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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. In some mid-altitude areas and drier lowland savannahs of sub-Saharan Africa, which are characterized by cool or hot long (≥5 months) dry seasons, the predator disappears from its habitat in the cassava apex during the dry season and reappears after the onset of rains. It is not known, however, where the predator remains during this time period. In this study, we conducted a field enclosure experiment of cassava plants with the objectives to determine if (a) *T. aripo* survives at very low densities in the apex, if (b) it survives in the soil or leaf litter below the cassava plant, and if (c) it recolonizes the cassava plant from the surrounding vegetation. Towards the end of the dry season, when the predators had disappeared from all cassava plants included in the experiment, five treatments were applied: (1) plants without enclosure; (2) plants with enclosure; (3) plants with enclosure, apices removed; (4) plants with enclosure, glue barrier around stem; and (5) plants kept free of *T. aripo*, without enclosure. Predator (re)appearance on cassava apices was monitored non-destructively at weekly intervals and 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

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reappeared first on the plants of the treatments (1), (2), and (4). With a time lag of 7–8 weeks, the predators appeared also on the plants of the treatments (3) and (5). The time pattern of the predator's (re)appearance in the cassava apex of the different treatments suggests that (a) *T. aripo* survives the dry season in very low densities in the cassava apex; this result is supported by an assessment of the efficiency of non-destructive visual in-field apex inspections which proved that about 10% of the cassava apices that had *T. aripo* were not recognized as such; (b) *T. aripo* does not survive in the soil or leaf litter, but we did document cases in a screenhouse experiment, where few individuals migrated down to the ground and walked over exposed soil until they reached the apex bouquet traps; additionally, microclimate measurements in various cassava plant strata 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; (c) *T. aripo* does not survive in the surrounding vegetation, which is supported by a vegetation survey, where *T. aripo* was not found on any other plant species than cassava.

Keywords Refuge · Predatory mites · *Manihot esculenta* · Migration · Biocontrol · Colonization · Canopy microclimate profile

Introduction

Arthropods respond to seasonally unfavourable environmental conditions, mainly heat, cold, or drought, in various ways (Tauber et al. 1986): Migration to an overseasoning habitat, dormancy ranging from quiescence to diapause, and acquired hardiness are three common adaptations that arthropods have developed to cope with temporarily 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. Phytoseiid mites cope with dry conditions in several ways. A common strategy is 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). Seasonal migration to specific structures on the host plant (Nyrop et al. 1994; Gurr 1997; Davies 2001) or to crop-surrounding wild vegetation (Tuovinen and Rokx 1991; Stanyard et al. 1997; Tixier et al. 1998, 2000; Kabicek 2003) is common with phytoseiid mites, whereby aerial and ambulatory dispersal occur (Sabelis and Dicke 1985; Croft and Jung 2001).

The neotropical phytoseiid mite *Typhlodromalus aripo* DeLeon (Acari: Phytoseiidae) was introduced into Africa in 1993 for the control of the neotropical phytophagous cassava green mite *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae) (Yaninek and Hanna 2003; Hanna et al. 2005). Today, *T. aripo* is established in 20 countries of sub-Saharan Africa (Hanna and Toko 2003). Whereas *T. aripo* persists throughout the year in the humid forest and the forest/savannah mosaic areas (Hanna et al. 2005; Onzo et al. 2005), it temporarily disappears from cassava fields in seasonally dry areas such as the savannahs of West Africa and the drier and colder mid-altitudes of southern Africa (Mebelo et al. 2003; Onzo et al. 2003; Hanna et al. 2005; Zundel et al., manuscript in preparation). In these areas, in the height of the dry season, the predators cannot be found in their daytime refuge—the cassava apices—by non-destructive in-field inspection. They reappear in the

apex only several weeks after the onset of the first rains of the subsequent rainy season. It is not known, where *T. aripo* survives the dry season: if 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, or if it migrates to the surrounding vegetation. 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. (Fabaceae), and from flowers of *Tridax procumbens* Linné (Asteraceae) in the beginning of the dry season (Zannou et al. 2005a).

The present study is one of a series designed to describe the establishment, persistence, and impact of *T. aripo* in the mid-altitudes of northwestern Cameroon. One particularity of the area is that the population cycles of the predator and its prey are asynchronous: Predator populations increase in the beginning of the rainy season, when prey populations decrease, and predator populations decrease in the height of the dry season, when prey populations increase (Zundel et al., manuscript in preparation). Despite this fact, the predators were able to persist for one cassava cropping cycle or longer, most probably because of their ability to survive and develop on alternative food, such as cassava extrafloral exudates, and maize pollen (Yaninek and Hanna 2003; Gnanvossou et al. 2005). These asynchronous population cycles are contradictory to the more typical dynamics of this acarine system, characterized by the predator densities following the prey densities with a time lag, as reported for Brazil by Magalhães et al. (2003) and for Benin by Hanna et al. (2005).

The objective of this study is to determine where *T. aripo* survives during the dry season. We had three hypotheses concerning the location of the dry season refuge of the predators. These were: (a) *T. aripo* survives at very low densities in the apex; (b) *T. aripo* survives in the soil or leaf litter below the cassava plant; and (c) *T. aripo* recolonizes the cassava plant from the surrounding vegetation. We conducted an enclosure experiment with treatments preventing the predators from recolonizing the cassava apices depending on the location of their dry season refuge. Four additional studies were conducted with regard to each of the hypothesized places of dry season survival: hypothesis (i): calibration of the efficiency of the visual in-field apex inspection method; hypothesis (ii): exploratory experiment on *T. aripo* cursorial movement over exposed soil; and assessment of microclimate within the cassava plant canopy; and hypothesis (iii): vegetation survey with collection of phytoseiid mites.

Materials and methods

Enclosure experiment

With the help of apex removal, glue barriers and enclosures, we wanted to determine if *T. aripo* survives at very low densities in the cassava apex or elsewhere on or nearby the cassava plant. The experiment had two phases: Phase 1 comprised release of predators and monitoring of their disappearance. Three weeks after the predators were no longer detectable by non-destructive in-field inspection, phase 2 started with imposing of treatments and monitoring of predator reappearance. The experiment was conducted near the town of Bamenda at 1,294 masl in the Northwest Province of Cameroon. It was established on-station during the rainy season (July) on a plot of 25 m × 40 m using 30 cm cuttings of the

cassava variety TMS 92/0326 which were planted in the field. 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 m within and between rows. The five treatments consisted of varying combinations of the elements: *T. aripo* addition/no addition, apex removal/no removal, glue barrier around stem/no glue barrier, enclosure/no enclosure. In the following, these elements are explained in more detail.

Typhlodromalus aripo addition

Since *T. aripo* had not (yet) established in this area, the plants on the experimental field were supplied with *T. aripo* (25 predators per plant on three successive releases at 2-week intervals between 3 and 29 October) to monitor disappearance and reappearance of the predators. *T. aripo* populations were provided by the International Institute of Tropical Agriculture (IITA), Biological Control Centre for Africa, located in Cotonou, Republic of Benin. The predators were imported from Bambuì 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 7 cm 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 20–30%. 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.

Apex removal

Apices of the cassava plants were removed to eliminate those predators from the cassava plant which remained in the apex at very low densities. Two weeks after apex removal, the apices had regrown to a size of 3.8 ± 0.2 mm (mean $\pm$ standard error) in diameter (apex size in treatments without removal at this time was 5.9 ± 0.4 mm), and were from thereon potentially suitable habitats for reappearing predators.

Glue barrier

A Tanglefoot glue barrier was applied to the base of the stem of the cassava plants to prevent those predators from recolonizing the cassva apices which had taken refuge in the soil or leaf litter.

Enclosures

Enclosures made from white polyethylene mesh (mesh size 0.2 mm; 1.5 m $\times$ 1.5 m $\times$ 1.5 m in L $\times$ W $\times$ H) with a wooden frame were placed over the experimental plants to prevent those predators from recolonizing the cassava apices

by aerial or ambulatory migration, which had taken refuge in the surrounding vegetation. Care was taken to cover the base of the enclosures with soil to prevent cursorial entry of *T. aripo* into the cages.

The following five treatments were applied: (T1) *T. aripo* was added in phase 1, but no enclosures were set in phase 2, to simulate natural conditions in an area where *T. aripo* is established. (T2) *T. aripo* was added in phase 1 and enclosures were set in phase 2, to prevent *T. aripo* from recolonizing the plants from the surrounding vegetation. (T3) *T. aripo* was added in phase 1 and enclosures were set and cassava apices were removed in phase 2. If *T. aripo* reappeared in (T1) and (T2), but not in (T3), we can conclude that it survived the dry season in low densities in the cassava apex. (T4) *T. aripo* was added in phase 1 and enclosures were set and glue barriers were applied at the base of the main stem in phase 2. If *T. aripo* reappeared in (T1) and (T2), but not in (T4), we can conclude that it survived the dry season in the soil or leaf litter around the plant. (T5) *T. aripo* was not added in phase 1 and no enclosures were set up in phase 2. If *T. aripo* reappeared in (T1) and (T2), but not in (T5), we can conclude that it survived the dry season somewhere close to the cassava plant. To avoid colonization of the plants of (T5) by *T. aripo* during phase 1, 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 m away from any cassava plants until they were transported to their respective positions in the plots. In a distance of 3 m from the experimental field, two border rows of the same cassava variety were planted at 1 m × 1 m spacing. To assure a source of predators that could colonize the sentinel plants, *T. aripo* was 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. The next cassava field was 10 m away from the experimental field.

A pre-release inspection had indicated that *T. aripo* was absent from all the experimental and border plants. Starting in phase 1, immediately after the first release of the predators, presence/absence of *T. aripo* was determined in weekly non-destructive inspections (i.e. thorough in situ visual inspection with 4× head lenses) of all plants. In phase 2, after *T. aripo* had disappeared and after the treatments were imposed, the enclosures were lifted once a week to monitor the return of *T. aripo* to the apices of the plants in the same way. The procedure lasted less than 10 min per plant. At the same time, though only in monthly intervals, *M. tanajoa* mobiles were counted on the first fully developed leaf of each experimental cassava plant. Because of the suspected relationship between *T. aripo* dynamics and relative humidity conditions, daily mean ambient relative humidity was calculated based on the measurements of a data logger (HOBO H8 Pro from Onset Computer Corporation) at 12-min intervals.

Calibration of the efficiency of the visual in-field apex inspection method

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) inspection under a dissecting microscope in the laboratory. The same apices were used to compare the two methods. After inspection in the field, they were kept in 75% alcohol until inspection under the microscope. Samples were taken on six occasions from December to February, on a total of 30 apices of the variety TMS 92/0326.

Typhlodromalus aripo migration to the ground and cursorial movement over exposed soil

To explore if it is possible that *T. aripo* migrates to the ground and walks over exposed soil in the dry season, we conducted a recapture experiment in a screenhouse at IITA in January, i.e. in the height of the dry season. Mean temperature in the screenhouse at this time was 31.6°C, and mean relative humidity was 65%. Cassava cuttings of variety TMS 92/0326 were planted in pots of 10 l volume. One week before the experiment started, the trial plants were infested with 50 females of *M. tanajoa* each. Cassava apex bouquets of the same variety were prepared by planting the apices in glass vials filled with water and sealed with parafilm around the shoots. Twenty-four hours before the beginning of the experiment, the bouquets were infested with 20 *M. tanajoa* females each. Six bouquets were vertically buried in each pot as attractant traps, with the vial rim being at ground level, at distances of 5, 15, and 25 cm from the plant stem. At trial strart, 30 *T. aripo* females were placed in each plant apex with camel-hair brushes. At this time, the plants had 15–20 leaves and were about 65 cm high, and obviously suffered from drought. During the experiment, the soil surface in the pots was kept moist with careful watering (0.25 l per pot per day) in the late morning, when the predators were not expected to migrate. Two treatments were applied: (1) Control—immediately after predator release, Tanglefoot glue was applied around the stem to prevent the predators from leaving the plant by ambulatory migration; (2) Migration—no glue application. Each treatment was replicated six times. The treatments were randomly arranged in blocks. Seventy-two hours later, phytoseiids were counted with the dissecting microscope on plant apices, leaves, and apex bouquet traps.

Microclimate in cassava plant canopy

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. The variety used is an early branching variety with low and dense canopy, uniformly green leaves, and hairy apices. Microclimate measurements were taken on 6 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 mm; length: 50 mm) 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 mm. Temperature and relative humidity measurements using both instruments were taken for the following plant strata: (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. Four

measurements were repeated with each instrument on each of the above-mentioned plant part within 1 min, 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 min.

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*. In addition to the enclosure experiment, we conducted a survey in February 2004 (towards the end of the dry season) in four villages between 800 and 1,300 masl in the Northwest Province of Cameroon. In each village, one cassava field was selected which had received *T. aripo* between 4 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 m 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). Plant samples were taken at a spacing of 1 m. Five leaves/plant parts distributed throughout the plant canopy were inspected with a 4× head lens. 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.

Data analysis

Since the dry season seemed to affect predator populations seriously, and the prey dynamics found in northwestern Cameroon were not sufficient to explain predator dynamics, we were interested to relate the pattern of *T. aripo* dynamics to changes in relative humidity. Two simple linear regressions with *T. aripo* presence (proportion of plants with predators on at least one apex; all treatments except T3 and T5 pooled) depending on ambient relative humidity (mean of daily means of a 2-week period prior to mite assessment) were calculated. In the first regression, the four dates within the period of *T. aripo* population decline were considered, i.e. beginning after the last release, on 19 November, and ending when *T. aripo* could not be detected anymore, on 18 February. The second regression covered the four dates within the period of *T. aripo* reappearance, i.e. beginning on 8 March, the last date when *T. aripo* was still absent, and ending on 8 June, when *T. aripo* had recovered 100% of the plants (Fig. 1).

For each of the three hypotheses of the enclosure experiment, we performed a generalized linear mixed model (GLMM) with a binomial error distribution and the logit-link function glmmPQL from the library MASS in R (R Development Core Team 2005) on proportion of plants with *T. aripo* (as dependent variable) in each treatment. For each of the three GLMM conducted, only those treatments were considered which were relevant to test the specific hypothesis. In each GLMM, the treatments T1 and T2 formed the group of control treatments and were compared to the group of treatments specific for each hypothesis. Treatment group and week of sampling were the two independent fixed variables and treatment was the subject variable. To find the optimal model, we did a step-wise backwards

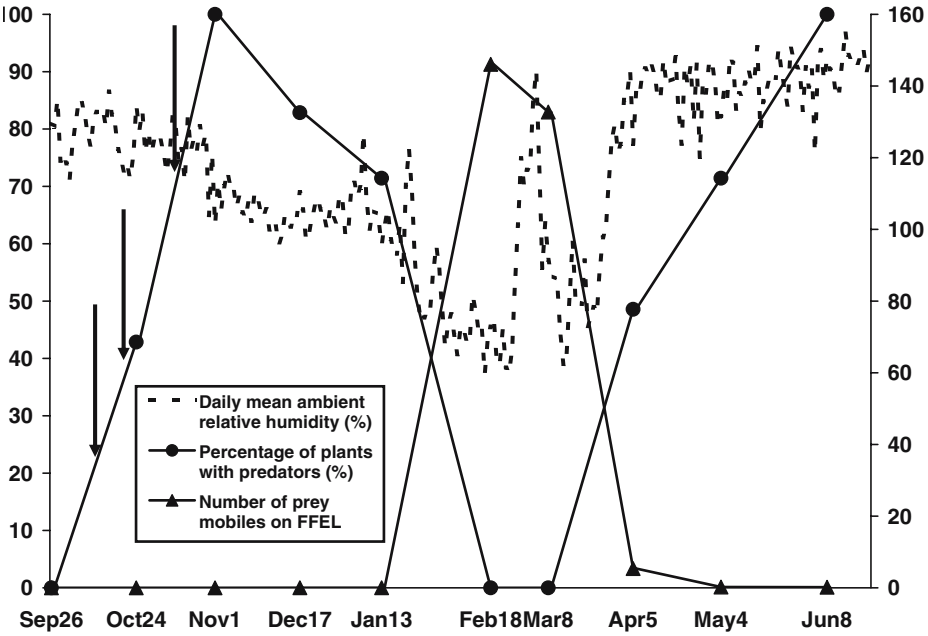

Fig. 1 Percentage of plants with *Typhlodromalus aripo* (*left y*-axis) and number of mobile *Mononychellus tanajoa* on the first fully expanded leaf (FFEL; *right y*-axis) of cassava plants in the enclosure experiment from the first release (3 October, 2003) to the end of the experiment (8 June, 2004). 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. *Dotted line* shows daily mean ambient relative humidity data (*left y*-axis). *Vertical arrows* indicate the release dates of *T. aripo*

selection by removing non-significant terms using likelihood ratio tests. Significant terms remained in the model. We started with the full model: $Y \sim$ treatment + week + week^2 + treatment*week + treatment*week^2|treatment 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 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. 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. T4). To test hypothesis (iii)—*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. T5).

Differences in microclimate between various cassava plant strata were compared with PROC GLM (*F*-test) and the Student–Newman–Keuls test (SAS 2003) 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).

Mean (arcsine transformed) recapture rates of females of the two treatments in the recapture experiment in the screenhouse were compared with a *t*-test.

Results

Enclosure experiment

The general population dynamics of predator and prey on the cassava plants of the enclosure experiment (pooled across treatments) from the first predator release until the end of the experiment (phase 1 and phase 2) are shown in Fig. 1. 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% of plants colonized on 19 November and declining thereafter to 0 by 18 February. The coefficients of the respective regression between predator population and mean ambient relative humidity showed that predator decline followed a corresponding decline in mean relative humidity ($R^2 = 0.95$; slope = 3.37; $p = 0.027$). The predators remained absent from all the plants for approximately 3 weeks, reappearing sometime between 8 March and 5 April and reaching 100% of plants colonized on 8 June. As a tendency, reappearance and increase of *T. aripo* populations were associated with a similar increase in mean relative humidity ($R^2 = 0.89$; slope = 3.44; $p = 0.057$), as the second regression coefficients showed. Prey was absent from the experimental plants until 13 January. The prey population had a sudden peak on 18 February, reaching a mean of 146 mobiles per leaf. Subsequently, the predator populations decreased and had completely disappeared on 4 May.

Figure 2 shows the time pattern of *T. aripo* reappearance on the cassava plants in phase 2 of the enclosure experiment, i.e. after the treatments were applied on 8 March until the end of the experiment on 8 June, depending on the treatments. Within 1 week of treatment application, *T. aripo* began to reappear in the apices of plants of the treatments T2 (*T. aripo* added, enclosures) and T4 (*T. aripo* added, enclosures, glue around stem base). Within 2 weeks of treatment application, the predators also reappeared in the apices of T1 (*T. aripo* added, no enclosures). Seven weeks after treatment application, *T. aripo* had colonized the apices of T5 (no *T. aripo* added, no enclosures), and 8 weeks after treatment application, they were also found in the regrown apices of T3 (*T. aripo* added, enclosures, apices removed).

Based on the fact that *T. aripo* reappeared on plants outside (T1) and inside (T2) the enclosures at about the same time, we concluded that enclosures do not affect reappearance of the predators. Thus, to test our three hypotheses, we compared the treatments T3, T4, and T5 against the group of the treatments T1 and T2.

On those plants which had received *T. aripo* and where the apices were removed (T3), the predator's pattern of reappearance was distinct from the two treatments where we had not removed the apices (T1 and T2) (GLMM; $df = 1$; $\chi^2 = 7.58$; $p = 0.006$). Data presented in Fig. 2 indicate that the predators came back much later on the plants where apices were removed which supports hypothesis (i)—that *T. aripo* survives in the apex.

Figure 2 shows that the predators appeared earlier on plants that received *T. aripo* and glue around the stem (T4) 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 T4, as the glue would have impeded *T. aripo*'s recolonization of the plant from the soil. Based on these results, we reject hypothesis (ii)—that *T. aripo* survives in the soil or in the leaf litter.

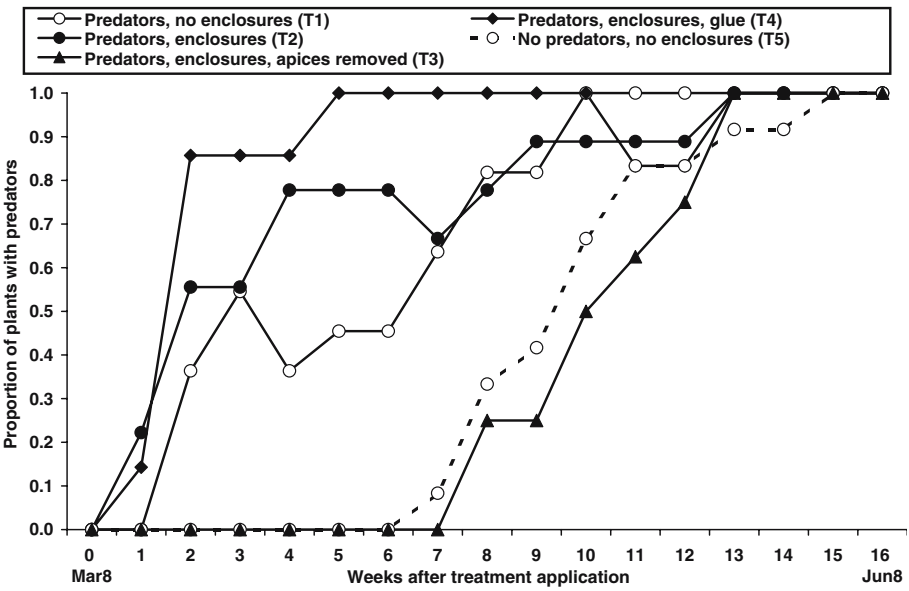

Fig. 2 Proportion of plants with *Typhlodromalus aripo* after treatment application (8 March/week 0) until the end of the experiment (8 June/week 16). Data points are proportions of plants with *T. aripo* in at least one apex

On plants of those treatments that received *T. aripo* and did not have any other predator excluding elements than enclosures (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 6 weeks of the new rains, the predators came back from near the plant. Thus, we reject hypothesis (iii)—that *T. aripo* survives in the surrounding vegetation.

Calibration of the efficiency of the visual in-field apex inspection method

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 were false negatives ($R^2 = 0.921$). These false *T. aripo* negatives contained on average 1.5 ± 0.3 (mean ± standard error) *T. aripo* individuals (females, males, and nymphs) which were not detected in the field.

Typhlodromalus aripo migration to the ground and cursorial movement over exposed soil

Mean recapture of *T. aripo* females in the apices of the test plants were not different in the two treatments ($p = 0.394$): On plants with glue barrier 20.5 ± 1.5 females were recaptured compared to 22 ± 1.0 recaptured females on plants without glue barrier. Four of the 36 apex bouquet traps in the plants without barrier were found

Table 1 Mean relative humidity, air temperature, and surface temperature and their standard errors measured in six different locations of the cassava canopy of variety TMS 92/0326 at 2 pm

	Relative humidity (%)		Air temperature (°C)		Surface temperature (°C)	
Apex	26.1 ± 3.1	ab	31.9 ± 0.5	c	24.9 ± 0.6	ab
FFEL	26.3 ± 3.4	ab	32.3 ± 0.4	bc	24.5 ± 0.7	b
Petiole base of FFEL	24.1 ± 2.9	c	32.5 ± 0.4	bc	26.5 ± 0.4	a
Petiole base of oldest leaf	23.9 ± 2.8	c	33.0 ± 0.8	ab	26.7 ± 0.5	a
Plant base	26.8 ± 3.1	a	33.5 ± 0.9	a	19.4 ± 0.7	c
Ambient	24.4 ± 2.8	bc	31.5 ± 0.7	c	–	–

Means with the same letter are not significantly different (Student–Newman–Keuls Test; $p = 0.05$)
FFEL = First fully expanded leaf

colonized by *T. aripo*, but none of the 36 sentinel apices in plants with barrier were colonized.

Microclimate in cassava plant canopy

Microclimate measurements showed differences among the various strata of the cassava canopy (Table 1). The highest relative humidity was found at the base of the 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 strata on the plant were the basal buds of the first fully developed leaf and the oldest leaf, which are similar to ambient relative humidity. Surface temperature of the plant strata 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 strata were intermediate (Table 1).

Phytoseiid mites on vegetation surrounding cassava fields

Eighty-two 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 are listed in Table 2. Eleven known phytoseiid species were found—*Euseius* sp.; *E. hutu* (Pritchard and Baker); *E. spermahyphus* (Ueckermann and Loots); *Neoseiulus* sp.; *Paraphytoseius multidentatus* Swirski and Shechter; *Phytoseius* sp.; *Phytoseius amba* Pritchard and Baker; *Phytoseius hongkongensis* Swirski and Shechter; *Typhlodromips* sp.; *Typhlodromips shi* (Pritchard and Baker); *Typhlodromus* (*Anthoseius*) *apoxys* van der Merwe. Two new species—*Neoseiulus yanineki* sp. nov., and *Typhlodromips cameroonensis* sp. nov.—were described for the first time (Zannou et al. 2005b). *T. aripo* was not found on any of the samples during the sampling period.

Discussion

Normally, predator population dynamics can largely be explained by the population dynamics of the prey. This is not the case in the acarine predator–prey system of

Table 2 Most common host-plant species of indigenous phytoseiid mites during the dry season in northwestern Cameroon

Plant species	Percentage of plant samples	Percentage of phytoseiids collected on this plant species
Chromolaena odorata (Asteraceae)	16	48
Asystasia schimperi (Acanthaceae)	1	3
Melinis minutiflora (Poacea)	3	5
Brachiaria ruziziensis (Poacea)	8	12
Erigeron floribundus (Compositae)	4	5

T. aripo and *M. tanajoa* in the mid-altitudes of northwestern Cameroon (Zundel et al., manuscript in preparation). Instead, as *T. aripo* cannot be found in their usual daytime refuge—the cassava apex—in the height of the dry season by visual in-field inspection, it seems that seasonal dynamics of *T. aripo* in this area is strongly affected by ambient relative humidity. The data presented in Fig. 1 show that the decline and resurgence in *T. aripo* populations during the dry season was 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. The question arose if *T. aripo* has a seasonal migration behaviour to a dry season refuge. Specifically, we wanted to determine if *T. aripo* remains on the cassava plant and its immediate vicinity or if it moves to the field surroundings from which it can recolonize cassava fields when conditions become favourable again.

Hypothesis (i): *T. aripo* survives in the apex

In the enclosure experiment (Fig. 2), *T. aripo* reappeared within a period of 1–2 weeks after treatment application (or 3–4 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 5–6 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. The mean error rate of 10.5% of our in-field sampling procedure at low *T. aripo* frequency indicates that undetected predators in the apices may have been the source for the recolonization of the plants where *T. aripo* had been added. If our conclusion holds true, the predators colonizing the plants of T3 7 weeks after treatment application must have come from other plants of the experimental plot, and must have entered into the enclosures. This assumption is supported by the colonization pattern of the sentinel plants of T5, which indicates that interplant movement by *T. aripo* within the experimental plot started 6 weeks after treatment application.

Hypothesis (ii): *T. aripo* survives in soil or leaf litter

In the enclosure experiment, resurgence of *T. aripo* was faster on plants with Tanglefoot glue barrier than on plants without the barrier. This means that at least part of

the predator population remained on the plant before the glue barrier was applied, most probably in the apex, as explained above. The beneficial effect of the glue barrier on *T. aripo* may indicate an interaction between the predator and the ground which was interrupted by the sticky barrier. The most likely explanation is that the predators left the plants without the barrier to some extent, probably in response to drought conditions. This migration behaviour left fewer individuals in the apices of the plants without glue than on those plants with glue. As a consequence it took longer to build up the population on the plants without glue in the new rainy season. Results of the screenhouse study indicate that, although no treatment effect could be found in the number of recaptures of the predators in the apices of the potted plants, at least a small number of a predator population did migrate to the ground and were able to walk over short distances of exposed soil. This is in line with other studies that 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). Gaede (1992) found positive hygrotactic responses of the predatory mite *Phytoseiulus persimilis* Athias-Henriot if they were suffering from a water deficit, and Perret (2003) described that the tick *Ixodes ricinus* Linné avoids dry conditions through migration behaviour. Thus, it seems possible that the high relative humidity at the stem base found in the study on microclimate within the cassava plant canopy attracted some individuals of the *T. aripo* population in the apex in both, the enclosure experiment and the screenhouse study. Another explanation for the earlier reappearance of *T. aripo* in the apices of the plants with glue barriers as compared to plants without glue barriers is that *T. aripo* on the plants without glue barriers 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.

Hypothesis (iii): *T. aripo* survives in the surrounding vegetation

In the enclosure experiment, *T. aripo* appeared earlier on enclosed plants where it was added than on plants where it was not added but was exposed to potential aerial colonization from surrounding vegetation. And, *T. aripo* was not found on any other plant than cassava in an extensive vegetation survey. Together, these results provide growing evidence that non-cassava vegetation is not a typical refuge for *T. aripo* during the dry season on the African continent. This corroborates existing knowledge about the host-plant specificity of *T. aripo* (Yaninek and Hanna 2003; Zannou et al. 2005a).

The more rapid resurgence of *T. aripo* in T2 (*T. aripo* addition plus enclosure) compared with T1 (*T. aripo* addition and no enclosure) as shown in Fig. 2 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 (T2) and outside (T1) 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.

Based on the interpretation above, we propose that *T. aripo* does not have an aerial long-distance migration behaviour to avoid dry climatic conditions, as is known of other phytoseiid mites (Sabelis and Afman 1994). This predator instead seems to stay in the apex, except for a few individuals that leave the plant by vertical migration to the ground. One option to compensate for water loss through transpiration and excretion may be to absorb water from feeding on prey and to produce water in the metabolism (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 indeed balance a large portion of water loss due to dry conditions. Second, *T. aripo* might also be capable of absorbing water from the air during the night, when ambient relative humidity is high, as has been shown for many phytoseiids (Gaede 1992; Yoder 1998). A third 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). The small refuge in the cassava apex would certainly support aggregation of the remaining *T. aripo* individuals. However, if this strategy can reduce water loss sufficiently in the few enduring predators must be questioned. Though low relative humidity has never been tested as a potential diapause-inducing cue for African phytoseiid mites (Veerman 1992; Bruce-Oliver et al. 1995), such behaviour seems unlikely in *T. aripo*, considering the fact that some individuals did migrate to the ground.

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 northwestern Cameroon with unimodal rainfall and a dry season of 4 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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