hill and multiple cropping area data showed that the predator's disappearance in the dry season was related to low relative humidity in the habitat, and to plant parameters indicating low plant vigour, low apex retention, small apex diameter and glabrous apices. For the predators' return in the rainy season, vigorous host plants and large apex diameter were more important than high relative humidity. In the grassland hill habitat type, *T. aripo* presence was low on all cassava genotypes. In the multiple cropping areas, the hairy genotype was able to host the predators longer and on a higher level than the semi-hairy and the glabrous genotype. *T. aripo* dynamics in the riparian forest sites were particular, and we discuss the possibility of an interaction with indigenous phytoseiids in this habitat type. The humidity effect, the substrate effect and their interacting effects on predator egg hatch could be confirmed in the growth chamber experiment, whereas the effect of

morphological features (i.e., apex hairiness) of the host plant was much weaker under controlled conditions compared to the field conditions. We suggest that *T. aripo* benefits from “services” of apex hairs which become effective only in the field (e.g. protection from wind, or macro-predation). We conclude that multiple cropping areas on fertile and humid soil are suitable as reservoirs for *T. aripo* in the dry season, in particular, if they are planted with a cassava variety with hairy apices.

Key words. Biological Control, *Typhlodromalus aripo*, phytoseiid, *Mononychellus tanajoa*, spider mites, *Manihot esculenta*, relative humidity, plant characteristics

INTRODUCTION

Seasonally changing climatic conditions, mainly temperature and humidity, challenge the survival of mites in temperate and tropical zones. In temperate zones, mites resort to a variety of strategies to cope with conditions that are either below or above their physiological development thresholds. The most common strategies are to pass winter in an environmentally resistant stage (i.e., as diapausing eggs or females), and/or to seek overwintering refuge in bark, scales, scars, or dormant buds (Gotoh 1987; Morewood 1993; Gurr et al. 1997; Koveos and Broufas 1999; Moreau et al. 2000; Golya and Kozma 2001; Popov 2003). Despite these overwintering strategies, mortality can still be as high as 80 to 90 % (Chant 1959; Gotoh and Kubota 1997). In tropical climates, it is usually the dry season that challenges mite survival. As the changes in monthly mean temperature over the entire year are smaller than the daily amplitudes, the tropical seasons are driven by rainfall and humidity rather than by temperature (Bakker et al. 1993). Thus, it is most likely low relative humidity which is difficult for the phytoseiids. For species which do not diapause or migrate to refuges, the habitat and its ability to mitigate the ambient climate become very important.

At the scale of mite environment, the leaf boundary layer of the host plant mitigates certain climatic conditions. Plant morphology and physiology can have an important influence on the microclimate just above the plant surface (Willmer 1986; Norton et al. 2001). The climate of the boundary layer is more relevant to small arthropods such as phytoseiid mites than ambient conditions (Ferro and Southwick 1984). While plant turgidity, and probably also leaf colour, affects plant surface temperature (Holtzer et al. 1988; Hanna et al. 1997; Zundel, unpublished data), relative humidity in the boundary layer is influenced by the physiological state of the plant and by leaf surface structures (Ferro and Southwick 1984; Schuepp 1993). As such, the boundary layer is especially accommodating to the more drought sensitive species and/or developmental stages (Bakker et al. 1993; Croft et al. 1993; Grostal and O'Dowd 1994; Shipp and van Houten 1997). The size of the boundary layer increases with decreasing air movement and obstructions at the plant surface (Nobel 1974; Gaede 1992; Norton et al. 2001), such as trichomes and domatia. Further, these structures can offer protection from macro-predators. Tufts of hair on leaves are also assumed to trap pollen and fungal spores, which represent additional food sources to generalist feeders (O'Dowd and Willson 1991; Norton et al. 2001). Which of the above mentioned mechanisms apply more than others, has been the subject of a variety of trials with contradicting results (Grostal and O'Dowd 1994; Roda et al. 2000; Roda et al. 2001; Norton et al. 2001; English-Loeb et al. 2002). But overall there is abundant evidence of the positive association between domatia and

pubescence on the leaf surface and higher densities of phytoseiid mites compared with leaves without these structures (Downing and Moilliet 1967; Duso 1992; Walter and O'Dowd 1992a; Walter and O'Dowd 1992b; Grostal and O'Dowd 1994, Karban et al. 1995, Walter 1996, Nyrop et al. 1998, Duso and Vettorazzo 1999; English-Loeb et al. 2002). Agrawal et al. (2000) showed that the presence of domatia on cotton plants not only increases phytoseiid populations, but also leads to lower densities of herbivore mites. In cassava, the crop of this study, the apices – consisting of the leaf primordia and the youngest, still folded leaves – can be considered as domatia (Sabelis et al. 1999), with hairy or glabrous expressions, depending on the cultivar.

In a field survey conducted in the previous year in twelve villages in the mid-altitudes of Cameroon, we found that the neotropical predatory mite *Typhlodromalus aripo* DeLeon, 1967 (Acari: Phytoseiidae), a predator of the cassava green mite *Mononychellus tanajoa* (Bondar, 1938) (Acari: Tetranychidae), was severely affected by the four months of the dry season (Zundel et al., manuscript in preparation). In about half of the villages, *T. aripo* had completely disappeared from the field, while in the other half they persisted in very low densities. Predator densities began to increase again after the first rains, also on fields where they had completely disappeared. Similar dynamics of *T. aripo* are known from other seasonally dry areas (Bakker et al. 1993), i.e., from Benin (Hanna et al. 2005; Onzo et al. 2005), and Zambia (Mebelo 1999).

The broad objective of this study was to identify options to prolong the predators' presence into the dry season to improve the suppression of damaging *M. tanajoa* populations on cassava. We wanted to investigate the potential benefit of reservoir habitats for fast recolonization of less favourable sites, and the role which cassava cultivars can play in the predator's dry season persistence. The hypotheses were: (i) Habitat type has an impact on *T. aripo*'s dry season presence; (ii) *T. aripo*'s disappearance in the dry season and its reappearance in the beginning of the rainy season are depending on relative humidity in the habitat; (iii) morphological features and the physiological state of the host plant are able to mitigate adverse climatic conditions in the habitat, and therewith have an effect on *T. aripo*'s dry season presence on the plant.

MATERIAL AND METHODS

Field study

Field selection and planting. To test the hypotheses (i) and (ii), a field experiment was conducted from July 2003 to July 2004 in a village (800 meters above sea level (m asl); 06°07'59'' N // 10°06'20'' E) near Bamenda in the North-West Province of Cameroon. The topography of the site is representative of the province and is characterized by a fragmented landscape of hills and valleys with diverse vegetation. The three predominant land cover types are described following the FAO land cover classification system of Di Gregorio and Jansen (2000): (a) closed grassland with sparse shrubs and agricultural fields, with a cover height of 0.03 to 3 meters and broad leafed semi-deciduous vegetation on a high-gradient hill slope (hereafter referred to as grassland hills). These grassland hills are increasingly cultivated with cassava; (b) cultivated areas with multiple herbaceous and fruit tree crops on scattered small sized fields in a rain fed, fallow-practising agricultural system, located at the gently undulating, low-gradient foot slopes (hereafter referred to as multiple cropping areas); and (c) closed forest with a cover height of > 14 meters with broad leafed evergreen vegetation, located on the valley floor in a fragmented landscape pattern (hereafter referred to as riparian forest). The dominant tree and shrub species of these three habitat types are listed in Table 1. Within a radius of about 300 meters, we selected three to five plots in each of the three typical land cover types. The four plots in the grassland hills were at an average distance of 200 meters from the hill-foot and were 50 to 300 meters apart, while the three riparian forest fields were scattered within the valley floor at about 400 meters apart. The two cultivated plots at the hill-foot were within 20 meters of each other. Each plot measured 48 x 10 meters and was surrounded by closed grassland with sparse shrubs on the grassland hills, by fruit trees, multiple cropping areas and fallow land at the multiple cropping sites, and by closed forest in the riparian forest. All the plots were between 810 and 920 m asl. In each plot we planted three cassava genotypes – TMS 92/0326 (hairy apices), TMS 92/0427 (semi-hairy hairy apices), and a local cultivar (glabrous apices) – providing a range of suitability to the predatory mite *T. aripo* (Zundel, personal observations). Seventy-two plants of each genotype were planted in randomly assigned plots within each experimental plot with a planting distance of 1 x 1 meter.

Table 1. Dominant tree and shrub species in the three habitat types included in the field study on *Typhlodromalus aripo* seasonal dynamics in northwest Cameroon.

Habitat type	Dominant species	Family
Grassland hills	<i>Annona</i> sp.	Annonaceae
	<i>Combretum</i> sp.	Combretaceae
	<i>Entada abyssinica</i> Steud. ex A. Rich., 1847	Mimosaceae
	<i>Terminalia mollis</i> Laws., 1871	Combretaceae
Multiple cropping areas	<i>Elaeis guineensis</i> Jacq., 1763	Palmae
	<i>Mangifera indica</i> Linné	Anacardaceae
	<i>Persea americana</i> Mill.	Lauraceae
	<i>Psidium guajava</i> Linné, 1753	Myrtaceae
Riparian forests	<i>Albizia</i> Durazz. sp.	Mimosaceae
	<i>Canarium schweinfurthii</i> Engler, 1883	Burseraceae
	<i>Carapa procera</i> DC., 1824	Meliaceae
	<i>Ceiba pentandra</i> (Linné, 1753) Gaertner, 1791	Bombacaceae
	<i>Elaeis guineensis</i> Jacq., 1763	Palmae
	<i>Entada abyssinica</i> Steud. ex A. Rich., 1847	Mimosaceae
	<i>Ficus</i> Linné sp.	Moraceae
	<i>Harungana madagascariensis</i> Lam ex Poir, 1804	Clusiaceae
	<i>Maesa lanceolata</i> Forssk., 1775	Myrsinaceae
	<i>Newtonia</i> Baill. sp.	Fabaceae
	<i>Polyscias fulva</i> (Hiern) Harms, 1894	Araliaceae
	<i>Raphia vinifera</i> P. Beauv., 1806	Palmae
	<i>Sorindea</i> Thouars sp.	Anacardiaceae
	<i>Tectona grandis</i> Linné	Verbenaceae
<i>Voacanga africana</i> Stapf, 1893	Apiaceae	

Origin of predatory mites and release. *Typhlodromalus aripo* (Bam strain) populations used in the experiments reported in this paper were provided by the International Institute of Tropical Agriculture, Biological Control Centre for Africa, located in Cotonou, Republic of Benin. The predators have been maintained in the laboratory on detached cassava leaves at 25 ± 1 °C and 80 ± 10 % relative humidity since 1997. The predators used in this study had been multiplied for at least three generations in rearing facilities in a greenhouse prior to packing

and shipping to Cameroon. Packing was done by aspirating 25 female predators into disposable seven centimeters long plastic pipette tips, which then were sealed with parafilm at one end while the other end was covered with mite-proof gauze (Mégevand 1997). At the time when the predators were released (less than 96 hours after packing), mortality in the tips was about 10 %. Releases were done twice within eight weeks to ensure solid establishment of the predators before the dry season. The first time (18 October 2003), we released on all the plants of each plot. We transferred five active predators with camel-hair brushes from the tips to the plants. Follow-up monitoring of predators on the released plants showed that they had established poorly. For the second release (28 November 2003), we attached the tips containing 25 predators each with scotch band to the stems of the sample plants only (see below), close to the apex.

Mite monitoring. Ten sample plants were randomly selected from the 72 plants of each genotype in a field, inspected for *T. aripo*, and tagged with a coloured polyethylene ribbon before the release. The same plants were monitored weekly for presence/absence of *T. aripo* in the cassava apex with 4 x head lenses in a non-destructive manner throughout the remainder of the experiment. To monitor densities of *M. tanajoa* and local phytoseiids, their mobile stages on the first fully expanded leaf of the terminal branch (as recommended by Yaninek et al. 1989; Yaninek et al. 1991) were counted with 4 x head lenses in monthly intervals. Samples of the local phytoseiids on the leaves were kept in alcohol for later identification. Several plant growth parameters such as plant height – measurements in centimeters, stay-green index – score from 1 (full canopy with turgid and green leaves) to 5 (complete defoliation of stem), apex retention index – score from 1 (first five leaves present) to 5 (none of the first five leaves present, dieback of apex), apex diameter – calliper measurements in millimeters, apex hairiness – score from 1 (glabrous) to 3 (very hairy), and flowering stage – score from 1 (no flower) to 5 (fruits set) were also recorded monthly. *T. aripo* sampling started on 29 December 2003, i.e., one month after the second predator release. The first sampling data for *M. tanajoa* after the second release of the predators was 16 December.

Climate monitoring. In each field, we recorded climate data at canopy height of the genotype TMS 92/0326 throughout the experiment. The self-contained loggers (HOBO H8 Pro, Onset Corporation, USA) recorded temperature with an internal sensor (accuracy: +/- 0.2 °C), and relative humidity (accuracy: +/- 3 %) in 12-minute intervals.

Growth chamber experiment

We conducted a growth chamber experiment (at the International Institute of Tropical Agriculture – IITA – in Cotonou, Benin) to determine the effects of cassava apex morphology (i.e., level of hairiness) and its potential interaction with relative humidity on *T. aripo* egg hatch. We tested two suppositions, which were: (i) Plant substrate effects and relative humidity effect interact (i.e., favourable plant substrate is more important under critical humidity conditions, but not under very humid or very dry conditions) and (ii) hairy apices are more favourable to *T. aripo* egg hatch than glabrous apices. For this purpose, the mid-altitude strain of *T. aripo* (originating from Bambui in Minas Gerais State in Brazil), which we used in several other studies, was collected from a field in Cameroon in May 2004, and was thereafter maintained in the laboratory on detached cassava leaves at 25 ± 1 °C and 80 ± 10 % relative humidity, at a photoperiod of 12L:12D until they were used in the present study. While in mass rearing, they were fed with *M. tanajoa* (all stages) and maize pollen. We worked with cohorts of eggs of the same age. Eggs are the developmental stage most susceptible to drought, because they can not compensate for water loss through feeding or water uptake (van Dinh et al. 1988; Croft et al. 1993), or escape through a behavioural response (Penman and Chapman 1988; Gaede 1992). The trial was designed as a two-factor experiment with three relative humidity (RH) levels and four substrates. The studies were carried out in two experiments with three replications of two RH levels (55 and 85 %) in the first experiment and three replications of all three RH levels (33, 55 and 85 %) in the second experiments. In choosing the RH levels to use in these experiments, we relied on the known response of *T. aripo* egg hatch to water vapour deficits (Bakker et al. 1993; Mebelo 1999), which showed that the LRH₅₀ (lethal relative humidity, which is analogous to LD₅₀) of *T. aripo* eggs maintained on glass slides was 67 % at room temperature. Humidity was controlled with oversaturated salt slurries (Winston and Bates, 1963) in round Perspex containers with lid (185 millimeters diameter x 80 millimeters height) containing 70 ml of KCl slurry for maintaining 85 % RH, 50 ml of Mg(NO₃)₂ * 6 H₂O slurry for 55 % RH and 50 ml of MgCl₂ * 6 H₂O slurry for 33 % RH.

The following four substrates were used in each RH level: hairy apices (cultivar ‘Agric’), glabrous apices (cultivar ‘Amala’), leaf lobe (cultivars ‘Agric’ and ‘Amala’), and a plastic mini-Petri dish. The apices and leaves were selected from 5-week old cassava plants grown in pots in a greenhouse free of mites. In preparing the apices and leaves, the unfolded leaves around the apex were removed and the stem was cut at about 3 centimeters below the

apex. The central lobe of the third leaf below the apex was used for preparing the leaf substrate. The leaf petiole was cut at about 3 centimeters below the leaf blade and the mid-lobe was cut at about 3 centimeters from the petiole. To keep plant apices and leaves fresh for the duration of the experiment, each apex or leaf were prepared with their stem or petiole base inserted in a glass screw cap vial (12 millimeters diameter x 45 millimeters height), filled with water and sealed with parafilm around the stem or petiole. The mini-Petri dishes had two opposite aeration holes of 2 millimeters diameter covered with mite-proof gauze. Each of the replicates consisted of four sample units of each substrate, to which five newly-deposited eggs were added. Eggs were not more than 12 hours old. The mini-Petri dishes were placed above the slurry, on polyethylene racks (168 millimeters diameter x 20 millimeters height) with a grid size of 2 millimeters, while the vials were placed upright with their base in the slurry. The humidity control containers were kept in the growth chamber at 22 °C, with a photoperiod of 12L:12D. Temperature and relative humidity were monitored with HOBO H8 Pro loggers (Onset Corporation, USA) inside the containers. After 72 hours, the shrivelled eggs, the viable eggs and the hatched larvae were counted. The containers remained tightly closed during the entire duration of the experiment.

Data analysis

Differences in temperature and relative humidity among habitat types. Weekly mean temperature and relative humidity values were calculated on the basis of daily mean (measured at 12-minute intervals) data. We used univariate repeated measures analysis (PROC MIXED, SAS Institute 2003) to test for differences in temperature and relative humidity among the three habitat types. The statistical analyses were conducted for the entire experimental period and then separately for the period of the dry season (29 December to 8 March) and the rainy season (15 March to 29 July). We used LSMEANS (SAS Institute 2003) to compare mean temperature and mean relative humidity of the habitat types.

T. aripo and M. tanajoa densities depending on habitat type and host-plant genotype. We used arcsine-transformed proportions of *T. aripo* infested plants and log-transformed numbers of *M. tanajoa* mobiles on the first fully expanded cassava plant leaf as dependent variables in mixed model autoregressive analysis (type 1) for repeated measures (PROC MIXED, SAS Institute 2003) to test for differences in *T. aripo* presence and *M. tanajoa* densities depending on the habitat type and host-plant genotype. The analyses were conducted for the entire experimental period (*T. aripo*: 29 December to 29 July; *M. tanajoa*: 16 December to 29 July),

and separately over the period of the dry season (*T. aripo*: 29 December to 8 March; *M. tanajoa*: 16 December to 25 February) and the rainy season (*T. aripo*: 15 March to 29 July; *M. tanajoa*: 24 March to 29 July). Non-significant interaction terms were stepwise removed from the model. Due to interactions between the two main effects, habitat type and genotype, the analyses were also conducted for each habitat type. Simple effects were separated with LSMEANS (SAS Institute 2003) and probability was adjusted with the Bonferroni procedure (Milliken and Johnson 1984).

Discriminant analysis and time series. We proceeded in two analytical steps to identify the variables that have an effect on the presence of *T. aripo* in the apices of the host cassava plant. First, we performed a linear discriminant analysis separating the plants where *T. aripo* was present from those where *T. aripo* was absent. We started with entering the following discriminator variables into the discriminant model: number of *M. tanajoa* mobiles on the first fully expanded leaf; plant height; stay-green index; apex retention index; index of flowering stage; apex diameter; apex hairiness; weekly mean temperature; and weekly mean relative humidity. Data collected on a monthly basis were interpolated to obtain data for each week. To adjust for the different scales of measurements, all variables were scaled to zero mean and standard deviation of one. Riparian forest data were excluded from the analysis because we suspected a strong interaction with indigenous phytoseiids, which may confound the relationships between *T. aripo* presence, prey densities, plant parameters and climate characteristics which shall be studied here. We applied backward selection using the Akaike Information Criterion (AIC) as optimizing criterion to identify variables that possibly have an influence on the presence of *T. aripo*. The discriminant factor analysis was performed (a) on the whole data set (29 December to 29 July), (b) on the dry season data subset (29 December to 8 March), and (c) on the wet season data subset (15 March to 29 July). In a second step, we modelled the relationship between presence of *T. aripo* and the variables identified in the discriminant analysis by the least squares method allowing for autocorrelations (gls; R core development team 2005). The autocorrelation structure was assessed beforehand for each variable by calculating the partial autocorrelations. All variables followed an autocorrelation structure of first order (AR1-process), except for weekly mean temperature in the dry season and stay-green index and apex hairiness in the rainy season, which showed no partial autocorrelation.

Growth chamber experiment. In a first step, we used a two-way ANOVA (glm; R Development Core Team 2005) to test for the effects of relative humidity and substrate (independent variables) on proportions of eggs hatched (dependent variable). As residuals were not normally distributed, we arcsine-transformed the proportions of eggs hatched. Since interactions occurred, we looked into each humidity level separately with a one-way ANOVA. If substrate proved to have a significant effect on the proportions of eggs hatched, a post-hoc multiple comparison test (Bonferroni) was performed.

RESULTS

Field study

Differences in temperature and relative humidity among habitat types. Weekly mean temperature increased continuously from the end of December to the end of March, and decreased thereafter until end of July in all three habitat types (Figure 1a). Relative humidity values continuously decreased from the end of December to mid-February, and remained low until the end of March, with a two-week increase coinciding with a brief rain at the end of February/beginning of March. Relative humidity rose in all habitat types from April through the end of the experiment (Figure 1b). In the repeated measures analysis, we found significant effects of habitat type on mean temperature and on mean RH in all three periods (whole period, dry season only, rainy season only) (Table 2). In all periods, mean ambient temperatures were higher in the grassland hill sites than in the riparian forest and the multiple cropping sites (LSMEANS; $p < 0.01$ for all relevant comparisons), whereas mean temperatures in the multiple cropping areas were not different from the mean temperatures in the riparian forest sites (LSMEANS; $p > 0.62$ for all relevant comparisons). Similarly, the grassland hill sites were drier than the other sites in all periods (LSMEANS; $p < 0.002$ for all relevant comparisons). Relative humidity in the multiple cropping sites was not different from RH in the riparian forest sites (LSMEANS; $p > 0.3$ for all relevant comparisons). The significant interaction between time and habitat type (Table 2) means that the linear change of mean temperature and RH with time differed between the habitat types, i.e. the difference in mean temperature and RH between the grassland hill sites and the other two habitat types were larger in the beginning of the study period than towards the end (Figure 1).

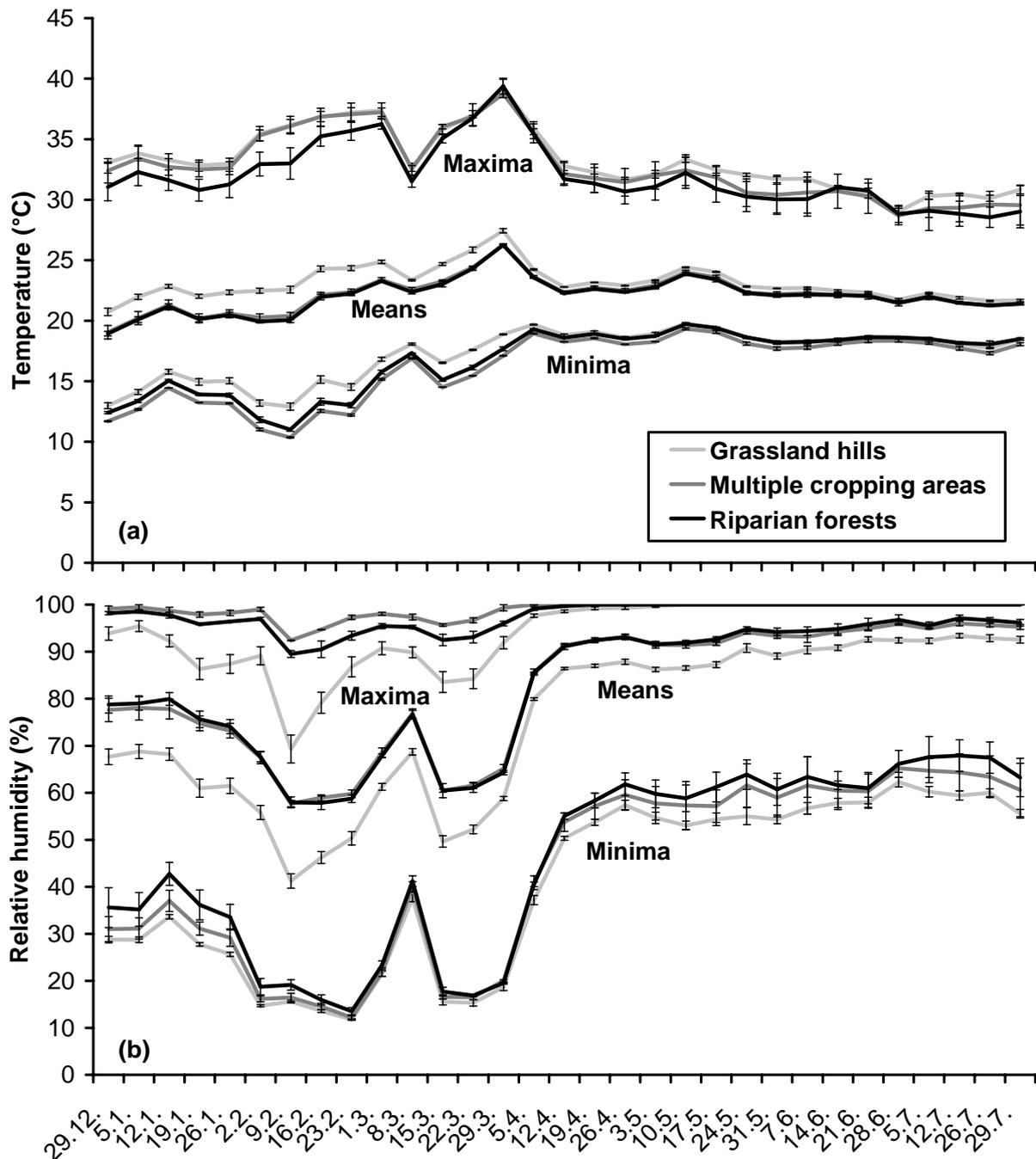


Figure 1. Maxima, minima and means of (a) temperature (°C) and (b) ambient relative humidity (%) three different habitat types on 800 m asl, Cameroon, from December 2003 to July 2004. Dates are last days of the 1-week observation periods. Data points are weekly means. Vertical bars are standard errors of the means.

Table 2. Results of mixed model repeated measures analysis on mean relative humidity and mean temperature depending on the habitat type, over the whole experimental period, over the dry season only, and over the rainy season only.

Source of variation	Num DF	Temperature			Relative humidity		
		Den DF	F-value	p-value	Den DF	F-value	p-value
<i>Whole period</i>							
Habitat type	2	6	16.60	0.0036	6	30.07	0.0007
Time	30	174	571.34	<0.0001	173	483.82	<0.0001
Habitat type*time	60	174	4.76	<0.0001	173	5.64	<0.0001
<i>Dry season</i>							
Habitat type	2	6	16.60	0.0012	6	28.23	0.0009
Time	10	58	512.30	<0.0001	56	279.52	<0.0001
Habitat type*time	20	58	5.67	<0.0001	56	7.53	<0.0001
<i>Rainy season</i>							
Habitat type	2	6	13.73	0.0058	6	26.05	0.0011
Time	19	110	654.97	<0.0001	111	589.81	<0.0001
Habitat type*time	38	110	2.72	<0.0001	111	3.38	<0.0001

Num DF = numerator degrees of freedom for this F-test; Den DF = denominator degrees of freedom for this F-test; p = error probability.

T. aripo presence depending on habitat type and host-plant genotype. In Figure 2, *T. aripo* presence is shown for the period of the dry season and the beginning of the subsequent rainy season depending on the host-plant genotype, for each of the three habitat types. When mite monitoring was started (29 December), the percentage of plants with *T. aripo* were low in the grassland hill (20 to 30 %) and in the riparian forest (7 to 39 %) habitat. In the multiple cropping habitat type, the percentage of plants with *T. aripo* was low on the local genotype (25 %), medium on TMS 92/0427 (45 %) and high on TMS 92/0326 (95 %). In the subsequent weeks, the percentage of plants with *T. aripo* decreased in all habitat types, and on all genotypes. Four weeks later, by 26 January, they had disappeared from all habitat types and from all genotypes, except for genotype TMS 92/0326 in the multiple cropping habitat type, where it persisted until 1 March. While *T. aripo* began to reappear in the apices of genotype TMS 92/0326 in the multiple cropping habitat three weeks after its disappearance (i.e., 22 March), its reappearance was delayed for another eight weeks (i.e., until 17 May) on

plants of TMS 92/0427 and of the local genotype. In the riparian forest, the predators reappeared first on 17 May, on plants of TMS 92/0326. Four weeks later, on 18 June, it was also back on TMS 92/0427. It did not reappear on the local genotype during the time period of this experiment. In the grassland hill habitat, the predators simultaneously reappeared on plants of TMS 92/0326 and TMS 92/0427 on 24 June. They never came back to plants of the local genotype. *T. aripo* colonized all sample plants of TMS 92/0326 in the multiple cropping habitat within seven weeks after its first reappearance (i.e., on 10 May). Plants of TMS 92/0427 reached 100 % coverage three weeks after its first reappearance on this genotype (i.e., 7 June), and it recolonized 70 to 80 % of all sample plants of the local genotype within five weeks after its first reappearance on this genotype (i.e., 24 June). While it lasted five weeks (i.e., until 24 June) from its first reappearance to a percentage of plants with *T. aripo* of 40 to 50 % in the riparian forest habitat on plants of TMS 92/0326, recolonization remained on a very low level in the forest on plants of TMS 92/0427 (3 to 13 %). In the grassland habitat, plants of TMS 92/0326 and TMS 0427 with *T. aripo* never exceeded 30 % and 20 %, respectively, during the time period of our observations.

The analysis over the whole experimental period showed strong interactions between habitat type and genotype (Table 3). If data of each of the habitat types were analyzed separately (Table 4), we found the following pattern: In the grassland hill habitat, over all three time periods, genotype did not have a significant effect on *T. aripo* presence. The same was true for the riparian forest habitat. In the multiple cropping habitat, genotype affected *T. aripo* presence if the whole experimental period or the rainy season was considered: Over the whole period and over the rainy season, TMS 92/0326 had higher proportions of plants with *T. aripo* than TMS 92/0427 (LSMEANS; $p < 0.02$ for all relevant comparisons). Proportion of plants with *T. aripo* was similar on TMS 92/0427 and on the local genotype over the whole time period (LSMEANS; $p = 0.963$), but TMS 92/0427 had higher proportions of plants with *T. aripo* in the rainy season (LSMEANS; $p = 0.005$). TMS 92/0326 had higher proportions of plants with *T. aripo* than the local genotype over the whole period (LSMEANS; $p = 0.005$). During the rainy season, TMS 92/0326 had higher proportions of plants with *T. aripo* compared with the local genotype (LSMEANS; $p = 0.001$). In the dry season, genotype effect was of borderline significance. Interaction with time was significant for all the relationships in the multiple cropping areas: The significant genotype effects remained over the whole period and in the rainy season, but not in the dry season, when interaction of genotype with time was omitted from the models, i.e. when a parallel development of *T. aripo* presence was assumed in the three genotypes over time.

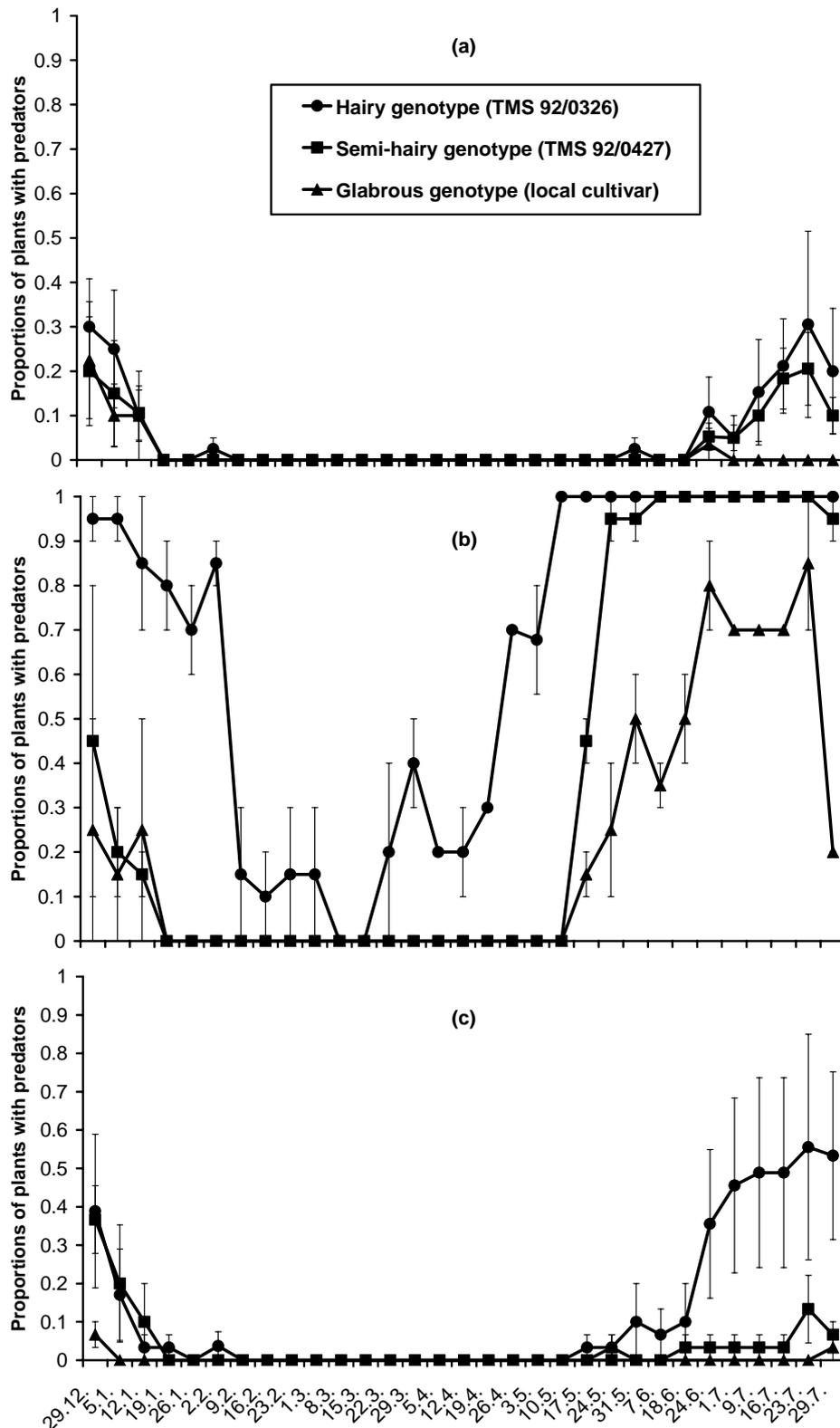


Figure 2. Proportions of plants with *Typhlodromalus aripo* on three different cassava genotypes (hairy: TMS 92/0326; semi-hairy: TMS 92/0427; glabrous: local genotype) on cassava fields (a) in the grassland hills; (b) on multiple cropping areas; and (c) in the riparian forest; on 800 m asl, Cameroon, from December 2003 to July 2004. Data points are mean proportions of plants with *T. aripo*. Vertical bars are standard errors of the means.

Table 3. Results of mixed model repeated measures analysis on *Typhlodromalus aripo* presence depending on habitat type and host-plant genotype over the whole experimental period, over the dry season only, and over the rainy season only.

Source of variation	Num DF	Den DF	F-value	p-value
<i>Whole period</i>				
Habitat type	2	15	20.82	<0.0001
Error: Field(habitat type)	3	15	1.17	0.3533
Genotype	2	15	33.46	<0.0001
Habitat type*genotype	4	15	10.72	0.0003
Time	30	540	14.10	<0.0001
Time*habitat type	60	540	4.32	<0.0001
Time*genotype	60	540	2.37	<0.0001
Time*habitat type*genotype	120	540	2.03	<0.0001
<i>Dry season</i>				
Habitat type	2	15	5.56	0.0156
Error: Field(habitat type)	3	15	2.72	0.0817
Genotype	2	15	10.85	0.0012
Habitat type*genotype	4	15	5.31	0.0072
Time	10	220	16.03	<0.0001
Time*habitat type	20	220	1.81	0.0212
Time*genotype	20	220	1.87	0.0158
<i>Rainy season</i>				
Habitat type	2	15	19.69	<0.0001
Error: Field(habitat type)	3	15	0.14	0.9347
Genotype	2	15	32.44	<0.0001
Habitat type*genotype	4	15	8.84	0.0007
Time	19	342	16.92	<0.0001
Time*habitat type	38	342	6.48	<0.0001
Time*genotype	38	342	2.58	<0.0001
Time*habitat type*genotype	76	342	2.85	<0.0001

Num DF = numerator degrees of freedom for this F-test; Den DF = denominator degrees of freedom for this F-test; p = error probability.

Table 4. Results of mixed model repeated measures analysis on *Typhlodromalus aripo* presence in each habitat type, depending on the host-plant genotype, over the whole period, over the dry season only, and over the rainy season only.

Habitat type	Source of variation	Num DF	Den DF	F-value	p-value
Grassland hills					
<i>Whole period</i>	Genotype	2	9	2.01	0.1895
	Time	30	330	4.23	<0.0001
<i>Dry season</i>	Genotype	2	9	0.40	0.6798
	Time	10	110	6.57	<0.0001
<i>Rainy season</i>	Genotype	2	9	2.19	0.1683
	Time	19	209	3.09	<0.0001
Multiple cropping areas					
<i>Whole period</i>	Genotype	2	3	62.66	0.0036
	Time	30	90	16.62	<0.0001
	Genotype*time	60	90	3.45	<0.0001
<i>Dry season</i>	Genotype	2	3	9.25	0.0521
	Time	10	30	5.33	<0.0001
	Genotype*time	20	30	2.08	0.0342
<i>Rainy season</i>	Genotype	2	3	265.19	0.0004
	Time	19	57	99.30	<0.0001
	Genotype*time	38	57	9.47	<0.0001
Riparian forest					
<i>Whole period</i>	Genotype	2	6	3.34	0.1060
	Time	30	240	2.52	<0.0001
<i>Dry season</i>	Genotype	2	6	1.65	0.2689
	Time	10	80	6.06	<0.0001
<i>Rainy season</i>	Genotype	2	6	2.45	0.1668
	Time	19	152	1.44	0.1158

Num DF = numerator degrees of freedom for this F-test; Den DF = denominator degrees of freedom for this F-test; p = error probability.

M. tanajoa densities depending on habitat type and host-plant genotype. Analysis of *M. tanajoa* densities over the whole period of observation and over the period of the rainy season showed significant differences between habitat types, but not between genotypes (Table 5). Cassava plants in the grassland hill sites had higher *M. tanajoa* densities than cassava plants in the riparian forest sites (LSMEANS; $p < 0.02$ for all relevant comparisons). In the dry season, neither of the two main effects was significant, nor was their interaction, although Figure 3 would suggest so: While *M. tanajoa* densities reached 150 ± 68 (mean \pm standard error) mobiles per leaf on the grassland hill sites in January, they remained low in the multiple cropping areas (20 ± 12 mobiles per leaf) and in the riparian forest (6 ± 2 mobiles per leaf) habitats.

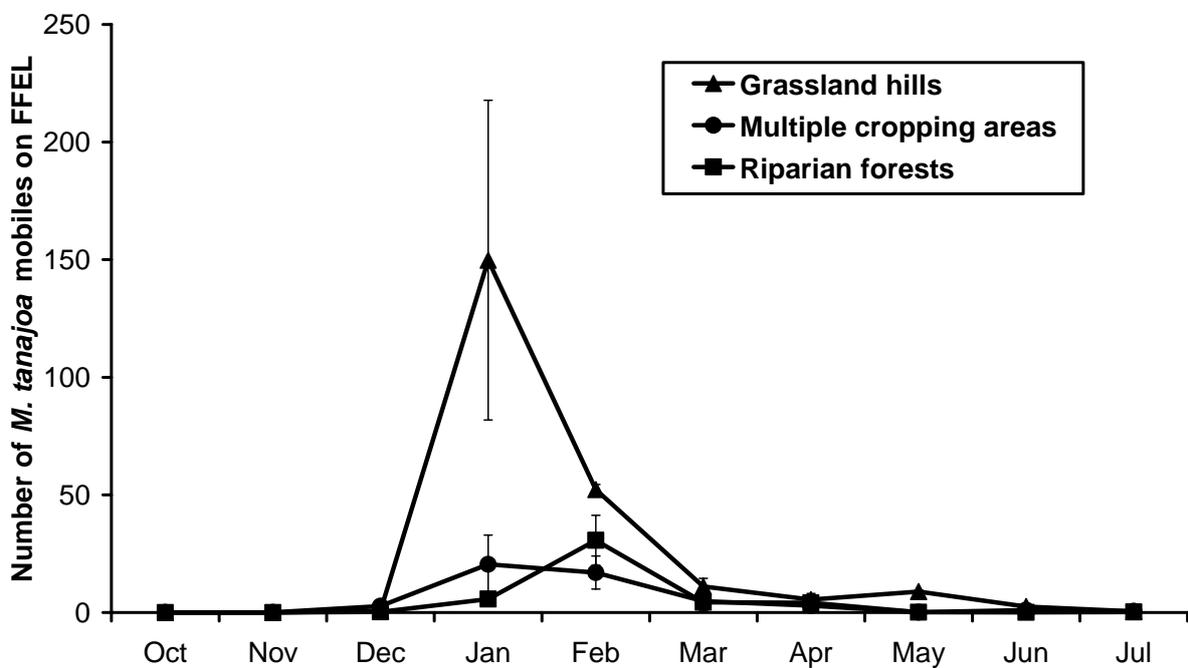


Figure 3. *Mononychellus tanajoa* densities in three different habitat types on 800 m asl, Cameroon, from October 2003 to July 2004. Data points are mean numbers of *M. tanajoa* mobiles on the first fully expanded leaf (FFEL) of the cassava host plant. Vertical bars are standard errors of the means.

Table 5. Results of mixed model repeated measures analysis on *Mononychellus tanajoa* densities depending on habitat type and host-plant genotype, over the whole period, over the dry season only, and over the rainy season only.

Source of variation	Num DF	Den DF	F-value	p-value
<i>Whole period</i>				
Habitat type	2	19	3.83	0.0401
Error: Field(habitat type)	3	19	1.70	0.2011
Genotype	2	19	2.14	0.1455
Time	7	166	21.41	<0.0001
Time*habitat type	14	166	3.75	<0.0001
<i>Dry season</i>				
Habitat type	2	19	0.31	0.7376
Error: Field(habitat type)	3	19	0.89	0.4639
Genotype	2	19	0.55	0.5859
Time	2	46	31.33	<0.0001
Time*habitat type	4	46	4.85	0.0024
<i>Rainy season</i>				
Habitat type	2	19	6.00	0.0095
Error: Field(habitat type)	3	19	3.34	0.0411
Genotype	2	19	1.93	0.1729
Time	4	96	6.91	<0.0001
Time*habitat type	8	96	3.42	0.0017

Num DF = numerator degrees of freedom for this F-test; Den DF = denominator degrees of freedom for this F-test; p = error probability.

Discriminant analysis and time series. In the discriminant analysis over the whole experimental period, we identified the variables of plant height, stay-green, apex diameter, apex hairiness, weekly mean temperature and weekly mean relative humidity which possibly have an effect on *T. aripo* presence in the cassava apex. Number of *M. tanajoa* mobiles on the first fully expanded leaf, apex retention and flowering stage did not have an influence. In the subsequent time series analysis, none of the variables tested had a significant influence on the presence of *T. aripo* in the cassava plant apex (Table 6). The discriminant analysis of the dry season subset indicated the variables of stay-green, apex retention, apex diameter, apex hairiness, weekly mean temperature and weekly mean relative humidity as being potentially influential on *T. aripo* presence. Number of *M. tanajoa* mobiles on the first fully expanded leaf, plant height and flowering stage were not regarded as potentially influential by the model. The time series analyses revealed a significant influence of stay-green, apex retention, apex diameter, apex hairiness and weekly mean relative humidity on *T. aripo* presence. In the rainy season subset, the parameters number of *M. tanajoa* on the first fully expanded leaf, plant height, stay-green, apex diameter, apex hairiness and weekly mean temperature showed a potential to be important variables for *T. aripo* presence. The time series analysis confirmed the variables of plant height and apex diameter to have a significant influence on *T. aripo* presence in the cassava apex.

Table 6. T-values and p-values of the discriminant (smallest model) and time series analyses for the variables that were identified to possibly have an influence on *Typhlodromalus aripo* presence in the cassava apex.

	Discriminant analysis (smallest model)				Time series analysis			
	Coefficients in the	Standard	t-value	p-value	Values	Standard	t-value	p-value
<i>Whole period</i>					<i>Autocorrelation=0.94</i>			
Plant height	0.1893	0.0069	27.47	<0.0001	0.23	0.48	0.45	0.6547
Stay-green	-0.0397	0.0055	-7.20	<0.0001	-22.64	15.26	-1.48	0.1511
Apex diameter	-0.0232	0.0068	-3.98	<0.0001	18.65	14.83	1.26	0.2206
Apex hairiness	0.0644	0.0053	12.32	<0.0001	-41.90	103.48	-0.40	0.6891
Mean temperature	-0.0766	0.0056	13.51	<0.0001	1.00	1.63	0.61	0.5448
Mean rel. humidity	0.0248	0.0063	4.13	<0.0001	0.11	0.25	0.44	0.6624
<i>Dry season</i>					<i>Autocorrelation=-0.84</i>			
Stay-green	-0.0265	0.0104	-2.64	0.0083	-88.37	5.61	-15.75	0.0001
Apex retention	-0.0350	0.0111	-3.09	0.0021	90.28	12.34	7.32	0.0019
Apex diameter	0.0396	0.0105	3.57	0.0004	121.44	9.95	12.21	0.0003
Apex hairiness	0.0369	0.0095	4.04	<0.0001	322.85	73.90	4.37	0.0120
Mean temperature	-0.1032	0.0114	-9.04	<0.0001	-3.77	1.38	2.72	0.0531
Mean rel. humidity	0.0649	0.0112	5.89	<0.0001	1.12	0.22	5.22	0.0064
<i>Rainy season</i>					<i>Autocorrelation=-0.16</i>			
<i>M. tanajoa</i>	-0.04056	0.0064	-6.38	<0.0001	-1.88	1.05	-1.78	0.0985
Plant height	0.2316	0.0078	29.56	<0.0001	2.03	0.24	8.42	<0.0001
Stay-green	-0.0341	0.0061	-5.61	<0.0001	-8.05	20.80	-0.39	0.7048
Apex diameter	-0.0448	0.0074	-6.03	<0.0001	-61.94	24.33	-2.55	0.0244
Apex hairiness	0.0781	0.0062	12.51	<0.0001	64.08	83.67	0.77	0.4575
Mean temperature	-0.0556	0.0068	-8.15	<0.0001	-1.66	1.81	-0.92	0.3766

Growth chamber experiment

The graphical presentation of the results (Figure 4) of the growth chamber experiment with proportions of *T. aripo* egg hatch as the dependent variable and humidity level and substrate as the two independent variables shows that *T. aripo* egg hatch rates increased with increasing relative humidity. At the lowest RH level of 33 %, almost none of the eggs hatched, with a few exceptions of the 'Amala' apex and the cassava leaf treatment. Under the conditions of the intermediary RH level of 55 %, eggs hatched with rates of more than 50 % on the treatments consisting of plant substrates (apices of cv. 'Agric', apices of cv. 'Amala', cassava leaves). Eggs hatched with rates of almost 100 % at the highest RH level (85 %) tested in this experiment. The general linear model showed that the interaction between relative humidity and substrate was highly significant ($df = 6$; $F\text{-value} = 46.75$; $p < 0.0001$). Relative humidity level ($df = 2$; $F\text{-value} = 901.96$; $p < 0.0001$) and substrate ($df = 3$; $F\text{-value} = 73.65$; $p < 0.0001$) had both highly significant effects on the proportion of *T. aripo* egg hatch. The subsequently conducted one-way ANOVA for each RH level showed that differences between substrates only got manifested at 55 % relative humidity. The post-hoc test revealed that proportions of egg hatch on the three plant tissue treatments (apices of cv. 'Agric', apices of cv. 'Amala', cassava leaves) were different from the proportions of egg hatch in the mini-Petri dish at an error probability level of $p = 0.05$.

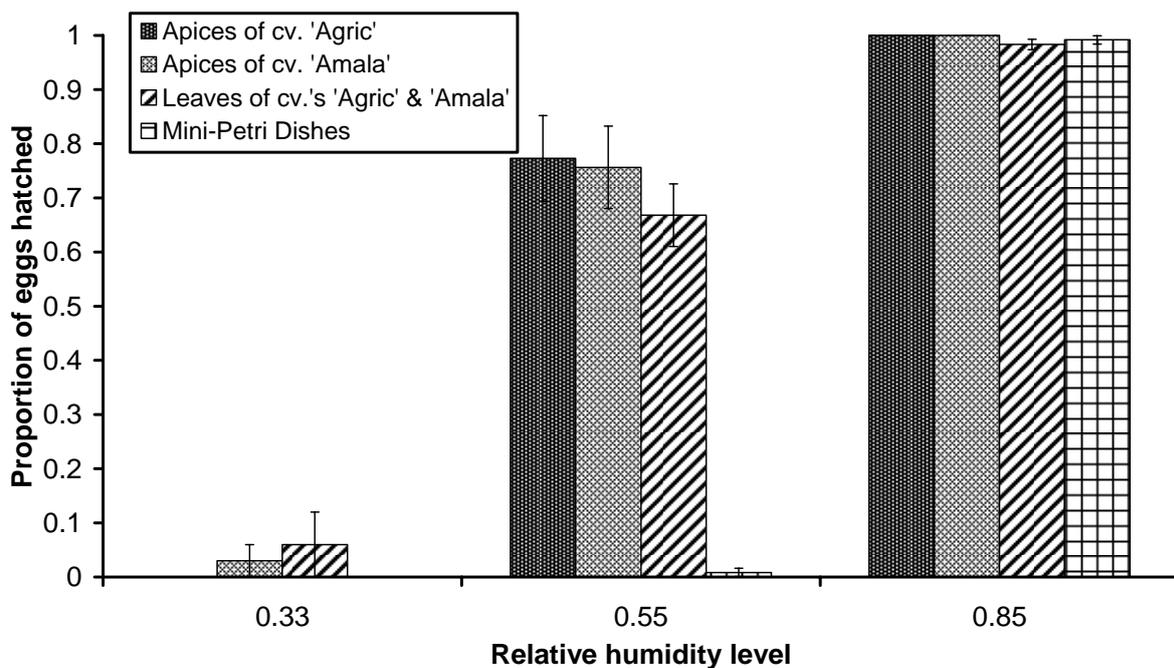


Figure 4. Egg hatch of *Typhlodromalus aripo* on four substrates under three humidity levels. Columns are mean proportions of eggs hatched. Vertical bars are standard errors.

DISCUSSION

Field study

Climate differences between habitat types. Located within a radius of ca. 300 meters, and within an altitude difference of 100 meters, the three habitat types differed in terms of ambient humidity and temperature, with the grassland hill sites being drier and warmer than the multiple cropping areas and riparian forest sites. Climatic differences were particularly pronounced during the dry season months. Whereas temperature differences levelled out in the beginning of the rainy season, the grassland hill sites remained slightly drier, also during the rainy period. Different combinations of topography, soil type, vegetation type and vicinity to open water surfaces may have led to these climate variations. The possibility for the predators to persist in favourable pockets within a few hundred meters of the harsh dry grassland hill sites was therewith provided. Surprisingly, the riparian forest sites were not more humid than the multiple cropping sites. It is possible that the clearing of the forest undergrowth prior to planting the trial field has affected relative humidity and temperature. The tall umbrella trees (*Albizia* sp., *Canarium schweinfurthii*, *Carapa procera*, *Ceiba pentandra*, *Elaeis guineensis*), 15 to 20 meters in height, may not have been effective enough in retaining relative humidity.

T. aripo presence depending on habitat type and host-plant genotype. The field trial data show clear seasonal patterns in *T. aripo* dynamics. Densities of this predator (measured in proportion of cassava plants with *T. aripo*) declined to zero during the dry season and began to increase gradually shortly after the beginning of the rainy season. How fast *T. aripo* populations decreased, when it disappeared, how long it was absent from the cassava plants, when it started to reappear and how fast it recolonized the cassava plants, depended on the habitat type and on the cassava host-plant genotype.

In the hot and dry grassland hill habitat, *T. aripo* levels were low throughout the experiment. The predators disappeared early in the dry season and were longer absent than in any of the two other habitat types. They recolonized the hairy and the semi-hairy genotypes, but not the glabrous genotype. Although the climate of the leaf boundary layer (which is affected by the genotype) is of more immediate relevance to the phytoseiids than the ambient climate (or canopy climate; Ferro and Southwick 1984; Holtzer et al. 1988; Cunningham et al. 1998), the importance of the latter should not be underestimated, as our study clearly shows: The microclimate on the plant largely depends on the conditions prevailing in the habitat type, as the mitigating capacity of the leaf boundary layer is limited. The importance of access to

water or high relative humidity spells for the uptake of water vapour from the air for phytoseiids is discussed in Gaede (1992), and (for house dust mites) in DeBoer et al. (1998). Evidently, in a dry habitat such as the grassland hills, it becomes increasingly difficult for predatory mites to balance water loss.

In the relatively cool and humid multiple cropping habitat, genotype differences in terms of suitability for *T. aripo* presence were clearly displayed, with the hairy genotype being the one with the highest *T. aripo* proportions over time, followed by the semi-hairy genotype. *T. aripo* also recolonized the glabrous genotype, although on a lower level than on the hairy and the semi-hairy genotype.

In contrast to what we had expected, the riparian forest habitat was not suitable for *T. aripo*, despite its cool and humid conditions, compared with the grassland hill habitat. The predators did not persist on the glabrous genotype, and they had difficulties persisting on the semi-hairy genotype. On the hairy genotype, they were able to colonize about 50 % of the cassava plants. We suspect an interaction with indigenous phytoseiids to be the cause for the low presence of *T. aripo* in the riparian forest sites: Indigenous phytoseiids were numerous (two phytoseiids per sample leaf) in the riparian forest sites in December 2003. Indigenous phytoseiid samples of that time consisted of 78 % of *Ueckermannseius* (syn. *Typhlodromalus*) *saltus* (Denmark & Matthysse, 1981) and of 22 % of *Euseius fustis* (Pritchard & Baker, 1962)). Experiences from greenhouse experiments show that, under shady conditions, *T. aripo* does not exclusively stay in the apex, but also dwells and oviposits on the top leaves (Onzo et al. 2003). Such behaviour increases the risk of encounters of *T. aripo* and indigenous phytoseiids inhabiting the same leaves: In a laboratory experiment of Zannou et al. (2005), *E. fustis* fed on eggs of *T. aripo*, whereas in a field experiment without shade (Onzo et al. 2003b), intraguild predation of *E. fustis* was not observed. A well controlled field experiment on shade, genotype and *E. fustis* effects would clarify these interactions.

We state that the host-plant genotype – most probably due to the feature of hairiness – was able to increase *T. aripo* presence in the dry season, given that the habitat was favourable. Under the unfavourable conditions of the grassland hill and riparian forest habitats, host-plant genotype was not able to mitigate these extreme conditions.

M. tanajoa densities depending on habitat type and host-plant genotype. The *M. tanajoa* population peak occurred in January, i.e., in the middle of the dry season. Similar seasonal dynamics have been found in other studies on pest and predatory mite dynamics in the mid-altitudes of the North-West Province in Cameroon (Zundel et al., manuscript in preparation).

The mixed model repeated measures analysis only showed higher *M. tanajoa* densities in the riparian forest sites compared to the grassland hill sites over the whole period of observation and in the rainy season. But based on Figure 3 we can assume that *M. tanajoa* densities were also higher in the grassland hill habitat type compared with the riparian forest and the multiple cropping habitat types in January, and probably also in February. This pattern has implications for *M. tanajoa* biocontrol, since a large – and increasing – share of cassava is grown on grassland hills. These sites are preferred for cassava production, because other staple crops such as maize would not perform well on these marginal soils (Bakia et al. 1999; Hillocks 2002; Howeler 2002). The low *M. tanajoa* densities in the multiple cropping habitat type can probably be explained by the high presence of *T. aripo* on these fields and their control effect on the pest mites. In the three genotypes used in the work described here, we did not observe a cassava genotype effect in *M. tanajoa* densities. It must be considered, though, that we selected the cassava genotypes for this study according to *T. aripo* preference criteria and not according to *M. tanajoa* resistance criteria.

Discriminant analysis and time series. The discriminant analysis and subsequent time series analysis over the whole experimental period indicated that none of the tested variables affected *T. aripo* presence in the cassava apex, probably because the two different climatic situations – dry season and rainy season – were confounded. When we split the experimental period into a subset of the dry season and a subset of the rainy season, we found that, in the dry season, more variables were important for *T. aripo* presence than in the rainy season. Whereas *T. aripo* was susceptible to poor stay-green, reduced apex retention, smaller apex diameter, low apex hairiness, and low relative humidity in the dry season, the predators only showed susceptibility to low plant height and small apex diameter in the rainy season. Mean relative humidity was not important at that time, because it was not limiting. Stay-green index and plant height are both measures for plant vigour. Our observations in the field point to the stay-green index being better related to *T. aripo* presence in the dry season and to plant height being better related to *T. aripo* presence in the rainy season. We conclude that plant vigour is important in both seasons. The same is true for apex diameter. Apex hairiness played a crucial role in the dry season, but it lost its importance in the rainy season. Since apex hairiness is a trait of the cassava genotype and is not affected by environmental conditions, this variable was constantly displayed in all its forms. We can therefore conclude that apex hairiness is more important in the dry season than in the rainy season. The possible role of apex hairs is discussed further below. Discriminant and time series analysis indicated that apex retention

was an essential trait in the dry season, but not in the rainy season. Unquestionably, apex retention is also important in the rainy season, since the predators are almost exclusively found in the cassava apices during daytime. The analysis did not provide this result, because apices were usually well retained in the rainy season, whereas the whole range from very poor to full apex retention was covered in the dry season.

Growth chamber experiment

In this experiment we attempted to further explore the effects of cassava apex morphology (i.e., level of hairiness) and its potential interaction with relative humidity on *T. aripo* egg hatch. The supposition that substrate and relative humidity interact, i.e., that a favourable substrate becomes more important under dry conditions, could be confirmed. However, the growth chamber experiment did not support the second supposition that hairy apices are more favourable to *T. aripo* egg hatch than glabrous apices. Whereas under very dry conditions (in the experiment represented by the RH level of 33 %) it was too dry for eggs to hatch – regardless on which substrate – we found that under conditions of critical relative humidity (in the experiment represented by the RH level of 55 %), it was important for high egg hatch proportions that the eggs lay on plant tissue. It did not matter, however, on which type of plant tissue they were lying. Egg hatch was not affected by the substrate under humid conditions (RH level of 85 %). The crucial role of the plant substrate under critical humidity conditions may be that the transpiring plant tissue is mitigating the low relative humidity level of the microclimate in which the predatory mites are dwelling.

T. aripo presence depending on habitat type, host-plant genotype, climate parameters, plant parameters and intraguild interaction

The results of the growth chamber experiment support the findings of the field study in many aspects: Both trials confirmed that the environment (growth chamber experiment: relative humidity level; field study: habitat type) had an essential influence on *T. aripo* thriving. They also showed that host-plant characteristics (growth chamber experiment: substrate; field study: genotype) have a crucial effect on the presence of the predatory mites. The interacting effects of environment and host-plant characteristics could be demonstrated in both trials, as well (i.e., host-plant characteristics play an important role under critical environmental conditions, but not under favourable or under harsh conditions).

The results of the two experiments diverged in the following aspect, though: In the field study, hairy cassava host-plant genotypes played a more important role for *T. aripo*

presence than it can be assumed from the results of the growth chamber experiment. Cassava genotypes with hairy apices also prompted higher *T. aripo* abundances as compared to genotypes with glabrous apices in a field experiment of Hanna et al. (2000). We assume that hairs are more important under field conditions than in the growth chamber because, in the field, they are able to protect the predators from the negative effects of wind. In the growth chamber, this effect becomes irrelevant. Other potentially beneficial mechanisms displayed by TMS 92/0326 in the field but not under the controlled conditions of the growth chamber are still climate-related, though not “hair-related”, i.e., the plant canopy mediating the diurnal weather dynamics, and plant vigour affecting microclimate. Plant morphology, in particular plant height, plant canopy and foliar density reportedly play a role in phytoseiid thriving (Nyrop et al. 1998; Pratt et al. 2002). Heinz and Parella (1994) and Rutledge et al. (2003) showed that the change of a single morphological trait in a cultivar can make a great difference to the predator – and, as a consequence, to the pest. Other potentially beneficial interactions, where hairy apices may play a role, are protection from macro-predators, and maybe provision of alternative food by trapping pollen (Karban et al. 1995; Bottrell et al. 1998; Sabelis et al. 1999; Cortesero et al. 2000). Protection from their own natural enemies is likely to be the most important of these suspected interactions (Agrawal et al. 2000; Roda et al. 2000; Roda et al. 2001; Norton et al. 2001). Prey densities may be less important than host-plant characteristics for predator presence, as is indicated by the work of Karban et al. (1995), Nyrop et al. (1998), Duso and Vettorazzo (1999), and Hanna et al. (2000).

As the discriminant analysis and subsequent time series analysis of the field study data showed, relative humidity contributed to explain the variance in the predator’s presence in the dry season. The variance in the predator’s reappearance in the different habitat types in the rainy season was not related to relative humidity, though. Relative humidity conditions were favourable (80 to 90 %) in each of the three habitat types as from April onward. The discriminant analysis and subsequent time series analysis let us assume that the habitat type effect in the rainy season elicited by the mixed model repeated measures analysis is not due to differences in relative humidity but to plant parameters such as plant height and apex diameter. Both plant parameters are related to general plant vigour, which in turn is affected by soil fertility and soil water tension. Our observations indeed confirm that the three habitat types are not only different in climate parameters but also in soil fertility.

It is well recognized that not only one single factor amongst prey abundance, intraguild competition, macro-predators, host-plant quality and (micro)climate is determining phytoseiid dynamics. It is rather their interacting effects, which are expressed differently in

each agricultural system (Agrawal et al. 2000), which are essential for the fate of predatory mite populations. A lot of research has been conducted on interacting effects with regard to the presence of predatory mites: on domatia interacting with host-plant resistance (Agrawal et al. 2000); on host-plant variety interacting with prey abundance (Duso 1992; Karban et al. 1995); on domatia interacting with super-predation (Norton et al. 2001); on domatia interacting with relative humidity (Grostal and O'Dowd 1994); and on plant substrate interacting with relative humidity (van Dinh et al. 1988). To our knowledge, the present study is the first looking into the interaction between genotype/hairiness and habitat climate and its effect on phytoseiids in the field.

Conclusions for M. tanajoa biocontrol

The overall objective in this study was to identify options to prolong *T. aripo*'s presence into the dry season to increase its predation on *M. tanajoa*. We wanted to investigate the potential benefit of reservoir habitats for the fast recolonization of less favourable sites after the dry season, and the role which cassava cultivars can play in the predator's dry season persistence. We established a field trial which reflected the fragmented landscape and land use patterns, and offered cassava genotypes with varying degrees of apex pubescence. *T. aripo* was present at high levels and over a long time in the humid and fertile multiple cropping habitat type. The potential of habitat reservoirs serving as a source for fast recolonization of less favourable areas in terms of *T. aripo*'s environmental requirements was therefore provided.

The hairy cassava genotype TMS 92/0326 was able to support high proportions of predators only in the fertile and humid multiple cropping habitat, where it most likely also reduced *M. tanajoa* densities. Here, the hairy TMS 92/0326 (or possibly other hairy cultivars) can be recommended, provided that farmers are satisfied with its agronomic performance. However, in sites unfavourable to *T. aripo*, resistant cassava genotypes are the better option to cope with pest mites.

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FIVE

Living at the threshold: Where does the neotropical phytoseiid mite *Typhlodromalus aripo* survive the dry season?

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ABSTRACT

The establishment of the neotropical predatory mite *Typhlodromalus aripo* in sub-Saharan Africa has resulted in broadly successful biological control of the cassava green mite *Mononychellus tanajoa* throughout the cassava belt of Africa. The predator has been less successful, however, in some mid-altitude areas and drier lowland savannas of sub-Saharan Africa. These areas are characterized by cool, long (\geq five months) and hot, long dry seasons, respectively. Here, the predator disappears from its habitat in the cassava apex during the dry seasons and reappears after the onset of rains. It is not known, however, where and how the predator remains during the dry season. In this study, we conducted a field enclosure experiment of cassava plants with the objectives to determine if (i) *T. aripo* recolonizes the cassava plant from the surrounding vegetation, if (ii) it survives in the soil or leaf litter below the cassava plant, and if (iii) *T. aripo* survives at very low densities in the apex. Because the mode of survival is expected to have an effect on the rates of recolonization, we compared the timing of the predator's reappearance in the cassava apex of the different enclosure treatments. Predator presence on cassava apices was monitored non-destructively at weekly intervals. The reappearance and subsequent resurgence of the predator was expressed as the proportion of plants with at least one apex with *T. aripo* per total number of plants of the treatment. The predators reappeared first on enclosed plants, except on the plants that had their apices removed. They appeared only one week later on plants without enclosure which had received *T. aripo*. The predators reappeared eight weeks later also in the enclosures where they had been released, but where the apices had been removed at the time when the enclosures were installed over the plants. At about the same time, the sentinel plants that have never received *T. aripo* were colonized by the predators. The study shows that *T. aripo* survives the dry season in very low densities in the cassava apex. Also discussed is the supportive value of the results of additional studies such as (a) a vegetation survey around release fields, (b) an assessment of efficiency of non-destructive visual in-field apex inspections, (c) an infested plant material transfer trial, (d) a screenhouse experiment on vertical migration, and (e) microclimate measurements in various cassava plant parts.

Key words: Refuge, predatory mites, *Manihot esculenta*, migration, biocontrol, colonization, canopy microclimate profile

INTRODUCTION

Over-seasoning in tropical climates is the mechanism of an organism to overcome more or less cyclic and rather long and unfavourable extremes in environmental conditions, mainly heat, cold or drought. Arthropods respond to such conditions in various ways (Tauber et al. 1986). Migration to an over-seasoning habitat, dormancy ranging from quiescence to diapause, and acquired hardiness are three common adaptations that arthropods have developed to cope with adverse climatic conditions. Tropical climates are generally characterized by rainy and dry seasons. Conditions during the latter can reach extreme levels of dryness that deeply challenge the survival ability of organisms.

The dry season is a time period with lack of precipitation, low daytime ambient relative humidity, and high daytime and low night-time temperatures. In the North-West Province of Cameroon, where the present study was conducted, the dry season typically starts in mid-November and extends through mid-March, with February being the driest month. During this period, average monthly relative humidity ranges from 62 to 77 % with upper and lower bounds of 23 to 49 % for the daytime and 84 to 98 % for the night-time (Zundel, unpublished data). Average monthly temperature for the same period ranges from 20 to 23 °C with an upper to lower bound of 12 to 15.5 °C for the minimum temperature and 29 to 33 °C for the maximum temperature. Together, these climatic conditions challenge the limits of tolerance of small arthropods like phytoseiid mites.

Phytoseiid mites cope with water deficits in several ways. First, water absorbed from feeding on prey and water produced in metabolism can compensate for water loss through transpiration and excretion (Gaede 1992). Since prey is abundant in the dry season (Onzo et al. 2003; Hanna et al. 2005; Zundel et al., manuscript in preparation), predation could therefore compensate for a large portion of water loss due to dry conditions. Second, predatory mites are also capable of absorbing water from the air, if ambient humidity is sufficiently high, as has been shown for many phytoseiids (Gaede 1992; Yoder 1998). Third, another common way to survive stressful periods is to enter diapause in the egg or adult-female stages in response to changes in temperature and photoperiod, where relative humidity can act as a modifying factor in diapause regimes of predatory mites (van Houten 1990). Diapause has never been reported, however, in tropical mites (Veerman 1992; Bruce-Oliver et al. 1995); and relative humidity, a critical factor during the dry season, has never been tested as a potential diapause-inducing cue for African phytoseiid mites (Bruce-Oliver et al. 1995). Furthermore, another strategy used by mites to cope with dry conditions is to aggregate and become immobile (for Orbatids: Smrz 1994; for Pyroglyphids: Glass et al. 1998) or to seek refuge in environments that are more

favourable for the phytoseiids' survival and reproduction (Swift and Blaustein 1980, cited in: Auger et al. 1999). Aerial and ambulatory seasonal migration is common with phytoseiid mites (Sabelis and Dicke 1985; Croft and Jung 2001), whereas structures on the host plant (Nyrop et al. 1994; Gurr 1997; Davies 2001) or surrounding wild vegetation serve as refuges for predatory mites of a crop (Tuovinen and Rokx 1991; Stanyard 1997; Tixier et al. 1998; Tixier et al. 2000; Kabicek 2003). Under dry conditions, predatory mites show positive hygrotactic responses if they are suffering from a water deficit (Gaede 1992).

The neotropical phytoseiid mite *Typhlodromalus aripo* DeLeon, 1967 (Acari: Phytoseiidae) was introduced into Africa in 1993 for the control of the neotropical phytophagous cassava green mite *Mononychellus tanajoa* (Bondar, 1938) (Acari: Tetranychidae) (Yaninek and Hanna 2003; Hanna et al. 2005). The latter was accidentally introduced into Africa in the early 1970s (Nyiira 1972). Where *T. aripo* has been established, it persists throughout the year, particularly in the humid forest and the forest/savanna mosaic agro-ecological zones (Hanna et al. 2005; Onzo et al. 2005). However, in seasonally dry areas such as the savannas of West Africa and the drier and colder sub-humid mid-altitudes of southern Africa, *T. aripo* disappears altogether from cassava fields during the height of the dry season and reappears approximately eight to 12 weeks after the onset of the first rains of the subsequent rainy season (Mebelo et al. 2003; Onzo et al. 2003; Hanna et al. 2005; Zundel et al., manuscript in preparation). It is not known, however, where *T. aripo* survives the dry season. The predator resides in the apex of the cassava plant during the day and migrates during the night down to the upper 20 % of the cassava plant foliage to forage on cassava green mite (Onzo et al. 2003). To date, the predator has been found only on cassava (Yaninek and Hanna 2003) with the exception of one record in which six individuals of *T. aripo* were collected from terminal shoots of *Cajanus cajan* (Linné) Millsp., 1900 (Fabaceae) and from flowers of *Tridax procumbens* Linné, 1753 (Asteraceae) in the beginning of the dry season (Zannou et al. 2005a).

The present study is one of a series designed to determine the establishment, persistence, and impact of *T. aripo* in the mid-altitudes of north-western Cameroon (Zundel et al., manuscripts in preparation). The broad objective of this study is to determine where *T. aripo* survives during the dry season. Specifically, we were interested in determining if (i) *T. aripo* recolonizes the cassava plant from the surrounding vegetation, or if (ii) it survives in the soil or leaf litter below the cassava plant, or if (iii) it survives at very low densities in the apex. Because the mode of survival is expected to have an effect on the rates of recolonization, we compared the timing of the predator's reappearance in the cassava apex.

To give support to the interpretation of the findings from the enclosure experiment, additional studies such as (a) a vegetation survey around release fields, (b) an assessment of efficiency of non-destructive visual in-field apex inspections, (c) an infested plant material transfer trial, (d) a screenhouse experiment on vertical migration, and (e) micro-climate measurements in various cassava plant were conducted.

MATERIAL AND METHODS

Phytoseiid mites on vegetation surrounding cassava fields

We were interested in knowing if the vegetation surrounding cassava fields serves as dry season refuge for *T. aripo*. We conducted a survey in February 2004 (towards the end of the dry season) in four villages between 800 and 1300 m asl (meters above sea level) in the North-West Province of Cameroon. In each village, one cassava field was selected which had received *T. aripo* between four and 16 months before the survey. *T. aripo* was present in all the fields prior to its disappearance from cassava in February of the same year (data presented elsewhere in Zundel et al., manuscript in preparation). At each field, one 60 meters transect in each of the four cardinal directions was established in the vegetation surrounding the fields (including cassava fields present within the specified transect distance). Two to five leaves distributed throughout the plant canopy were inspected with a 4x head lens during a period of two to ten minutes depending on the size of the plant. Special attention was given to plant parts which were turgid, hairy (or providing other types of domatia), or providing pollen. All phytoseiids found were collected with camel-hair brushes and kept in 75 % alcohol and later identified to genus or to species level where possible.

Enclosure experiment

Typhlodromalus aripo is known to inhabit the apex of the cassava plants during the day and to forage on cassava leaves during the night. Estimates of population size of this predator are generally based on counts from cassava apices during the daytime. It is not known, however, if during the dry season, when *T. aripo* 'disappears' from the plant – i.e., it can no longer be found in the apices and upper canopy leaves – it seeks refuge in other parts of the plant such as basal leaf buds or the base of the plant including leaf litter and top soil. In the enclosure experiment, we were interested to determine if *T. aripo* (i) recolonizes the cassava plant from the surrounding vegetation, or if (ii) it survives in the soil or leaf litter below the cassava plant, or if (iii) it survives at very low densities in the apex. Because the mode of survival is

expected to have an effect on the rates of recolonization, we compared the timing of the predator's reappearance in the cassava apex in the different treatments.

The experiment was conducted near the town of Bamenda at 1294 m asl in the North-West Province of Cameroon. It was established on-station during the rainy season (July) on a plot of 25 x 40 meters using 30 centimeters cuttings of the cassava variety TMS 92/0326. This variety is known to be a suitable host for *T. aripo* because of its hairy apex (Zundel et al., manuscript in preparation). Five treatments were randomly assigned to single cassava plants, with 12 plant replicates per treatment and a planting distance of 3 meters within and between rows. The following treatments were applied: (T1) *T. aripo* added to plants without enclosures, (T2) *T. aripo* added to plants with enclosures, (T3) *T. aripo* added to plants with enclosure and with Tanglefoot glue barrier at the base of the main stem of the plant (with only one stem per plant), (T4) *T. aripo* added to plants with enclosures and with cassava apices removed, and (T5) control consisting of plants where *T. aripo* was not added, and where no enclosures were set up. The control plants were used as sentinel plants to indicate the timing of *T. aripo* reappearance on individual plants that had remained free of *T. aripo*. To avoid infestation of the plants in the control treatment by *T. aripo*, they were planted in large pots (ca. 50 l) at the same time as the plants for the other four treatments and were grown in an isolated place at least 200 meters away from any cassava plants until they were transported to their respective positions in the plots. Two weeks after apex removal, the apices of T4 had regrown to a size of 3.8 ± 0.2 millimeters in diameter (apex size in the other treatments at this time was 5.9 ± 0.4 millimeters), and were from thereon potentially suitable habitats for reappearing predators.

In addition to the treatment plants, the plot also included two border rows of the same variety planted at 1 x 1 meter spacing. In the predator addition treatments, *T. aripo* was added at the rate of 25 predators per plant on three successive releases at two-week intervals between 3 and 29 October. Predators were also added to the border plants during the first two releases at the rate of 25 predators on each of 40 plants evenly distributed throughout the border rows. White polyethylene (mesh size 0.2 millimeters) enclosures (1.5 x 1.5 x 1.5 meters in L x W x H) were placed over the plants in the three enclosure treatments on 8 March, three weeks after *T. aripo* was no longer detectable in the cassava apices (Figure 1). Care was taken to cover the base of the enclosures with soil to prevent cursorial entry of *T. aripo* into the cages.

Typhlodromalus aripo populations used in the experiments reported in this paper were provided by the International Institute of Tropical Agriculture, Biological Control Centre for

Africa, located in Cotonou, Republic of Benin. The predators were imported from Bambui in Minas Gerais State in Brazil and were maintained in the laboratory on detached cassava leaves at 25 ± 1 °C and 80 ± 10 % relative humidity since 1997. The predators were multiplied for three generations in cassava rearing facilities in a screenhouse prior to packing and shipping to Cameroon. In preparation for shipping, the predators were aspirated into disposable seven centimeters long plastic pipette tips, each tip containing 25 female predators. The pipette tip was sealed with parafilm at one end while the other end was covered with mite-proof gauze (Mégevand 1997). At the time when the predators were released (96 h after packing), mortality in the tips was 20 to 30 %. The predators were released by attaching the pipette tips containing the predators with scotch band to the stem close to the apex, followed by removal of the seal.



Figure 1. White polyethylene (mesh size 0.2mm) enclosures (1.5 x 1.5 x 1.5 meters in L x W x H), which were placed over the cassava plants according to the various treatments.

Infestations by *T. aripo* were determined in weekly non-destructive inspections (i.e., thorough in situ visual inspection with 4x head lenses) of all apices starting immediately after the first release of the predators. A pre-release inspection had indicated that *T. aripo* was absent from all the experimental and border plants. The cages were lifted once a week to monitor the return of *T. aripo* to the apices of the plants. The procedure lasted less than ten minutes per plant.

To determine the efficiency of the method of visual in-field inspections (with minimal disturbance to the apex), we compared the frequency of *T. aripo* using (a) the in-field

inspection method and (b), on the same apices which were removed, inspection under a dissecting microscope in the laboratory. Samples were taken on six occasions from December to February, on a total of 30 apices of the same variety.

Microclimate of cassava plants

To determine which stratum or structure of the cassava plant might provide a favourable temperature and relative humidity environment for *T. aripo* during the dry season – December 2003 through February 2004 – we characterized the relative humidity and temperature profile of the various strata of the cassava variety TMS 92/0326 which was used in the experiment. This is an early branching variety with low and dense canopy, uniformly green leaves, and hairy apices. Microclimate measurements were taken on six days at 2 pm (which is the driest and hottest period of the day) on the same cassava plant in a plot adjacent to the enclosure experiment. Relative humidity was measured with a probe (Hygroclip®, Rotronic; diameter: 4 millimeters; length: 50 millimeters) containing a humidity sensor (ceramic capacitance; ± 1.5 %) and a temperature sensor (Pt 100; ± 0.3 K). Plant surface temperature, which is more relevant to *T. aripo* development than the temperature recorded by the probe, was measured with an infrared gun (Inspacto 900, Infrapoint®; accuracy ± 1 % of the measured value) on a spot size of 2 millimeters. Temperature and relative humidity measurements using both instruments were taken for the following plant parts: (a) inside the first folded leaves covering the apex – where *T. aripo* resides; (b) on the lower surface of the first fully developed leaf – where highest densities of the prey *M. tanajoa* are found; (c) on the base of the petiole of the first fully developed leaf; (d) on the base of the petiole of the oldest leaf; (e) in the area of the stem at the interface with the ground which is normally surrounded by plant litter. (f) Ambient conditions at the level of the apex were measured with the probe. The measured plant parts are illustrated in Figure 2. Four measurements were repeated with each instrument on each of the above-mentioned plant part within one minute, which were then averaged to give the measurement for a particular plant part on a day of measurement. All measurements were completed within a period of 30 minutes.

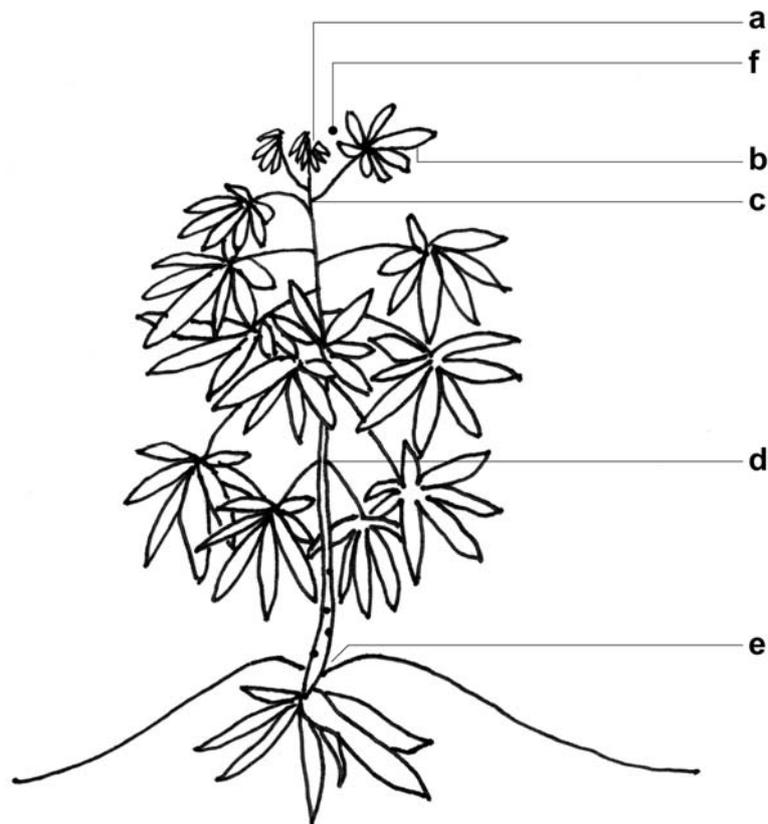


Figure 2. Precise location of the microclimate measurements in the cassava canopy: (a) inside the first folded leaves covering the apex; (b) on the lower surface of the first fully developed leaf; (c) on the base of the petiole of the first fully developed leaf; (d) on the base of the petiole of the oldest leaf; (e) in the area of the stem at the interface with the ground which is normally surrounded by plant litter; (f) ambient conditions at the level of the apex

Data analysis

To test the three hypotheses of the enclosures experiment i.e., if (i) *T. aripo* survives near the cassava plant; if (ii) *T. aripo* survives in the soil or leaf litter; and if (iii) *T. aripo* survives in the apex, we performed a generalised linear mixed model (GLMM) with a binomial error distribution and a logit-link function for each of the hypotheses. We used the function `glmmPQL` from the library `MASS` in R (R Development Core Team 2005). The dependent variable was the proportion of colonized plants within each group. The treatment combinations, according to the hypotheses, and week, were the two independent fixed variables. The subject variable was defined as the five groups of plants of the five treatments. To find the optimal model, we did a step-wise backwards selection by removing non-significant terms using likelihood ratio tests. Significant terms remained in the model. We

started with the full model: $Y \sim \text{treatment} + \text{week} + \text{week}^2 + \text{treatment} * \text{week} + \text{treatment} * \text{week}^2 \mid \text{group}$, where Y is the proportion of plants with *T. aripo*. The treatment factor was constructed as follows: To test hypothesis (i) – *T. aripo* survives near the cassava plant – we compared the treatments where we expected *T. aripo* to appear (i.e., T₁ and T₂) with the treatment where we did not expect it to appear, if it had survived near the cassava plant (i.e., T₃). To test hypothesis (ii) – *T. aripo* survives in the soil or leaf litter – we compared the treatments where we expected *T. aripo* to reappear (i.e., T₁ and T₂) with the treatment where we did not expect it to reappear, if it had survived in the soil or leaf litter (i.e., T₃). To test hypothesis (iii) – *T. aripo* survives in the apex – we compared the treatments where we expected *T. aripo* to reappear (i.e., T₁ and T₂) with the treatment where we did not expect it to reappear, if it had survived in the apex of the cassava plant (i.e., T₄).

The correlation between *T. aripo* presence and ambient relative humidity (Figure 3) was calculated with a linear model using generalised least squares (glS; R Development Core Team 2005).

Differences in microclimate between plant parts for each instrument were compared with PROC GLM (SAS 2003) and the Student-Newman-Keuls Test with day of measurement as a replicate. This is justifiable since the plants did not change much during the period when the measurements were taken (data not shown).

RESULTS

Phytoseiid mites on vegetation surrounding cassava fields

Eighty two (82) plant species (including cassava) were inspected during the survey of the vegetation surrounding the four cassava fields. Phytoseiid mites were found on 26 plant species. The most common host-plant species for phytoseiids were (1) *Chromolaena odorata* (Linné, 1759) R.M. King & H. Robinson (Asteraceae), representing 16 % of plant samples and harbouring 48 % of phytoseiids collected; (2) *Asystasia schimperi* T. Anders. (Acanthaceae), representing 1 % of plant samples and harbouring 3 % of phytoseiids collected; (3) *Melinis minutiflora* Palisot de Beauvois, 1812 (Poaceae), representing 3 % of plant samples and harbouring 5 % of phytoseiids collected; (4) *Brachiaria ruziziensis* R. Germain & Evrard, 1953 (Poaceae), representing 8 % of plant samples and harbouring 12 % of phytoseiids collected; and (5) *Erigeron floribundus* (H.B. & K., 1820) Sch. Bip. 1865 (Compositae), representing 4 % of plant samples and harbouring 5 % of phytoseiids collected.

Eleven known phytoseiid species were found – *Euseius* sp.; *E. hutu* (Pritchard & Baker, 1962); *E. spermaphyphus* (Ueckermann & Loots, 1988); *Neoseiulus* sp.; *Paraphytoseius multidentatus* Swirski & Shechter, 1961; *Phytoseius* sp.; *Phytoseius amba* Pritchard & Baker, 1962; *Phytoseius hongkongensis* Swirski & Shechter, 1961; *Typhlodromips* sp.; *Typhlodromips shi* (Pritchard & Baker, 1962); *Typhlodromus (Anthoseius) apoxys* van der Merwe, 1968. Two new species – *Neoseiulus yanineki* sp. nov., and *Typhlodromips cameroonensis* sp. nov. – were described for the first time (Zannou et al. 2005b). *Typhlodromalus aripo* was not found on any of the samples during the sampling period.

Enclosure experiment

The data from the enclosure experiment are presented in Figures 3 and 4. Figure 3 shows pooled *T. aripo* infestation levels on all plants where the predator was added (i.e., all plants of all treatments except the sentinel plants (T₅) and those plants from which the apices were removed (T₄)). The predator was absent from all the plants in the experiment on the first inspection (26 September). Densities of *T. aripo* began to increase soon after its release on 3 October, peaking at 100 % infestation on 19 November and declining thereafter to zero by 18 February. The fit showed that this decline followed a corresponding decline in average relative humidity ($p = 0.0022$). The predators remained absent from all the plants for approximately three weeks, reappearing sometime between 8 March and 5 April and reaching 100 % infestation on 8 June. The reappearance and increase is associated with a similar increase in average relative humidity ($p = 0.0014$).

Figure 4 shows the data for *T. aripo* infestation on plants after the enclosures were installed on 8 March, two weeks after the predators were no longer detectable on any of the plants in the experimental field. Within one week from the placement of the enclosures, *T. aripo* began to reappear in the apices of plants of some of the treatments. On plants that received *T. aripo* (T₁ and T₂), the predators appeared considerably earlier than on plants to which the predators were not added (T₅) (GLMM; $df = 1$; $\chi^2 = 13.04$; $p < 0.001$), indicating that previous presence of the predators plays a significant role in (re)colonization of a cassava plant after the dry season. At least in the first six weeks of the new rains, the predators came back from near the plant, which allows us to compare the treatments in the remaining hypotheses (ii and iii) against T₁ and T₂. Figure 4 shows that the predators appeared earlier on plants that received *T. aripo* and glue around the stem (T₃) than on plants that received the predators but where we had not applied the glue (T₁ and T₂) (GLMM; $df = 1$; $\chi^2 = 24.74$; $p < 0.001$). Had *T. aripo* migrated to the soil or litter, we would have expected it to reappear

earlier on T₁ and T₂ compared with T₃, as the glue would have impeded *T. aripo*'s recolonization of the plant from the soil. On those plants where we removed the apices (T₄) and which had received *T. aripo*, the predator's pattern of reappearance was distinct from the two treatments where we did not remove the apices (T₁ and T₂) (GLMM; df = 1; $\chi^2 = 7.58$; p = 0.006). Data presented in Figure 4 indicate that the predators came back much later on the plants where apices were removed which supports hypothesis (iii) – that *T. aripo* survives in the apex.

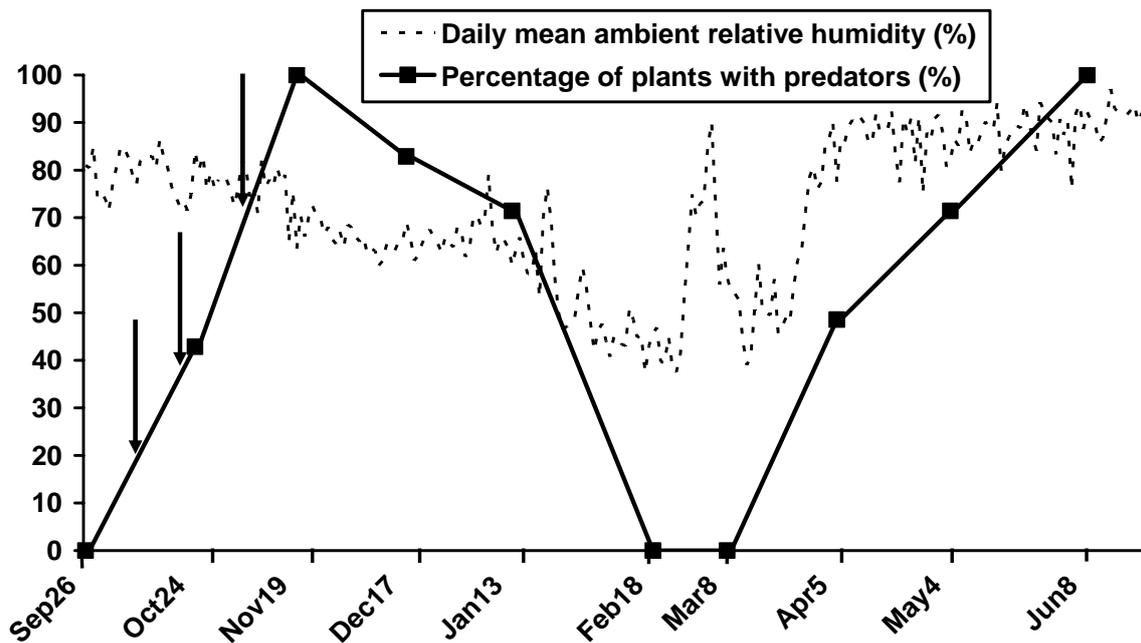


Figure 3. Proportions of plants with *Typhlodromalus aripo* in the enclosure experiment from the first release (3 October, 2003) to the end of the experiment (8 June, 2004). The treatments were applied on 8 March, 2004. The plants of all treatments with *T. aripo* release (except for the treatments where the apices had been removed) are pooled (n = 27). Data points are proportions of plants with *T. aripo* in at least one apex. Dotted line shows daily mean ambient relative humidity data, based on the measurements with a data logger (HOBO H8 Pro from Onset Computer Corporation) at 12-minute intervals. Vertical arrows indicate the release dates of *T. aripo*.

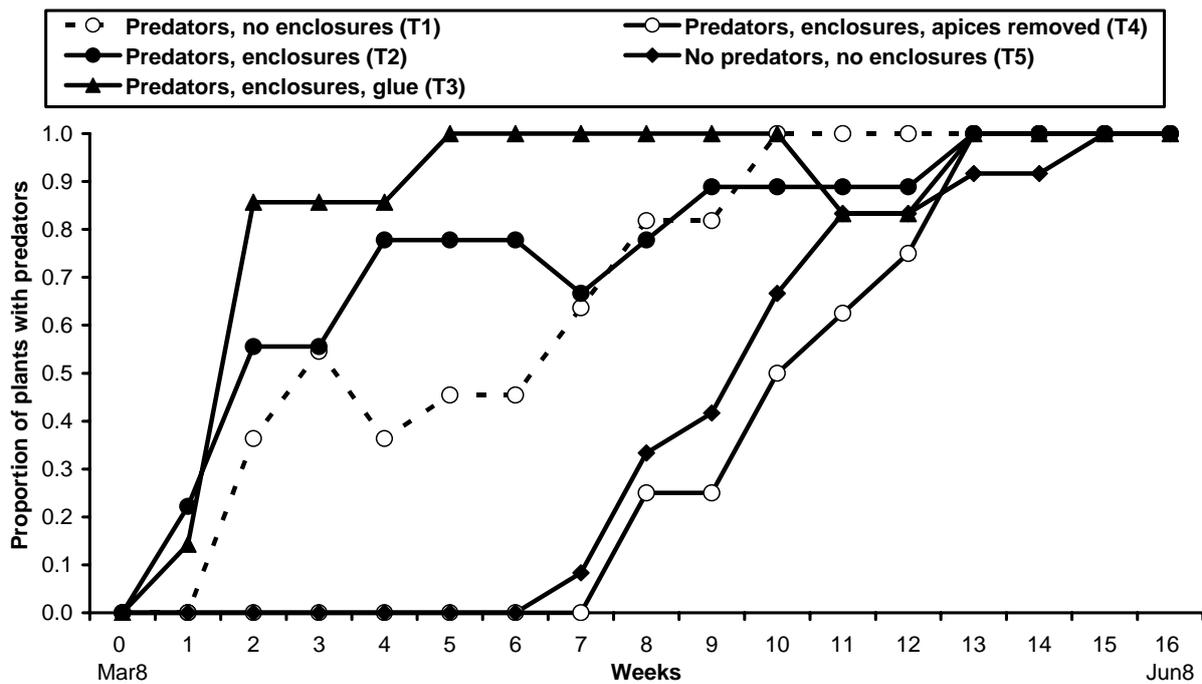


Figure 4. Proportion of plants with *Typhlodromalus aripo* after treatment application (Mar8/w0) until the end of the experiment (Jun8/w16). Data points are proportions of plants with *T. aripo* in at least one apex. The arrow indicates the period used in the analysis (week 0 to week 6).

In summary, our results show that: (i) *T. aripo* survives near the cassava plant; (ii) *T. aripo* does not survive in the soil or leaf litter; but we have reasons to assume an interaction between the pattern of *T. aripo*'s reappearance and the glue and / or the soil, since it came back faster on plants with glue than on plants without glue, which was the opposite of what we expected; and (iii) *T. aripo* survives in the apex since *T. aripo* started to move between cassava plants beginning with week 6, as indicated by the time of appearance of *T. aripo* on the sentinel plants (T₅). The other treatments lost their usefulness in eliciting the place of dry season refuge of the predators after week 6.

Inspection of a sample of apices under a dissecting microscope in the laboratory showed that contrary to visual in-field inspection, 10.5 % (with a range of 0-22 % for the six sampling dates) of the apices ($R^2 = 0.921$) were false negatives. These false *T. aripo* negatives contained on average 1.5 ± 0.3 (mean \pm standard error) *T. aripo* individuals (females, males and nymphs) which were not detected in the field.

Microclimate of cassava plants

Microclimate measurements showed differences among the various parts of the cassava canopy (Figure 5). The highest relative humidity was found at the base of plant at the interface between the ground and the stem. But that was not significantly different from relative humidity on the first fully developed leaf and the apex. The driest spots on the plant were the base of the first fully developed leaf and the oldest leaf, which are similar to ambient relative humidity. Surface temperature of the same plant parts measured by the infrared gun showed that the plant base was the coolest and differed by 7.02 and 7.35 °C respectively from basal buds of first fully developed leaf and the oldest leaf. Surface temperatures of the remaining two plant parts were intermediate (Figure 5).

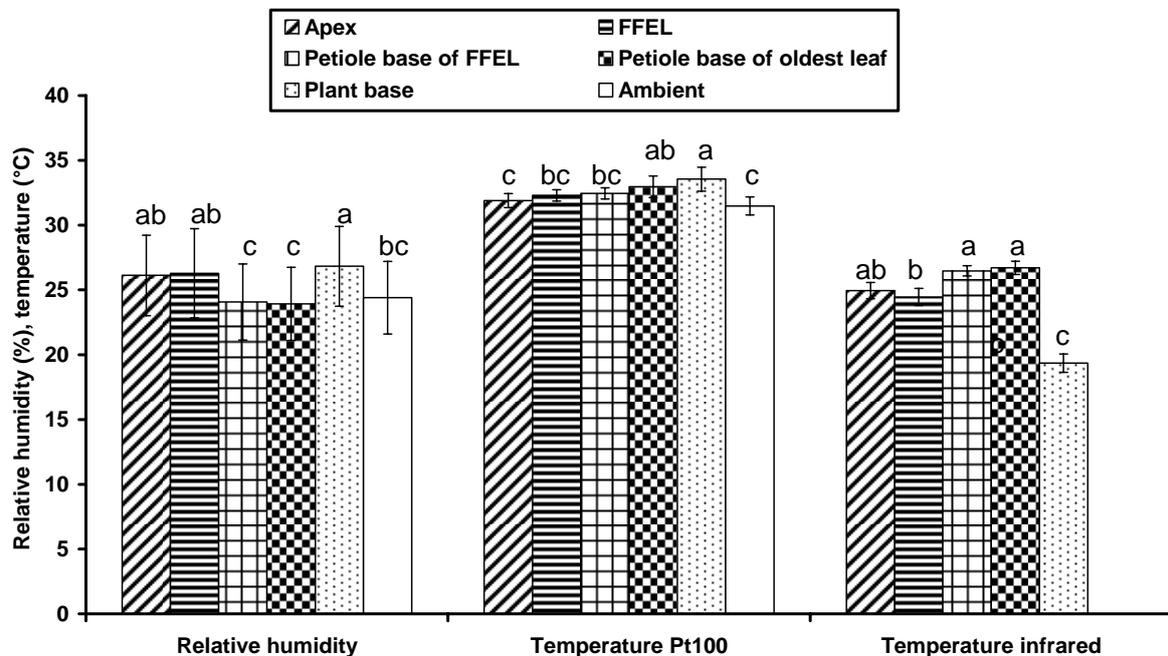


Figure 5. Mean relative humidity (%), temperature measured with a Pt 100 sensor (°C), and temperature measured with an infrared gun (°C) in six different locations (FFEL = first fully expanded leaf) of the cassava canopy of variety TMS 92/0326 at 2 pm. Vertical bars are standard errors of the means. Means with the same letter are not significantly different (Student-Newman-Keuls Test; $p = 0.05$).

DISCUSSION

In this study, we were interested in answering the broad question of where *T. aripo* resides in the dry season. Specifically, we wanted to determine if *T. aripo* moves to the field surroundings from which it can recolonize cassava fields when conditions become favourable, or if it remains on the cassava plant and its immediate vicinity. Our results provide convincing evidence that *T. aripo* does not utilize non-cassava vegetation, which corroborates existing knowledge about the host-plant specificity of *T. aripo* (Yaninek and Hanna 2003; Zannou et al. 2005a). It is now abundantly clear that non-cassava vegetation is not a typical refuge for *T. aripo* during the dry season on the African continent. This conclusion leaves two options: adults that survive the dry conditions remain on the cassava plant at very low numbers (and possibly undetectable by non-destructive methods). Or, they seek refuge at the base of the plant in soil and leaf litter, where the microclimate may be more favourable than on the plant canopy.

The enclosure experiment, including the sentinel plants, was designed to determine if *T. aripo* reappearance is from predators that stay on the plant in the field or from aerially dispersing migrants that colonize cassava from habitats with favourable conditions. The data presented in Figure 3 shows that the decline and resurgence in *T. aripo* populations during the dry season is associated respectively with a parallel decline and increase in ambient relative humidity, with an intervening period during which the predator apparently disappeared from the plants. In the enclosure experiment (Figure 4), *T. aripo* reappeared within a period of one to two weeks after enclosure installation (or three to four weeks after its disappearance) on plants where the predator had been added and where the apices remained intact. In contrast, predator appearance on the sentinel plants (that never had any *T. aripo*) lagged another five to six weeks, similar to the plants from which apices were removed after they had received the predators in October. Apex removal from plants kept them free of predators thereafter, which points to an essential role of the plant apex in the dry season survival of *T. aripo*. Together, the two patterns (i.e., short and long lags) of *T. aripo* resurgence strongly suggest that the predator had remained on the plants where it was added but was not detected by the non-destructive inspection method used in this study. Moreover, that the predators lagged five to six weeks on the sentinel plants indicates that there was no interplant movement by *T. aripo* within the experimental plot during the first six weeks after enclosure installation. This is further supported by the lagged appearance of *T. aripo* on enclosed plants from which the apices were removed, which also indicates that during the seven-week period prior to the

resurgence of *T. aripo* on these plants there was no colonization of enclosed plants from outside the enclosures. Taken together, the patterns of first reappearance of *T. aripo* and its subsequent resurgence strongly indicate that the early reappearance of *T. aripo* on the enclosed and non-enclosed plants with intact apices was from predators that had remained all along on the plant.

Based on the observations and considerations above, we propose that *T. aripo* does not have an active migration behaviour to avoid dry climatic conditions, as is known about aerial long-distance dispersal of phytoseiid mites (Sabelis and Afman 1994). This predator instead seems to stay in the apex where it is subject to high mortality when conditions worsen. That *T. aripo* reappeared first on plants it inhabited prior to its apparent disappearance in the height of the dry season may be explained by two alternative hypotheses: (1) the predator remained on the plants but was not detected by our sampling procedure, and/or (2) the predator left the apices and hid on other parts of the plants or in leaf litter or soil. We tested these hypotheses with several supplementary experiments.

First, in February, one week after *T. aripo* had disappeared from all the cassava plants, 50 cassava plants which were grown close to the enclosure experiment, and that had received *T. aripo* in October, were dissected into seven stem sections and three canopy levels. Leaves were screened with 4x head lens, and stem buds were inspected with 10x hand lenses. *T. aripo* was not found on any of the plant parts. In the immediate neighbourhood of the enclosure experiment described above, and at about the same time, we transferred plant material (a: leaf litter; b: stems and woody branches cut in pieces of 20 centimeters; c: top soil around stem; d: no transfer) from cassava plants of the variety TMS 92/0326 where *T. aripo* had been released four months before, to plants of the same variety which always had been free of *T. aripo*, and enclosed them with cages, as described above. The treatments were replicated eight times in blocks. As a control, we monitored eight plants without enclosures. The enclosures were removed two months after the setup of the experiment, and apices were inspected for *T. aripo*. The predator was not found on any of the plants inside the enclosures, regardless of type of plant material transferred into the enclosure. However, the predators were present in the apices of seven of the eight control plants without enclosures, where *T. aripo* had not been released in October.

Second, we determined the reliability of our sampling procedure, particularly at low *T. aripo* frequency or during its apparent absence. The average error of 10.5 % shows that the predators in apices reach abundance levels that were no longer detectable with field

inspections, which may have been the source for the recolonization of the plants where *T. aripo* had been added.

Third, that resurgence was faster on plants with Tanglefoot glue barrier (T_3) than on plants without the barrier (T_2) may indicate a possible interaction between the predator and the ground, which was interrupted by the sticky barrier. The most likely explanation is that the predators were at least partially leaving the plants without the barrier, probably in response to drought conditions. We tested this hypothesis in a screenhouse experiment using plants of the genotype TMS 92/0326 which were water-stressed for three weeks (Zundel, unpublished data) and infested with females of *M. tanajoa* and females of *T. aripo*. A Tanglefoot glue barrier was applied to one group of plants while the other group remained without a barrier. Sentinel cassava apices (with stem end inserted in parafilm-sealed glass vials filled with water) of the same genotype were placed in the soil surface around the base of the plant and checked after 72 hours of exposure. Average recapture of *T. aripo* adults in the apices of the test plants were similar in both plants with barrier and those without barrier, whereas four sentinel apices were found infested with *T. aripo* in the plants without barrier (36 sentinel apices in total), but none of the sentinel apices in plants with barrier (36 sentinel apices in total) were infested with *T. aripo*. Although no treatment effect could be assessed in the recapture of the predators in the apices of the potted plants, the few captures on the sentinel apices showed that, at least, *T. aripo*'s downward movement range extends to the ground. Other studies have shown that ambulatory dispersal by phytoseiid mites is directed away from wilting plants (Auger et al. 1999) and can occur over bare ground (Janssen 1999), however, with considerable losses of individuals (Jung and Croft 2000). It is also possible that *T. aripo* may have an active migration behaviour to avoid dry conditions as shown for *Phytoseiulus persimilis* Athias-Henriot, 1957 (Gaede 1992) and for the tick *Ixodes ricinus* Linné, 1758 (Perret 2003). It is also possible that *T. aripo* was preyed upon by ground predators that forage on the cassava plants. Even though this phenomenon was not found in extensive diurnal monitoring of within plant distribution of mites on cassava (Onzo et al. 2003) it may require further investigations.

Fourth, the rapid resurgence of *T. aripo* in T_2 (*T. aripo* addition plus enclosure) compared with T_1 (*T. aripo* addition and no enclosure) may be partially explained by higher average temperature (+ 1.1 °C) inside the enclosures compared to non-enclosed plants. It is unlikely that among-treatment differences in *M. tanajoa* densities may have affected the pattern of *T. aripo* reappearance in (T_2) and outside (T_1) the enclosures, as we did not find any differences in average *M. tanajoa* densities in and outside the enclosures: *M. tanajoa* densities

were 182.0 and 104.3 ($p = 0.187$) in February inside and outside the enclosures respectively, while in March average *M. tanajoa* densities were 119.3 and 115.6 ($p = 0.777$). Means were compared with a *t*-test using log-transformed mite densities.

In this study we established, indirectly, that *T. aripo* is likely to survive at a very low frequency in the cassava apices in environments similar to the mid-altitudes of north-western Cameroon with unimodal rainfall and a dry season of four months. Additionally, we suspect that *T. aripo* interacts with the ground below the cassava plant; however, the nature of this relationship is not yet sufficiently clear. Because of the essential role of the apices in *T. aripo* dry season survival, we suggest that further studies focus on the identification of those apex traits which are favourable for the predators' dry season survival. Based on our observations, we assume that apex hairiness and apex turgidity are traits which make a cassava variety suitable for *T. aripo* during the dry season. Varieties with young leaves shading the apex might also be favourable, as shade reduces temperature and therefore increases relative humidity. Cassava varieties having these traits (in addition to other pest and disease resistance traits and to characteristics preferred by farmers) should be made available in areas where *T. aripo* dry season survival is at stake.

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SIX

Developing cassava cultivars for a diverse environment in the mid-altitudes of Cameroon: How to build on farmers' own experimentation

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ABSTRACT

What is the most effective way of cassava cultivar selection in an agro-ecologically diverse environment in Central Africa? The low multiplication rate of cassava (about ten plants out of one plant per year) is a specific challenge which requires that selection, targeted promotion, multiplication and distribution are optimally interlinked. By means of a formal on-farm variety trial, of farmer-designed variety trials, of field visits, of semi-structured farmer interviews and of an assessment of farmers' ability to differentiate between new varieties, we explored to which extent decentralized and participatory cassava variety selection are useful, and how much we can build on farmers' own experimentation. We found that, due to high heterogeneity between farmers' fields, decentralized selection with one to three trial sites per village is a prerequisite to give farmers access to the information they need to take decisions concerning new varieties. Farmers' number one preference criteria for varieties is high yield to best exploit the opportunity related to the high, mainly urban, demand of gari. In addition, they prefer varieties which can be consumed after simple boiling. The on-farm variety trial showed that heterogeneity in terms of cassava variety performance was more pronounced between fields with low ($< 8.6 \text{ Mg ha}^{-1}$) mean yields, as compared to fields with high ($> 8.6 \text{ Mg ha}^{-1}$) mean yields. We found some evidence that the present pattern of distribution of local cassava cultivars has its reason in genotype x environment interaction. The cassava variety experiments designed by farmers were set up in a systematic way that allowed comparisons between the new varieties. To farmers, cassava cultivar testing is a long-term process. In each cropping cycle, emphasis is given to specific objectives. In the first cropping cycle, some experiences are collected, and the planting material is multiplied. In a second cropping cycle, the cultivars are tested in mixtures and/or on different soils. Selection starts earliest in the second cropping cycle. The proposed cassava variety selection scheme largely builds on farmers' own experience in cassava cultivar testing, and on their ability to distinguish between varieties that are new to them. The availability of planting material at the time of field preparation is a major bottleneck in cassava crop management and forces farmers to exchange large quantities of planting material. This common exchange of planting material between farmers will grant a fast and effective (though not systematic) dissemination of new genetic material.

Key words. Agricultural research methodology, farmer experimentation, participatory variety selection, variety identification, cassava cropping system, genotype x environment interaction

INTRODUCTION

Farmer experimentation has a longstanding tradition. Sometimes it is so naturally integrated into the production process that it goes unrecognized by the farmers themselves – and by outsiders asking them about their latest experiments or innovations. And sometimes experimentation and innovation are an explicit element in the farming culture (Millar 1993; Bentley 1994; Stolzenbach 1997). The fact that farmers do their own experimentation has now begun to trickle into the consciousness of the formal research community – and with it the question of how this asset could be best exploited. Two broad lines of opinions can be distinguished: Some see it as an opportunity to learn something about the farmers' concerns and the way they approach them. In order to produce results that are more acceptable to farmers, agricultural researchers want to build their own research priorities and methods on the farmers' way of experimenting. At the same time, however, they are warning from imposing formal research concepts on farmers – because the “extra” which farmer experimentation can add to knowledge gain would be lost (Millar 1993; Okali et al. 1994; Stolzenbach 1997). Others feel encouraged to collaborate with farmers by the fact that they can work with somebody who has an understanding for the nature of experimentation. But, in their view, farmer experimentation needs modification to produce results which can be communicated to other partners in the innovation chain and which eventually comply with scientific standards (Ashby et al. 1995).

The objective of the work presented here was to find the most efficient combination of these two attitudes and to translate it into practical steps of a participatory selection scheme for cassava varieties in an agro-ecologically diverse environment in Central Africa. The low multiplication rate of cassava (about ten plants out of one plant per year) is a specific challenge which requires that selection, targeted promotion, multiplication and distribution are tuned to each other.

Farmers insist that they need to grow the new varieties in their own fields to assess them. This suggests genotype x environment (G x E) interactions in cassava cultivar performance in the project area. As a consequence a high degree of decentralization of variety testing is required which is only feasible if farmers bear the lion's share of responsibility.

To develop a participatory variety selection (PVS) scheme fitting our purposes, we need to answer a series of questions which will affect the shape of the scheme:

- How big is the farmers' interest for new cassava varieties?
- What is the magnitude of cassava G x E interaction in the project area?

- What is the actual cultivar portfolio of the area, how do farmers deal with new cassava varieties, and are there potential channels for further dissemination?
- What are the farmers' own experimentation practices?
- Can farmers differentiate between new cassava varieties?

History and importance of cassava in the NWP

Cassava reached today's North-West Province (NWP) of Cameroon from the coastal areas only between 1918 and 1920, as a consequence of the influenza pandemic, which had caused labour shortage and had hampered the timely planting and harvesting of traditional crops like yams (Ohadike 1981; Warnier 1984). Mainly produced for home consumption in the beginning, cassava became one of the most important staple food crops of the area around the mid-20th century. Today, cassava is also a cash crop. Its processed products, in particular gari¹ and waterfufu², are very popular with the urban population, because they are easier to prepare and can be kept longer than other staple crops of the area. In the NWP, as everywhere in Cameroon, cassava is produced by small scale farmers (Simeu Kamdem 1996). The trend to produce more cassava is furthermore promoted by the fact that this crop can be grown under a wide range of biophysical conditions and on soils which are too depleted for the successful production of other staple crops (Prudencio and Al Hassan 1994; Bakia et al. 1999). In the NWP, as everywhere in Cameroon, cassava is produced by small scale farmers (Simeu Kamdem 1996). Our preliminary studies have shown that it is rather labour than land availability which limits cassava farming, since cassava can be grown on marginal soils. How much area can be grown to cassava, when the planting can be done, how much care (weeding) can be given to the crop, and which quantity can be processed into gari largely depends on labour availability, i.e., on the family situation, on the health state of the farmer, and the possibility to hire labour. In the humid savannas of Cameroon (to which the NWP belongs), 80 % of the farmers who are growing cassava also plant it as a sole crop (for commercial purposes). Only 20 % grow it as an intercrop (for home consumption), exclusively. Neither manure nor fertilizer nor direct plant protection measures are applied. The planting density of 20800 plants per hectare is twice as high as recommended (Okeleye et al. 2001). Harvesting is done continuously, and in small quantities. Farmers only harvest what they can process within a few days. Large quantities are only harvested when big sums of money are needed.

¹ Processed (grated, fermented and roasted in palm oil) cassava tubers. The dry yellowish granules are ready for consumption after mixing with water.

² Processed (fermented, pounded and sieved) cassava tubers. The white paste can be kept up to four weeks. It is eaten with leafy vegetables.

Processing is done at home or in community infrastructures. Gari is a predominant source of income, but plays an important role in home consumption, too. Bags of gari are sent to the children staying in the boarding schools during the term, since food is not provided by the school.

Demand for new cassava varieties

Considering the growing demand for cassava products, especially gari, in the NWP, high yielding varieties with high dry matter content are required. Basically, this would comprise either a few varieties with a stable performance across farmers' highly variable agro-ecological conditions or a broad cultivar portfolio consisting of varieties specifically adapted to small pockets under the same agro-ecological conditions (Prain et al. 1991; Witcombe et al. 1996; Ceccarelli et al. 2000). The pest and disease situation in the NWP requires cultivars that are resistant or tolerant to the African Cassava Mosaic Virus (ACMV) and the Cassava Green Mite (CGM). The difficult long-term establishment of the predatory mite *Typhlodromalus aripo* deLeon, 1967 (Acari: Phytoseiidae) to control CGM could be facilitated by a significant proportion of cassava plants with hairy and year-round turgid apices (Zundel et al., manuscript in preparation). In the NWP, presently, only about 3 % of the cassava plants in farmers' fields have hairy apices.

G x E interaction

Cassava breeding largely relies on selection of F1 clones over several clonal generations. Material performing well in advanced multi-location yield trials of the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria, is then passed to cassava programs in other countries and to other IITA research sites. In this context, about 200 new cassava clones were introduced for evaluation in the year 2000 into the humid forest station of IITA in Nkolbisson, 700 m asl (meters above sea level), near the Cameroonian capital Yaoundé. Introduced cassava clones used in the trials reported here or obtained for further work at the Rural Training Centre Fonta (RTC Fonta) had been developed by IITA in Ibadan.

RTC Fonta which is located about 20 kilometers east of the provincial capital Bamenda has been involved in cassava improvement since 1994 (Bakia et al. 1999). Since then it has been receiving new cultivars through the Ecologically Sustainable Cassava Plant Protection (ESCaPP) Project. At the beginning a series of several hundred local cultivars collected in Cameroon (hereafter referred to as ESCaPP varieties) were obtained. A second batch of 10 new clones from IITA – hand-picked on the basis of their performance in Nigeria

and their resistance to ACMV – was obtained in 1999 and widely used in the context of the present study. Since then RTC has obtained over 100 additional clones after evaluation at IITA-Nkolbisson. All IITA material was introduced into Cameroon through the IITA-Nkolbisson station to comply with phytosanitary regulations. And all the material provided so far had been bred and selected in altitudes below 1000 m asl. It has been demonstrated many times (Iglesias et al. 1994; Tan and Mak 1995; Dixon and Nukenine 1997; Dixon and Nukenine 2000), that G x E interactions are important in cassava farming. Owing to the fact that large parts of the cassava growing area of the NWP are located above 1000 m asl, and that all previous breeding and selection stages have been done in low-altitude areas the need for a further selection and dissemination step in the NWP is obvious.

Farmers' experimentation

The main differences between farmers' experimentation and formal research often reported are (Potts et al. 1992; Millar 1993; Sperling et al. 1993; Bentley 1994; Ashby et al. 1995; Stolzenbach 1997):

- Farmers have a goal to make their practices more successful. Formal researchers have a hypothesis which they want to confirm or reject.
- Thus, farmers' treatments are dynamic which means that they are continuously adapted in the course of an experiment in order to achieve the goal, whereas formal research makes a point of implementing the treatments as planned beforehand, to be able to confirm or reject the hypothesis.
- In farmers' experimentation, the various steps of an experiment are done in parallel, i.e., analysis is done as observation goes on and the conclusions from it are immediately applied – probably even in the on-going experiment – and eventually copied by neighbouring farmers and relatives. In contrast, formal research is done in a serial way – one step beginning only after the previous step has been concluded.
- Farmers select marginal and heterogeneous sites for their experiments to avoid the risk of planting a cultivar which is not adapted to their harsh environments. Formal research does experiments on fertile soil to avoid problems with poorly performing crops and plot heterogeneity.
- Farmers have the control treatment in their minds. Formal research has it on a plot next to the new treatments.

- Farmers use intra-plot variation to explain interacting effects. Formal research uses multifactorial treatments.
- Farmers' replicates are in time and sometimes in neighbours' fields. Formal research has simultaneously running treatment replicates, usually on the same experimental field.

In the present study we intended to examine to what extent these experiences hold true for the project area. This helps to integrate farmers' experimentation optimally in the cassava variety development scheme.

Farmers' skills to differentiate between cassava varieties

Mkumbira et al. (2003) found that Malawian farmers have excellent skills to tell apart cassava cultivars: Whereas farmers clearly distinguished between 10 cultivars (which proved to have distinct genotypes in molecular analyses), the botanical key for morphological cassava variety classification (Nweke et al. 1994) which had been adapted by the authors and then used, was only able to single out one cultivar. This study was conducted in an area where cassava has been present for 100 to 200 years, and on cultivars which have been grown by the farming community for more than 50 years. We were interested in finding out whether the farmers of the NWP, who have been growing cassava for a few decades only, have similar skills to distinguish between varieties.

In this work – in order to put in place a participatory selection scheme for cassava varieties in the agro-ecologically diverse environment of the RTC Fonta client farmers – we wanted to (a) assess G x E interaction in cassava varieties occurring in the area; (b) study farmers' cassava cultivar portfolio and how they deal with new varieties in order to identify potentials for further dissemination of varieties; (c) study farmers' own way of experimenting with new varieties; and (d) assess the ability of farmers to distinguish between new cassava varieties.

MATERIAL AND METHODS

Farmers involved in the study

The farmers involved in the work presented here were smallholders of the ethnic group of the Bafut in the Mezam Division, North-West Province of Cameroon. The farmers selected for this study grow cassava as a cash crop for the rural and urban market and have several years of experience with the crop. Twenty-nine out of the 32 farmers were women.

Farmers' evaluation of an on-station variety trial

On the station of RTC Fonta, a variety trial with 10 varieties (Table 1) was planted in June 2002. The basic purpose of the trial was to assess yield performance and parameters relevant to biocontrol in a mid-altitude environment. Each variety was replicated four times and each replicate consisted of 12 x 12 plants which were planted on ridges. Distance between the ridges and distance between the plants was one meter. The trial plot (100 x 70 meters) was bordered by two ridges planted with a cultivar labelled ESCaPP 23 (the number is an internal label given by RTC Fonta), which is known to be very susceptible to ACMV and which was considered as a good source of inoculation. Before cassava planting, the plot had been used as pasture land for three decades. After the first tillage, a green manure mixture was grown for 12 months. The green manure biomass was incorporated in the ridges before planting. No fertilizer was applied, no crop protection measures were taken, and weeding was done according to farmers' practise, i.e., three to four times per year.

Farmers were invited on two occasions to evaluate the varieties: when the crop was 12 months old (above-ground evaluation) and a second time 24 months after planting, i.e., at the time of harvest (above- and below-ground evaluation). For the first evaluation, farmers were invited in small groups of two to four persons. In total, 12 farmers participated in the evaluation on five consecutive days. All farmers and their cassava fields had been visited by the project team at least once before the evaluation. After an introduction to explain the purpose and the history of the trial, the farmers were given some time to stroll through the field. The subsequent semi-structured discussions covered the following topics: observations concerning the above-ground appearance of the different varieties and respective implications for field management and yield expectations; preferences for specific varieties at the present growth stage; and a ranking of the importance of the preference criteria. The varieties appearing in the top-three ranks of at least one farmer were selected for the on-farm variety trial (see below). In the second evaluation at the time of harvest, a similar procedure was applied but with the addition that four plants per variety were harvested and five tubers per variety were boiled and served to the participating farmers in a tasting session. At the end of the day, farmers could select planting material to take home and grow on their own fields (see below).

Table 1. List of varieties included in the on-station variety trial at RTC Fonta.

Variety	Origin	Name given by farmers	Yield (Mg ha ⁻¹) Means \pm se)	Cooking/processing quality (assessed by farmers)	Appearance (assessed by farmers)	ACMV resistance	CGM resistance	No. of farmers selecting the variety for their own trial*
ESCaPP 30	Cameroonian cultivar	Bitter purple	17.4 \pm 0.29	Very bitter; very white; for gari	Tall; attractive leaf colour	Slightly susceptible	Moderate	12
TMS 92/0057	Improved	Small long leaves	16.8 \pm 0.18	Nice taste; cooks well	Tal	Resistant	Susceptible	14
ESCaPP 32	Cameroonian cultivar	Agric pawpaw leaf	13.9 \pm 0.11	Slightly bitter; for gari or waterfufu	Tall	Susceptible	Resistant	15
TMS 92/0427	Improved	Short short stem	13.5 \pm 0.49	Nice taste; cooks well	Short	Resistant	Moderate	5
ESCaPP 23 (as borders)	Cameroonian cultivar	Shake and pull	(High)	?	Tall	Very susceptible	?	Not available
Fonta cassava	Local	Fonta cassava	9.8 \pm 0.06	Doesn't cook; for gari or waterfufu	Tall	Susceptible	Susceptible	2
TMS 92/0236	Improved	Njamahnjamah leaf	9.3 \pm 0.03	Nice taste; cooks well	Short, branching	Slightly susceptible	Susceptible	0
TME1	Nigerian cultivar	Plum leaf	8.7 \pm 0.25	Nice taste; cooks well	Tall	Slightly susceptible	Tolerant	13
TMS 94/0239	Improved	Small no be sick	8.0 \pm 0.14	Nice taste; cooks well	Short	Resistant	Resistant	4
TMS 92/0235	Improved	Trouble maker	7.8 \pm 0.09	Nice taste; fibrous; for gari or waterfufu	Cross-branching	Resistant	Tolerant	0
TMS 30572	Improved	Folded leaves	6.6 \pm 0.16	Poor taste; for gari	Short	Resistant	Moderate	0

ESCaPP = Ecologically Sustainable Cassava Plant Protection Project; Mg = megagrams; ha = hectares; se = standard error; ACMV = African Cassava Mosaic Virus; CGM = Cassava Green Mite; * maximum of 18 farmers.

On-farm variety trial

In order to get an idea of the dimensions of the genotype x environment interaction, we planted an on-farm variety trial covering five villages within a circumference of 10 kilometers, with a total of 11 fields which were considered as replicates. At each site, we planted the same five varieties, which had been selected by farmers at the occasion of an on-station variety evaluation in Fonta (see above). These were: TMS 92/0057, TMS 92/0427, TME 1, and two farmers' cultivars from Cameroon labelled as ESCaPP 30 and ESCaPP 32. The farmers were asked to add one of their local cultivars as a local check. The trials were planted in August 2003 on ridges across the slopes in the same manner as noted above, with each variety stretching vertically (i.e., across the ridges). Each trial field was bordered by at least four border plants of a local cultivar. The fields were visited together with the farmers in three-month intervals. Semi-structured interviews on the farmers' observations concerning crop development, yield expectations and perspectives regarding an eventual integration of the new varieties into their portfolio were conducted. The fields were harvested in April 2005, i.e., 20 months after planting. It is well known that favourable environments are relatively homogeneous while marginal environments can be marginal in many different ways and are therefore more heterogeneous. Thus, in addition to the analysis including all fields, we stratified the fields using the mean yield (8.6 Mg ha^{-1}) for separation into six high-potential and five low-potential fields. This was done to test the hypothesis that variety effects are displayed more clearly on high-potential than on low-potential fields. The "farmers' variety" was excluded from the analysis since this "variety" was different on each field. Data on yield (Mg ha^{-1}) and on the proportion of plants still standing at harvest were analyzed with a mixed model (NCSS 2000), with variety as a fixed factor and field as a random factor. Differences between factor levels were tested with a post-hoc test (Bonferroni).

In another approach to assess G x E interaction, we looked at the distribution of the five most common local cassava cultivars in six villages of the NWP (Bambui, Fonta, Akossia, Asanje, Nibe and Mfoya) which are situated within a circumference of 10 kilometers. Since there is a lively interaction between these villages through family relations, farming groups, processing mills, market days, church activities, etc., we can assume that the existence of any specific cultivar is known in all the villages and that the present cultivar distribution pattern is a response to specific adaptation. We applied Fisher's exact test to see if these cultivars are randomly distributed, or if there is a relationship between cultivar and village.

Farmer-designed variety trials on-farm

The aim of this work is to design a variety selection methodology that builds on farmers' own ways of variety testing in order to involve them more in the selection process which in turn should become more efficient, i.e., generating "lower costs per unit of additional income due to the new varieties adopted by farmers". The objective of this specific study was to find out how farmers test new varieties if they are not instructed by researchers.

For this purpose, the 18 farmers participating in the second variety evaluation on-station were invited to choose their preferred cassava cultivars among the 11 ones presented. They were free to select whatever material they wanted. But they were allowed to take only as many stems as they could carry on their own (no transportation vehicles allowed) which typically resulted in 15 to 20 stems of ca. one meter length and provided around 60 cuttings in total. The farmers' choice is shown in Table 1.

The farmers were told that they could plant the varieties in any way they wanted to in order to find out as much as possible about the varieties in a short time. Thirteen of these 18 farmers were followed up in two visits over one year. At the same time, the farmer-designed variety trials served as an entry point to discuss farmers' management of old and new cassava varieties in general. A semi-structured interview was conducted with open questions and routes for probing, field observations and visualization exercises. By asking about the flow of planting material, we aimed at getting ideas on how best to address the question of dissemination, building as much as possible on farmers' own practices and strategies.

On-station variety recognition test

In any variety development scheme, the skills of farmers to differentiate between different cultivars, to recognize them and to relate the appearance in the field to qualities visible only after harvest (yield, tuber appearance, cooking and processing quality) are crucial. Earlier experiences have found that African farmers have excellent observation skills (Stolzenbach 1997) and can identify a specific cultivar at any stage between crop planting and consumption of its products. This holds especially true when the crop in question is an important staple food crop like cassava. As farmers in the NWP plant cassava sometimes in cultivar mixtures, we assessed these skills by asking them to identify the different varieties in mixtures planted on RTC station. We invited farmers who participated in the studies described above, as well as farmers without previous exposure to new varieties, to assess their differentiation skills. As a control group, we invited technical staff from non-governmental organizations (NGOs) who work in the field with cassava (self-declaration). In a second test, we assessed farmers' ability

to memorize and recognize new cassava varieties in the short term. These two exercises were carried out to determine what variety differentiation skills and variety recognition capabilities farmers have to build a participatory variety selection scheme upon.

To test the ability of farmers to differentiate between varieties, we planted four different mixtures of 40 plants (four rows x 10 plants; one meter spacing) each. On plot (1), we planted a main variety (Fonta cassava; 22 plants) and three new varieties with typical leaf colour and branching habit (ESCaPP 32, TMS 92/0324 and TMS 92/0326; six plants each) in a randomly mixed pattern. On plot (2), we randomly mixed a main variety (Fonta cassava; 28 plants) and two new varieties of similar height and leaf colour (TMS 92/0057 and TME1; six plants each). Plot (3) consisted of a main variety (Fonta cassava; 28 plants) and two new varieties with distinct height, branching habit and leaf colour (ESCaPP 30 and ESCaPP 32; six plants each). On plot (4), the main variety (a local, very common cultivar called Pawpaw Leaf; 32 plants) was intercropped with another local and common variety (Fonta Cassava; six plants), both of similar height, branching habit and leaf colour. At the time of the differentiation test, the plants were about 10 months old. The 12 farmers, whom we had been working with in the frame of other activities as described above, the eight farmers without previous exposure to new cassava varieties and the six technical staff from NGOs were introduced to the test and its purpose and asked to work in groups of two. The groups rotated between the mixture plots in a 15-minute interval. The participant groups visited three to four of the four plots. In total, we had 46 observations of all participant groups on all the plots. In order to acquaint the participants with the various plots, we first asked them how many varieties they saw in the respective plots. We also asked them to point out one plant of the main variety in each of the plots. After that they were given ribbons of five different colours and they were asked to mark the odd plants of a plot in a way that the plants of the same variety would carry the same ribbon colour. The main variety was not supposed to get any ribbon. After the test ribbon distribution was noted down and the plants with correct differentiation were counted for each group of two on each plot.

In order to establish that the participants are able to differentiate between varieties, we compared their number of correct identifications with the number of correct identifications of computer-aided random ribbon allocation. This simulation was generated with the statistical software R (R Development Core Team 2005) as follows: In a first step, we randomly assigned to each plant on a plot, with equal probability, if it belonged to the main variety or to the group of odd varieties. In a second step, the plants which were determined to belong to the group of odd varieties were given, again randomly and with equal probability, one of five

ribbon colours. This random simulation was repeated as many times as participant groups had visited the respective plot (total of all plots: 46 times). Correct identifications were counted for each simulation. The number of correct identifications of the random simulations was compared with the number of correct identifications of the participants with a t-test with Welch correction for unequal variances. Within each group, the number of correct identifications was normally distributed, as assessed graphically.

To check whether the participants' background of experience had an effect on the number of correct identifications and whether there were interactions between background of experience and plots, we performed a mixed model ANOVA with number of correct identifications as dependent and background of experience and plot as fixed independent variables and participant groups as random independent variable. We tested the interaction between background of experience and plot by comparing the models with and without interaction terms with a Likelihood Ratio test. We started with the full model containing the interaction term and did a backward selection as long as the Likelihood Ratio test between the actual model and the model reduced by one term was not significant (as suggested by Crawley 2005). To verify if the assumptions of the model were met, we plotted the fitted values against the residuals and checked with a Q-Q-Plot whether the random effects were normally distributed. The confidence intervals for the means were obtained by bootstrapping and by taking the 0.025 and 0.975 percentiles as limits of the 95 % confidence interval.

To test the ability of the farmers to memorize the phenological appearance of a variety within a short time, we established a variety mixture plot with 20 cassava plants (four rows x five plants; one meter spacing) consisting of eight randomly selected varieties with an unbalanced number of plants of each variety. About 20 meters away, hidden behind another cassava field, we planted 12 varieties, including the eight varieties planted in the test plot, in pure stands and labelled them with their folk names and an associated pictogram. The test participants, again in groups of two, had 10 minutes time to stroll through the labelled "cassava garden" and to memorize the 12 varieties. They were then given small labels in excessive numbers carrying each the folk name and the associated pictogram of a variety. Participants were asked to identify the plants in the mixture plot by assigning the correct labels. Five groups of experienced farmers, three groups of non-experienced farmers and two groups of technical staff participated in this memory test. The number of plants that were correctly identified was counted and the means for each experience group were compared. We applied an ANOVA with proportion of correct identifications as dependent and background of

experience as independent variable. The residuals were normally distributed, as assessed in a graph.

RESULTS

Genotype x environment interaction

The on-farm variety trial in three villages on 11 fields, with five new varieties plus one cultivar added by the farmers showed no significant variety effect on yield (Table 2; Figure 1). When grouped into high-potential fields (mean over all varieties $> 8.6 \text{ Mg ha}^{-1}$; $n = 6$) and low-potential fields (mean over all varieties $< 8.6 \text{ Mg ha}^{-1}$; $n = 5$), we found a variety effect in the high-potential fields but the difference could not be attributed to a specific variety with the post-hoc test. No significant variety effect was found on the low-potential fields. Percentage of plants still standing at harvest over all fields depended on the variety (ESCaPP 30, ESCaPP 32 and TMS 92/0427 having a higher plant survival rate than TME1). While this effect was not evident on the high-potential fields, it was clearly displayed on the low-potential fields (ESCaPP 30 having a higher plant survival rate than TME1). In both the low-potential and the high-potential sites, we found the field effect on yield to be highly significant, but the field effect on plant survival was not significant.

Another study to quantify G x E interactions was based on the geographical pattern of local cultivar use. Table 3 presents the distribution of the five most common cultivars over six villages. Only one cultivar (Local Pawpaw Leaf) was grown in all six villages. One variety (Fonta Cassava) was grown in five villages, one (Nkong) in four villages, one (Mambo) in three villages, and one (Nsongwa) in two villages. Fishers' exact test ($p < 0.001$) showed that there is an association between villages and cultivars.

Table 2. Yield and plant survival of six cassava varieties in high and low potential fields (means and probability levels of variety effects and field effects).

Field stratum	Parameter	Mean	Probability levels	
			Variety effects	Field effects
All fields	Yield (Mg ha ⁻¹)	8.9	0.1588	< 0.0001
	Proportion surviving plants	0.86	0.0004	0.3686
Fields with yields > 8.6 Mg ha ⁻¹	Yield (Mg ha ⁻¹)	12.3	0.0473	0.0008
	Proportion surviving plants	0.87	0.0634	0.4261
Fields with yields < 8.6 Mg ha ⁻¹	Yield (Mg ha ⁻¹)	4.9	0.2559	0.0018
	Proportion surviving plants	0.84	0.0250	0.3404

Mg = megagrams; ha = hectares.

Existing cultivar portfolio, farmers' way to deal with new varieties, and potential dissemination channels

Preference criteria. Interviews, a variety evaluation on-station and the farmer-designed variety trials confirmed that the most important criterion for cassava preference was yield. According to farmers planting sole cassava, this crop is grown and appreciated for its high yield. Other positive (but optional) traits were whether the cultivar could be consumed as boiled cassava (only needs a short time to get prepared, nice taste, not bitter), whether it was early maturing, and whether it allowed continuous harvesting over a long period. We found that mediocre yield is a killer criterion for the selection of a cultivar, no matter how preferable the other characteristics are (see examples of TMS 92/0326 and TMS 92/0239 in Table 1). Bitterness was always referred to in a negative way, but still, it was accepted if the cultivar was a high yielder (e.g. ESCaPP 30). Generally, “curled leaves” (ACMV) were not liked by farmers. Here again farmers would still accept “curled leaves”, if other features (e.g. stem diameter) pointed to a high yield (ESCaPP 23).

When evaluating plants of new varieties before harvesting, the more experienced cassava farmers tended to prefer varieties which resembled the ones they grew themselves, whereas the less experienced cassava farmers were keen on trying something which looked

completely new. For example, they preferred the short varieties over the tall ones, whereas the experienced farmers favoured the tall varieties.

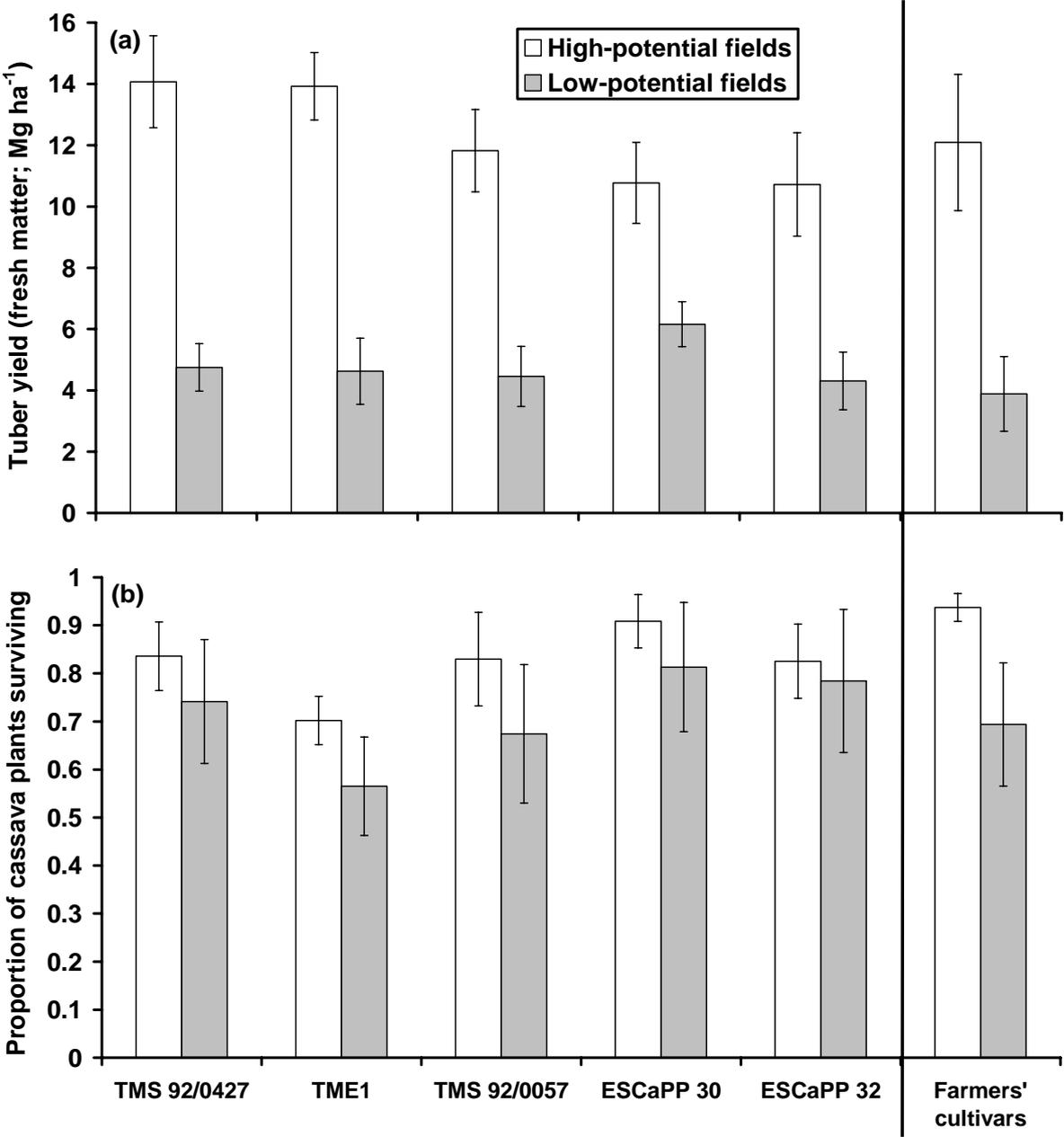


Figure 1. Yield (a) and proportions of surviving plants (b) of five different varieties and the farmers' own cultivars on high-potential fields (n = 6) and on low-potential fields (n = 5). Data points are means. Vertical bars are standard errors of the means.

Portfolio management. In the six villages of our study, we identified about 16 different cassava cultivars, five of them are grown on a larger scale. We heard of at least four more cultivars which farmers once tried to grow, but then abandoned because of one reason or another. Eleven of the 16 cultivars were “sweet” and could be consumed as boiled cassava. The remaining five cultivars were either “bitter” (which correlates with a high cyanogenic potential), or did not get soft when boiled, and had to be processed into gari or waterfufu. Farmers typically grew three different cultivars, ranging from farmers who had only one, to farmers who had six cultivars. One quarter of the interviewed farmers grew one or two more cultivars on a very small scale (a few plants only). This was the case with cultivars which were not very much preferred but where the farmers had decided to keep them in stock. And it was the case with new cultivars where the farmer had only a few cuttings to plant.

All farmers said that they would always want to have a cultivar which can easily be boiled and eaten. Farmers with four and five cultivars would replace a low yielder with a new one, if the new one was really good. Farmers with only two cultivars wanted to add one or two good ones of the new varieties to the portfolio. Based on these observations, we conclude that four to five cassava cultivars are the optimum size of a cultivar portfolio of a farmer growing sole cassava. This is in accordance with an experienced farmer who said that three or four cultivars were enough, if they yielded well. However, many others said that having many cultivars was good in order to be prepared for risks. They found seven to 20 cultivars to be ideal. Another aspect of cultivar portfolio management is the maintenance of rare genetic material. For instance, one very old cultivar which was nice to eat and which had a flexible harvesting period was planted on a small scale by two farmers just for the purpose of maintaining the material. Sharing planting material with other farmers was another strategy to maintain cultivars.

Table 3. Number of visited farmers per village and number of farmers who grow a specific cultivar.

Village	Mfoya	Nibe	Asanje	Akossia	Bambui	Ndoka
Visited farmers	11	2	2	3	3	7
Fonta Cassava	10	2	2	0	1	1
Local Pawpaw Leaf	10	2	2	3	2	3
Nkong	10	2	2	3	0	0
Nsongwa	0	0	0	0	3	7
Mambo	0	0	2	0	1	6

Pure stands versus cultivar mixtures. In our survey, we found that cassava cultivars were sometimes planted in pure stands and sometimes in mixtures. We wanted to know whether it was a deliberate act of farmers to plant in mixtures, and if yes, which intentions were behind it. We found that cassava farmers with large areas usually planted in pure stands. If cassava cultivars were deliberately planted in mixtures, it was either done to avoid the risk of a complete crop failure – to have a crop which was more stable, especially for plantations on marginal soils or sites with unknown characteristics – or to achieve a specific blend of tubers for gari production. Unintended mixtures occurred, if farmers did not have enough planting material of one cultivar, or if the planting material had been harvested a long time ago and the cultivar could not be identified anymore. Good management (i.e., harvesting at the right time) of fields with unintended mixtures was said to be very difficult. To find the right cultivars in mixtures to avoid competition was also mentioned as a challenge.

Management of planting material. The scarcity of planting material at the time of planting is a major bottleneck in cassava farming. Planting material is available in large quantities at the time of harvest. But this is not always the right time when farmers want to plant a new cassava field. We found the following constraints for planting: no land available, peak of labour in other crops, health or other problems rendering the farmer unavailable for planting or the beginning of the dry season. Farmers collected stems as planting material from the harvested field and kept it in a shady and cool place or they left the stems in the field and eventually went back to select planting material when they needed it. Once the tubers were harvested, the stems were gradually losing their vigour as planting material. It is not advisable to keep planting material for longer than one to two months. Farmers were very

much aware of that and attempt to plant the material as freshly as possible. Consequently, if a farmer wanted to plant a new cassava field but did not have enough planting material, she asked neighbours, relatives or farming group members if they could provide planting material, in particular, if the mature plants of the other person's field looked vigorous. Large distances between fields were another reason why planting material changed hands easily. If a farmer had harvested her mature field on one hilltop and had land available for a new cassava field on another hilltop, she asked the neighbours of her new field if they could provide cuttings rather than carried her own stems from one hill to the next. In return, she was ready to give away her own planting material to other farmers. Smaller quantities of planting material were extracted before harvest by cutting single stems from plants having several stems. This method has the advantage that the stems are usually fresh and farmers could actually do a selection for ACMV-free plants. If planting material was selected when mature cassava was harvested, the leaves were too senescent to detect and identify ACMV symptoms reliably. However, when selecting planting material, farmers gave more attention to strong and vigorous stems from plants with high yield than to healthy leaves.

How farmers deal with new varieties. The triggers to try other cultivars were either the lack of planting material, which forced the farmers into something new, or the high yield reputation of a cultivar. The planting material of the new cultivars usually came from friends from nearby villages, relatives and contractors with whom the farmers worked. The farmers did not have much information about a cultivar when they decided to try it: Most often the reputation of a cultivar to yield well was sufficient to go for it. Some farmers considered the agro-ecological conditions of the origin of the new cultivar and compared it to their own environment before they took the decision to try. Farmers grew as much of the new cultivar as they could get planting material for. In some cases this was a few cuttings and sometimes they planted a whole field.

Potential dissemination channels for new varieties. If possible, the stems were collected at the time of tuber harvest and were immediately re-planted. If this was not feasible, which was very often the case, farmers either kept their own planting material for a few weeks or they relied on planting material from other people. Exchanging cuttings as gifts or requesting cuttings from somebody who had nice cassava was very common. This free exchange of planting material between farmers could be an important basis for a low-cost and efficient dissemination of new varieties, at least within a specific interest group.

Farmers' own experimentation with new cassava varieties

The variety trials which were designed by the farmers themselves were visited one year after the farmers had selected the planting material from the RTC station. These field visits and interviews revealed the following:

Representativeness of test location. Most of the farmers (11 out of 13) planted their test plot close to their compound (not more than five minutes of walk), in mixed cropping areas. Only two farmers had planted further away from the house on typical cassava hills. Farmers explained that they had more control over the crop if they planted close to the house. Mixed cropping made them to go regularly to the test field, e.g. for weeding or harvesting of the other crops. This would give them the opportunity to also look after the cassava and to observe it well. Other reasons given for the particular plot choice were: The trial plot should be located on their own land (and not on rented land) which secures cropping on a longterm; the trial plot should have good soil fertility; or the plot chosen was the only plot available at the time of planting. We concluded that the test sites and plots were chosen deliberately although not representatively (see below). All farmers had planted other crops in-between the cassava cuttings, as they usually do in their production fields. After harvesting of these other crops, about half of the farmers planted a second batch of crops. These farmers had planted cassava in one row per ridge. The farmers who left cassava as a sole crop after the harvest of the first associated crop of maize and beans had planted cassava in two rows per ridge.

Additionally to the test plot, farmers had between two and five more cassava fields. The size of the field containing the test plot ranged from 6 to 28 % (average: 12.4 %) of the total farm area under cassava cultivation. As a tendency, these plots were smaller than the average cassava field.

Uniformity of the plot. Except for one field, all test fields were of a reasonable to good uniformity.

Replications. None of the farmers split her planting material and planted it in replications. Two farmers had in principle planted the new varieties ridge by ridge, but had mixed in varieties from other ridges, though not in a systematic way. Farmers explained that they wanted to test the varieties on different parts of the field. We assume that they felt the need for some kind of replications but did not implement them in a systematic way.

Spatial arrangement of varieties. The majority of the farmers planted the new varieties in a ridge-by-ridge arrangement. If the planting material of a ridge was not enough to fill the ridge, another variety was used to fill it. Two farmers planted the varieties patch-wise across ridges in an unsystematic pattern.

Local cultivar as a control. Four out of the 13 participating farmers had their own cultivar planted at the same time adjacent to the new varieties. However, only one farmer did it deliberately in order to compare the new varieties to her own. The other three farmers had their own cultivars nearby because the new varieties occupied only a small portion of the land which they had reserved for their cassava planting. They filled it up with their own cultivar. When asked how they were able to tell if the new varieties performed better or worse than their own local cultivar, they replied that they could estimate how much their own cultivar would yield on the test plot soil. In the first instance, it was not important for the farmers to compare their own cultivars with the new varieties. They rather wanted to find out which varieties among the new ones would do well. Very often, farmers mentioned their intention to test the best new varieties against their own only in a second or third cropping cycle though it is unclear, in what way and how many “best new varieties” will be selected.

Cultivar testing and adoption as a long-term process. Three farmers explained how they will proceed with the new varieties they got from RTC Fonta. In the first cropping cycle, the only purpose is to get to know the varieties and to multiply the planting material. No selection will be done at that time. In the second cycle, the new varieties will either be planted in mixtures, or they will be planted alongside with the local cultivars. Some selection may be done after the second harvest. Discussions about earlier experiences with new varieties showed that a new cultivar was often tested on different soils for up to three cropping cycles before it was perhaps abandoned. The transition from test phase to adoption seems to be gradual. The cultural habit of the region is not to discard cultivars, unless their yields are poor throughout the area. Instead, farmers try to find a niche for a cultivar where it does well. Farmers’ reports on their earlier experiences with new cassava cultivars show that out of 15 new cultivars, seven can now be considered as adopted, four as abandoned, two as lost by accident (stolen) and two are still in the test phase.

Quantitative capacity for tests. When invited to the RTC station to evaluate 10 new varieties, farmers wanted to test all the varieties on their own, not just those ranking best. They still insisted in trying all varieties even though the total number of cuttings which they could take home was limited. They said that they need to grow all varieties on their own soils before they could assess which of them was doing well. When we let them select a maximum of 60 cuttings per person one year later, the same farmers chose between two and five varieties of the 10 available, resulting in 12 to 30 cuttings per variety (Table 4). This is in accordance with the 10 to 30 plants which farmers say to be ideal in order to evaluate a cultivar.

Table 4. Number of farmers (out of 11) who picked a specific number of varieties (10 varieties were on offer) for their own home-testing. Picking more varieties meant picking less planting material per variety, since total cuttings per farmer were restricted to 60.

Number of varieties picked	0	1	2	3	4	5	6-10
Number of farmers	0	0	1	3	7	5	0

Farmers' observations. At the occasion of the field visits, we asked the farmers what they could tell us about the present appearance of the plants of the different varieties, or what they had observed at an earlier stage. The first observation was usually associated with the state of the planting material (“cuttings were weak”, “cuttings were tiny”), and with the emergence of the young plants (“some died”, “grew fast in the beginning”). The young stage did not trigger many comments, except if a variety was still suffering from the poor planting material or if it was susceptible to ACMV (“curled leaves”). The first weeks after the end of the dry season when plants were ca. 12 months old were of more interest to the farmers. Varieties with dried leaves and die-back of branches were compared to varieties which looked fresh. Few farmers commented on the plant architecture, i.e., on the branching habit. Somebody said that late side shoots were useless and that she usually removes them. At the occasion of the first weeding in the new rainy season, most farmers removed the top soil from a few tubers to estimate their size and shape and to do a first approximation of the yield to be expected. At this stage, stem diameter was also mentioned to be a good indicator for yield. In general, farmers felt attracted to plants with a healthy and fresh looking canopy. However, most of the farmers could not explain why. One farmer said, that she concludes from above ground performance to yield, because she thinks that the leaves were “the kitchen of the plant”. Maturity was determined by

test harvesting of a few plants after 18 months. Stem appearance (colour, woodiness) was also used as an indicator for maturity.

Farmers' skills to differentiate between cassava varieties

In order to establish that farmers (and technical staff of NGOs) are able to differentiate between varieties, we compared the number of correct identifications of farmers and technical staff with the number of correct identifications of randomly distributed differently coloured ribbons. Based on the performed t-test ($df = 72$; $p < 0.001$), we conclude that the participants recognized phenological differences between cassava plants and grouped them along variety traits.

In a preliminary analysis of the data with the Linear Mixed Model, we identified an outlier in the participants groups, which was thereafter omitted from the model. We found a significant interaction between plot and background of experience in their effects on the number of correct identifications (Linear Mixed Model; $df = 6$, Likelihood Ratio = 25.17; $p < 0.001$) (Figure 2).

Over all the plots, the group of the experienced farmers had 33 ± 1.8 (mean \pm standard error) correct identifications out of 40 possible. The group of non-experienced farmers had 33 ± 1.9 scores, the group of non-experienced farmers had 33 ± 1.9 scores and the NGO staff had 31 ± 2.7 scores. On plot (1) (30 ± 2.4 scores) and (2) (30 ± 2.1 scores) participants scored low when compared to plot (3) (35 ± 1.8 scores) and (4) (35 ± 1.4 scores) where higher scores were achieved. On plot (1), the experienced farmers scored higher than the other two groups. On plot (2), the non-experienced farmers excelled the other two groups. On plot (3), the three groups were close together, with the non-experienced farmers scoring higher than the experienced farmers (who had a high variance). On plot (4), no difference between the groups can be made out because of the high variance of the non-experienced farmers. The experienced farmers had similar scores on the plots (1), (3) and (4), but they scored less on plot (3). The non-experienced farmers scored with a large variance on plot (1) and (4), and they achieved their highest scores on plot (2) and (3). The technical staff did better on the plots (3) and (4) than on the plots (1) and (2).

The test on the ability of participants to memorize phenological appearance of cassava varieties on a short term depending on their background of experience resulted in a means of 49 % correctly labelled plants for all participant groups. Background of experience had no effect on the number of correct identifications ($df = 2$; $F = 0.436$; $p = 0.663$).

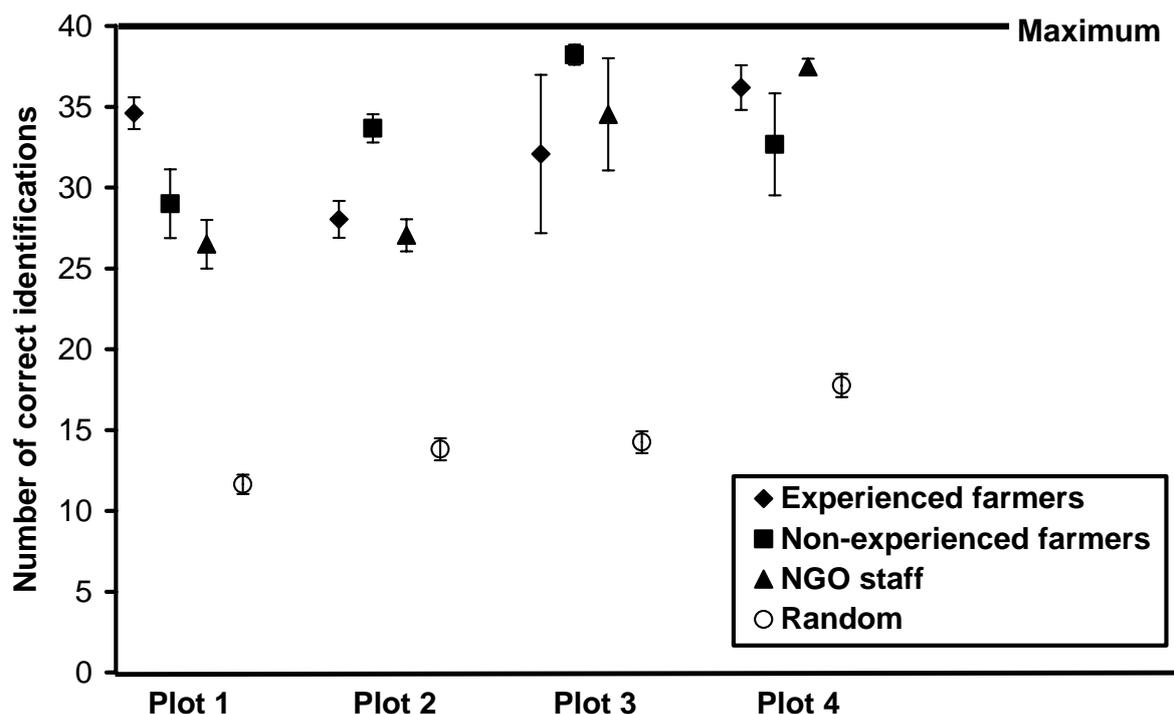


Figure 2. Number of correct identifications (out of 40 possible) in a cassava variety differentiation test with experienced farmers, non-experienced farmers and technical staff from NGOs on four plots with different cassava variety mixtures. In addition, the number of correct identifications generated by random simulation is shown. Data points are mean number of correct identifications. Vertical bars are standard errors of the means.

Farmers' suggestions for a cassava variety selection scheme at RTC Fonta

The great part of the interviewed farmers explicitly expected RTC Fonta to provide new varieties at frequent and regular intervals, rather than to multiply existing genetic material, despite frequent shortages in planting material and subsequent requests for mass supply of cuttings. Farmers estimate their own testing capacity to be around three to five cultivars per year. This is in accordance with the fact that farmers, at the occasion of the RTC on-station variety evaluation, selected between two and five varieties out of a possible 11 to take home and test. Farmers were of the opinion that RTC should grow the varieties first before distributing them to farmers. Farmers found it necessary that they come and select the varieties themselves. Ideally, they would want to come three to four times during the cropping cycle: three months after planting (to see those varieties with weak youth development); 12 months after planting (after the first dry season; fully developed canopy; possible diseases well expressed); 18 months after planting (for a first yield and harvesting time estimation by

digging some tubers); and at harvest. The identification of these crucial phases is supported by what the farmers usually observe in their own fields (see above). For the dissemination of the preferred varieties, 50 cuttings per variety and farmer are considered ideal.

DISCUSSION

Genotype x environment interaction

In the on-farm trials with five new varieties at 11 sites, we found that variety effects on yield are more visible on high-yielding fields than on low-yielding fields. Ranking of varieties regarding yield in low-potential fields was different from ranking in high-potential fields, pointing to a G x E interaction. This is confirmed by the present distribution of local cultivars in the area: The planting of many of the local cultivars was restricted to a few villages, although exchange of planting material was common, also across villages. The interviews showed that farmers had a clear idea of G x E interaction. Farmers were able to tell on which soil and in which village a specific local cultivar performs well and where it does not. If farmers considered trying a new cultivar, they took into account the environment where the respective cultivar is presently grown and compared it to their own environmental conditions.

The lower the yield potential of a site, the more difficult it is to propose the “right” cultivar and the more important a broad range of choice becomes. It is also evident that each village, if not each farmer, must have the possibility to test the new genetic material and to draw the conclusions just for the small pocket of land which really matters for their farming success.

Because of the evident variety effect on plant survival, emphasis should be given to developing varieties with hardy planting material and with a fast and strong youth development, both under dry and wet conditions. In a recent trial on viability of planting material in Fonta, it was found that some varieties tolerated prolonged storage of planting material better than others (Scheidegger et al., unpublished data).

Need for new varieties

The study shows that farmers know their own cultivars and their possible uses very well, and that they manage their cultivars (i.e., scale of planting, allocation to suitable sites) in a conscious way. If cultivars were grown in mixtures because of too little planting material of one cultivar, the farmers recognised the different cultivars in their fields, and may have harvested them plant-wise, depending on the intended use. It appears that farmers did not

strive for a wonder cassava, but instead try to put to use as many cultivars as possible, and seek the best growing conditions for each. This attitude facilitates cultivar development and helps to maintain high genetic diversity in cassava farming, even if improved varieties are used.

Considering the diverse agro-ecosystem, not only in the NWP or within a specific village, but also among the fields of a single farmer, the number of cultivars presently grown is small. Indeed, many farmers wished to have more cultivars. In terms of processing capacities, although gari demand is increasing and more and more farmers go into this business, farmers also desire to have cultivars that can be boiled and eaten without any further processing. This is to satisfy their household need for fresh cassava. Another reason may be that labour availability within the family is sometimes scarce or difficult to plan. Yet gari production is labour intensive. Growing cassava also apt for fresh consumption gives them more flexibility in organizing their manpower. Finally, cultivars with a flexible harvesting time and cultivars which produce sufficient and good quality planting material are also important to allow a smooth management of the cassava crop.

Farmers' own experiments

Independently from RTC's activities farmers had always been looking for the possibility to try out new cultivars. Most often, they had gotten them through relatives, neighbours or members of the same farming group, church or saving group. How much area was given to the new variety depended on its performance. High yielding cultivars were scaled up and medium yielding cultivars were kept at an intermediate level. Even low yielding cultivars were kept over several cropping cycles and tested under different conditions, although on a smaller scale, to find the niche where they did well and hopefully even better than others.

In their own experiments with varieties picked at RTC Fonta, farmers did not try to make a generally valid statement on the performance of a specific variety. In the first cropping cycle, their intent was to get to know the varieties and to multiply the planting material. In contrast to Sthapit et al. (1996), where farmers tested new rice varieties first on their worst land and subjected them to the severest abiotic stresses to avoid the risk of a failure on good land, the NWP cassava farmers planted their experiments not on the poorest of their soils, but on a site which they could easily observe and where they could be sure not to lose the crop. The experimental fields were reasonably uniform. As reported by many others (Sperling et al. 1993; Ashby et al. 1995; Stolzenbach 1997), only few farmers established a control plot with their own cassava cultivar. Farmers argued that they know the

performance of their own cultivars on the given plot, and that they therefore do not need a control – in particular not at this stage, because selection would be done in a later cropping cycle.

None of the farmers planted the material in systematic replicates, although at least two felt the need for it and mixed the varieties on one ridge. Farmers see cassava cultivar testing as a long-term process that goes over several cropping cycles, to test the new varieties on different soils and in different cultivar mixtures. In a way, they apply replicates in time. We found that farmers are excellent observers who focus their observations on stages and aspects (plant establishment, dry season survival, maturing) which are of relevance to cropping success.

Farmers' skills to differentiate between cassava varieties

A comparison with a random differentiation has shown that farmers, experienced and non-experienced, are able to differentiate between cassava varieties which were introduced to the area only recently. The ranking from “easy” plots to “difficult” plots corresponded largely with what we had expected. Plot (3) with two odd varieties with distinct characteristics was an easy task for all groups, no matter of their background of experience. Also plot (4) with one local and well known cultivar mixed into the stand of another (similar looking) local and well known cultivar was well mastered by most of the groups. Plot (2) was difficult to read, as expected, because participants were not familiar with the odd varieties which, to make the task more difficult, were of similar appearance. Our expectation that scoring on plot (1) would achieve a better result than on plot (2) was not confirmed even though the three odd varieties had distinct features. The varieties on plot (1) were considerably more difficult to identify than the ones on plot (3) where two odd varieties with distinct features were grown. It seems that the more varieties there are in a variety mixture the more challenging it becomes to distinguish between the different varieties – even if they have characteristic phenotypes. Farmers classified the plants on the mixture plots as well as the technical staff from NGOs did. Why the non-experienced farmers performed better on plot (2) than the experienced farmers is difficult to explain.

In the memory test, we found that farmers (and technical staff) who had never been exposed to the new varieties were able to memorize the morphological appearance of a cassava variety in a short time and to achieve similar results as farmers which had planted some of these varieties before. This shows that farmers are able to identify a new variety after a very short time of exposure.

Conclusions for an effective and efficient cassava variety selection and dissemination scheme

The need for a decentralized selection scheme emerges from the G x E interactions in cassava cultivars, even on a small spatial scale. Kornegay et al. (1996) found that in Colombian bean growing differences between farmers' fields are as big as differences between researchers' and farmers' fields. It is therefore not sufficient to have a few on-farm trial sites. Many on-farm trial sites are needed. Decentralized selection is also advocated by Sperling et al. (1993) for bean selection in Rwanda, by Joshi and Witcombe (1996) and Sthapit et al. (1996) in rice breeding in Nepal and by Ceccarelli et al. (2000) for barley selection in Syria. Useful decentralized selection in the case of cassava in the NWP of Cameroon would ideally mean three or more trial sites per village.

Prain et al. (1993) and Ceccarelli et al. (2000) see two ways to cope with G x E interaction. One option would be to find a few stable varieties that suit everywhere. The other option would be to find different varieties (many in total) which are each specifically adapted to a particular environment. Our approach would allow us to do both: We may find a few cultivars that perform well in many villages. Since these cultivars seem to be stable over a wide range of conditions, we may decide to directly promote them also in new areas. But beyond this, no extrapolation is needed. We rather opt for simple testing in each village. It is not necessary that farmers take quantitative yield data. A ranking of the varieties' performance and its feedback to the breeders serves the purpose completely. It is no disadvantage, if we find in each village another set of best varieties since there is no need or pressure to narrow promotion to a few of the tested varieties. (The only pressure would be existing seed laws which make the release of many varieties expensive.) Each village and each farmer has the possibility to grow the varieties best liked. It is of minor importance if they happen to be the same as in other villages or with other farmers.

Decentralized selection does not automatically mean participatory selection since they are independent processes. In practice, however, farmers' participation is indeed needed to make a decentralized selection affordable (Ceccarelli et al. 2000). It has to be kept in mind that the handing over of selection from an institution to farmers does not mean an elimination of costs but a different distribution of costs (Morris and Bellon 2004).

Based on our study, we advocate shifting a large part of the responsibility for cassava variety selection from the institutions to farmers. A large part of the farmers' own experiments deal with new varieties (Bentley 1994; Ashby et al. 1995; Defoer et al. 2000). To test new cassava varieties on their own is therefore in line with farmers' research and can

build on their experience of how varieties can be tested (and at the same time be integrated in the production process) most efficiently. Farmers are not only capable of differentiating between varieties (Mkumbira et al. 2003; this paper) they are also very efficient in selecting varieties which yield highly in their own farms (Sperling et al. 1993; Kornegay et al. 1996; Ceccarelli et al. 2000). In addition, farmers may interpret and extrapolate the results from a peer more readily than those from a formal trial. One of the reasons may be that a formal experiment reduces complexity to a level that is confusing to the farmer.

The issue of the local check is controversial. On the one hand, it is doubtful whether farmers can really, based on earlier performance of their cultivar, reliably predict the yield of their local cultivar under the circumstances in which the new varieties are grown. One reason is that farmers generally (as anyone else) tend to remember the past better than it actually was, as a study of Defoer et al. (2000) on yield perception showed. On the other hand, insisting on a control treatment may be counter-productive, as it might make farmers loose ownership of and thus interest in the trial.

Organisation and backstopping of a decentralized, participatory selection scheme need to rely on institutions (NGOs) operating at the local level and playing the role of an effective interface between breeders and farmers. The responsibilities of such variety hubs in Cameroon are outlined in the following.

As a basis for farmers to select the varieties they want to test in their village, the varieties should be grown by the variety hub on suitable land (“station”). If done in a replicated trial, multiplication of planting material and feedback to the breeders on performance of these varieties can go hand in hand. Planting material of new varieties should be provided to interested village groups continuously over a certain time period.

How many cultivars can farmers handle? In the literature (Sperling et al. 1993; Bänziger and Cooper 2001; Gridley et al. 2002; Witcombe et al. 2002, in: Witcombe et al. 2005), we find that mother trials host 60 to 80 cultivars, while baby trials managed by farmers may have one to 10 cultivars. According to our interviews, farmers want to test about three to five new varieties in a year. If farmers keep the varieties for testing during two cropping cycles of two years each, and will get five new varieties each year, they will simultaneously manage 20 new varieties.

The schedule for farmers’ cassava evaluation on the station can be derived from the periods when farmers usually observe their cassava crop very closely, i.e., three months after planting (emergence and youth development); twelve months after planting (after the dry season; canopy fully developed; eventual diseases clearly expressed); eighteen months after

planting (ex-ante yield assessment and estimation of harvesting time); and at harvest. To keep the system running smoothly, the variety hub needs to allocate resources that are able to provide about 50 cuttings per variety and per experimental site.

The breeder and the variety hubs need to collaborate in a way which allows getting many new cassava varieties to the target area. That means, as soon as cassava clones pass the advanced yield trials and are introduced to Cameroon they should also be shipped to the variety hubs in the mid-altitudes. Since selection is done in the low-altitudes, many cultivars which could have been highly performing in the mid-altitudes might otherwise be dropped. Sperling et al. (1993) emphasize an early involvement of farmers to prevent loss of genetic material which could potentially be of interest to the end user areas. This is for an area where the breeding station is located within the target farmers' area. Indeed, many more varieties got adopted there because farmers were involved earlier in the selection process. A pre-requisite for the functioning of the proposed scheme is the regular arrival of new genetic material. Good contacts and smooth collaboration between the breeder and the variety hubs is therefore the backbone of the whole program. More important than a high number of new varieties is the regular provision of about the same number of new varieties to the hubs to allow for constant use of the capacities built up.

This implies a more systematic way to work with farmers. A two-stage approach for variety exposure to farmers (similar to Sperling et al. 1993) could help: One or two lead farmers per village or farming group are invited to evaluate the material on the land of the variety hub (e.g. RTC) and take interesting material home for testing. This allows a hub to cover a wide area with planting material. Moreover, the village test fields are closer to the farmers, both in terms of agro-ecological conditions and in terms of distance. Farmers then select varieties from the test fields in their own village and try them on their own land. In the case of RTC, trainees with some experience in cassava farming are ideal to bring home varieties from "their hub" at the end of their course, and to establish a test field in their village.

Based on the results of our field visits and interviews, the hubs should not be concerned about multiplication and dissemination of the new varieties to all farmers. It should rather concentrate on providing nuclei of material to many villages. Once these nuclei are established in the villages, the new varieties will naturally be tested and disseminated through neighbourhoods, farmers' groups and relatives.

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SEVEN

General discussion and conclusions

The exploration of the agro-ecological requirements of *T. aripo* showed that this predatory mite, which successfully controls the pest mite *M. tanajoa* in the low altitudes of sub-Saharan Africa, has difficulties to establish in altitudes above 1100 meters above sea level (m asl) in northwest Cameroon: *T. aripo* did not spread to neighbouring fields above 1100 m asl after one cropping cycle. As a consequence, the predators disappeared from the area, once the last release field was harvested. The fact that predator and pest mite have asynchronous population cycles is not encouraging either. Although this asynchrony does not seem to affect predator survival, probably because of abundant alternative food such as pollen and fungi, it does question the potential control effect of the predators on the pest mite. The introduction of a new *T. aripo* strain (*Bam*) which was supposed to be better adapted to the mid-altitude temperatures, could not make a difference in long-term establishment of the predator. The only factor we found to have a significant effect on *T. aripo* long-term establishment was altitude: In areas below 800 m asl, the predators did spread to neighbouring fields within a few months time. However, asynchrony of the cycles of predator and prey remained the same. Unexpectedly, though, the *Pir* strain had an advantage over the *Bam* strain in the first three months after release, which coincided with the dry season. This result was consistent with the result of the greenhouse experiment. A possible reason may be that the *Pir* strain which originates from a dry area in Brazil was better adapted to the dry season months than the *Bam* strain. Based on these experiences, it is recommended that in a next expedition to the origins of *T. aripo* to collect more strains for release in Africa, drought resistance is added to the priority selection criteria.

Multiple cropping areas on fertile and humid soil are suitable as reservoirs for *T. aripo* in the dry season, in particular, if they are planted with a cassava variety with hairy apices. Basically, it might be possible that farmers cultivate their *T. aripo* reservoir in favourable places on varieties preferred by predators and distribute apices infested with *T. aripo* to other areas for faster recolonization after the dry season. However, since *T. aripo* needs some time to restore high population levels after their population breakdown in the dry season, it is doubtful if apex transfer can achieve a control effect on the pest population (which is naturally collapsing at this time of the year) in the same season. There is a possibility, though, that the predators recolonise the pest prone hill sides before the next *M. tanajoa* peak one year later.

The enclosure experiment elicited the essential role of the apices in *T. aripo* dry season survival. Apex hairiness, high apex turgidity and large apex diameter are traits which can increase the rate of *T. aripo* surviving the dry season. An improved availability of cultivars combining these traits with high agronomic performance could make a difference to predator persistence in areas where *T. aripo* dry season survival is at stake.

Because of the results discussed above, we did not find it useful to go into developing options together with farmers to settle *T. aripo* – with the exception of developing a variety selection and dissemination scheme together with farmers and RTC Fonta: Our previous work with *T. aripo* made obvious that cassava varieties will play an important role in the control of *M. tanajoa*. Either cassava cultivars with hairy apices are needed to foster the establishment of *T. aripo* or, if *T. aripo* fails to establish, resistant or tolerant cassava cultivars have to be developed as an alternative option to reduce *M. tanajoa* damage. Addressing the *M. tanajoa* problem through resistant or tolerant cultivars is promising, because (a) resistant and valuable cultivars are available (i.e., ESCaPP 30, ESCaPP 32 and TMS 92/0427), (b) other problems in cassava cropping (e.g., low yields, susceptibility to the African Cassava Mosaic Virus) can be addressed at the same time, and (c) farmers are very interested in testing new varieties. Because of the high heterogeneity of sites and soils in the project area, a variety selection and dissemination scheme must be organised in a decentralized and participatory way. Our experiences with farmers designing their own cassava variety trials have shown that farmers set up their own experiments in a purposeful way which allows them to make comparisons between the new varieties, and to assign each new variety to a specific agro-ecological niche. Therefore, we propose a cassava variety selection scheme that builds on a decentralised variety hub and on farmers' own experience in cassava variety testing. Once new cultivars have reached the farmers, planting material will be disseminated through neighbourhood and family networks.

SUMMARY

Cassava (*Manihot esculenta* Crantz) is a main staple in many parts of Africa. In the processed form of gari¹, it constitutes an essential income source for the rural women in certain areas. This holds certainly true for the target area of this project, the North-West Province (NWP) of Cameroon. There, one of the most important biotic constraints to cassava cropping is the cassava green mite *Mononychellus tanajoa* (Bondar, 1938) (Acari: Tetranychidae). To reduce cassava yield losses caused by *M. tanajoa*, the neotropical predatory mite *Typhlodromalus aripo* DeLeon, 1967 (Acari: Phytoseiidae) was first introduced into Africa in 1993. At present, *T. aripo* is established in 20 countries of sub-Saharan Africa. But the predator has been slow in colonizing and establishing in mid-altitude regions. This is particularly the case in latitudes above 4° North and South where temperatures are cooler and relative humidity in the dry season is lower than in the low altitudes and in areas closer to the equator. The objective of this thesis was to develop biocontrol strategies against *M. tanajoa* in the mid-altitudes of the NWP of Cameroon by enhancing the establishment of *T. aripo*.

In a field release study in the years 2002 to 2004, the population dynamics and establishment of a strain of *T. aripo* from the mid-altitudes (*Bam* strain from Minas Gerais, Brazil) was examined and compared to a lowland strain (*Pir* strain from Bahia, Brazil) used earlier. Both strains were released in cassava fields in the lower (600 to 850 meters above sea level) and the higher (1100 to 1300 meters above sea level) range of our mid-altitude study area in northwest Cameroon. Additionally, we conducted a greenhouse population-level experiment with the objective to determine the short-term dynamics of the *Bam* and the *Pir* strains of *T. aripo* and their effects on *M. tanajoa* populations.

In view of establishing dry season predator reservoirs, the population dynamics of predator and pest were studied in three habitat types: (a) on dry grassland hill sites with low soil fertility where cassava predominates; (b) on multiple cropping sites, which are more humid and more fertile and have a highly diverse cropping system; and (c) on riparian forest sites, which are humid and shady. Earlier studies had shown that *T. aripo* abundance is generally higher on cassava cultivars with pubescent apices, where *T. aripo* seeks refuge during the day. We introduced two cassava cultivars, one with hairy apices and one with

¹ Processed (grated, fermented and roasted in palm oil) cassava tubers. The dry yellowish granules are ready for consumption after mixing with water.

semi-hairy apices, and compared them in all three habitat types with a glabrous local cultivar in terms of their suitability to the predators.

In the above-mentioned studies we saw that *T. aripo* disappeared from the cassava apex – where it usually stays – during the dry seasons and reappears after the onset of the rains. We conducted a field enclosure experiment of cassava plants with the objectives to determine if (i) *T. aripo* recolonizes the cassava plant from the surrounding vegetation, if (ii) it survives in the soil or leaf litter below the cassava plant, and if (iii) *T. aripo* survives at very low densities in the apex.

The studies outlined before had shown that *T. aripo* may not be an efficient option to control *M. tanajoa*. To make *M. tanajoa* resistant or tolerant cassava cultivars available to farmers seemed to be a promising alternative approach. By means of a formal on-farm variety trial, of farmer-designed variety trials, and an assessment of farmers' ability to differentiate between new varieties, we explored to which extent decentralized and participatory cassava variety selection are useful, and how much we can build on farmers' own experimentation.

We found that, unlike in other regions of sub-Saharan Africa, *M. tanajoa* populations peaked at the end of the dry season (or shortly after the beginning of the rainy season) and not shortly after the onset of the dry season. Concurrently predator abundance dropped to very low levels in the dry season and recovered only four to eight weeks after the beginning of the rainy season. Despite the asynchrony with its prey, *T. aripo* was able to persist in both lower and higher altitudes for more than one year. However, in contrast to the lower altitude range, the predators were not able to persist beyond one cropping cycle in the higher altitudes, because they did not spread to neighbouring fields. The introduction of a new *T. aripo* strain (*Bam*) – which was supposed to be better adapted to the mid-altitude temperatures than the strain used earlier (*Pir*) – had no effect on the long-term establishment of the predators. Unexpectedly, though, the *Pir* strain had an advantage over the *Bam* strain in the first three months after release, which coincided with the dry season. This result was consistent with the result of the strain evaluation in the screenhouse. Possibly, the *Pir* strain, which originates from a dry area in Brazil, was better adapted to the dry season months than the *Bam* strain.

Typhlodromalus aripo disappeared earlier and came back later in grassland hill and riparian forest sites, as compared to the multiple cropping sites. The predator's disappearance in the dry season was related to low ambient relative humidity in the habitat, and to plant parameters indicating low plant vigour, low apex retention, small apex diameter and poor

apex hairiness. For the predators' return in the rainy season, plant parameters indicating strong host-plant vigour and large apex diameter were the most important factors. In the multiple cropping habitat type, the hairy cultivar was able to host the predators longer and on a higher population level than the semi-hairy and the glabrous cultivar. *T. aripo* dynamics in the riparian forest sites was particular, and we suspect an interaction with local phytoseiids in this habitat type.

The timing of the predator's reappearance in the cassava apex of the different treatments of the field enclosure experiment suggests that *T. aripo* survives the dry season in very low densities in the cassava apex. This result is supported by additional studies: (a) In the course of a vegetation survey, *T. aripo* was not found on any other plant species than cassava. Instead, two new indigenous phytoseiids were discovered. (b) An assessment of the efficiency of non-destructive visual in-field apex inspections proved that about 10 % of the cassava apices that had *T. aripo* were not recognised as such. (c) A plant material transfer trial showed that predator-free plants could neither be infested with stems of previously infested plants, nor with leaf litter or top soil collected from the surroundings of the previously infested plants. However, there are also two studies that point to a possible role of the ground in *T. aripo* dry season survival: (d) A screenhouse experiment on vertical migration revealed that *T. aripo* sometimes does leave the cassava plant and walk over bare ground. (e) Micro-climate measurements in various cassava plant parts proved that the cassava apex and the cassava stem base are the locations with the highest relative humidity during the dry season – which makes the stem base a potentially interesting refuge.

The formal on-farm variety trial showed no differences between varieties despite the use of 11 replications. This let us suspect strong interactions between varieties and fields. Due to the high heterogeneity between farmers' fields, decentralized selection is a prerequisite to give farmers access to the information they need to take decisions concerning new varieties. The trial also showed that heterogeneity in terms of cassava variety performance was more pronounced between fields with low mean yields ($< 8.6 \text{ Mg ha}^{-1}$), as compared to fields with high mean yields ($> 8.6 \text{ Mg ha}^{-1}$). Farmers set up their own experiments in a systematic way that allowed comparisons between the new varieties. To farmers, cassava variety testing is a long-term process. In each cropping cycle, emphasis is given to specific objectives. Selection starts earliest in the second cropping cycle. We propose a cassava variety selection scheme that largely builds on farmers' own experience in cassava variety testing, and on their proven ability to distinguish between varieties that are new to them. The cultural habit to exchange

planting material freely with neighbours and relatives grants a fast and effective (though not systematic) dissemination of new genetic material.

In summary, this thesis shows that the potential of *T. aripo* in suppressing *M. tanajoa* populations in the mid-altitudes of northwest Cameroon is limited because of the asynchronous population cycle of predator and prey and because of the slow dispersal of the predatory mite. Cassava cultivars resistant to *M. tanajoa* may represent a better option to reduce pest mite damage. To introduce new cultivars to the area, a cassava variety selection and dissemination scheme is proposed that builds on farmers' own experimentation and expertise.

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APPENDIX

Zannou I D, Zundel C, Hanna R, de Moraes G J (2005)

**Two new species of phytoseiid mites (Acari: Phytoseiidae) from Cameroon, Central
Africa**

Zootaxa 1093:55-59