Environment and host-plant genotype effects on the seasonal dynamics of a predatory mite on cassava in sub-humid tropical Africa

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Abstract

1 In tropical dry seasons, survival of small arthropods such as predatory mites is often negatively affected by low relative humidity (RH). For species that do not diapause or migrate to refuges, the ability of the habitat to mitigate climatic conditions becomes crucial.

2 The relative effect of macro-habitat (dry grassland hill, humid multiple cropping area, humid riparian forest) and microhabitat (host-plant genotypes with hairy, semi-hairy and glabrous apices) on the seasonal dynamics of the phytoseiid mite *Typhlodromalus aripo*, a predator of *Mononychellus tanajoa* on cassava, was examined in a field experiment during a dry season. The effect of RH and plant genotype on *T. aripo* egg survival was determined in an environment control chamber.

3 Predator abundance was higher in humid multiple cropping areas and on hairy cassava compared with the other habitat types and cassava genotypes.

4 Discriminant and regression analyses showed that the predator's dry season persistence was related to high RH, high plant vigour and hairy apices, but not to prey abundance.

5 In the controlled climate experiment, the effect of host-plant morphology was evident only at the intermediate RH level of 55%. An effect of apex hairiness was not found.

6 It is concluded that the effect of genotype on *T. aripo* persistence diminishes under low RH conditions, and that supportive effects of apex hairs become effective only in the field, probably through protection from wind and/or intraguild predation. Humid multiple cropping areas planted with hairy and vigorous cassava genotypes are suitable dry season reservoirs for *T. aripo*.

Keywords Apex pubescence, classical biological control, *Manihot esculenta*, *Mononychellus tanajoa*, plant–predator interaction, relative humidity, *Typhlodromalus aripo*.

Introduction

Seasonally changing climatic conditions, mainly temperature and humidity, challenge the survival of small arthropods such as mites in all climatic zones (Leather *et al.*, 1993). In tropical climates, it is usually the dry season that jeopardizes mite survival. Because the differences in monthly mean temperature over the year are smaller than the daily amplitudes, the

tropical seasons are characterized by rainfall and humidity rather than by temperature (McGregor & Nieuwolt, 1998). Thus, low relative humidity (RH) has a greater influence on small arthropods such as mites during the dry season than high or low temperature. For species that do not diapause or migrate to refuges, the habitat and its ability to mitigate ambient climate become critical in the survival of mites. The microhabitat of plant-inhabiting mites is the leaf boundary layer; thus, plant morphology and physiology can have considerable influence on the microclimate of mite habitat

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(Willmer, 1986; Norton *et al.*, 2001). The size of the leaf boundary layer increases with the presence of obstructions such as trichomes and domatia at the plant surface because of their calmative effect on air movement (Nobel, 1974; Gaede, 1992; Norton *et al.*, 2001). Relative humidity in the leaf boundary layer is influenced by photosynthetic activity of the plant (Ferro & Southwick, 1984; Schuepp, 1993). High RH in the leaf boundary layer is especially accommodating to the more drought sensitive species and/or immature stages of mites (Bakker *et al.*, 1993; Croft *et al.*, 1993; Grostal & O'Dowd, 1994; Shipp & van Houten, 1997). There is abundant evidence of the positive association between domatia or pubescence on the leaf surface and higher densities of a large group of predatory mites (Acari: Phytoseiidae) compared with leaves without these structures. However, it is not clear whether this effect can be attributed to favourable RH or to other beneficial effects (Downing & Moilliet, 1967; Duso, 1992; Walter & O'Dowd, 1992a, b; Grostal & O'Dowd, 1994; Karban *et al.*, 1995; Walter, 1996; Nyrop *et al.*, 1998; Duso & Vettorazzo, 1999; Roda *et al.*, 2001; 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.

The neotropical phytoseiid mite *Typhlodromalus aripo* DeLeon (Acari: Phytoseiidae) was released for the first time in Africa in 1993 to control another neotropical species, the herbivorous mite *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae), a serious pest on cassava. Subsequently, the predator has established in 20 countries of sub-Saharan Africa. Although *T. aripo* persists throughout the year in the humid forest and the forest/savannah mosaic areas, it is severely affected by the long dry seasons of the higher latitudes of sub-Saharan Africa (Yaninek & Hanna, 2003; Hanna *et al.*, 2005; Onzo, *et al.*, 2005; Zundel, 2006). The predator does not migrate to dry season refuges (Zundel *et al.*, 2007), nor is it known to have a diapausing stage. Populations often decline to few individuals in the apices of the cassava host plants and it takes weeks or months of rainfall before they have recovered. Cassava apices, consisting of the leaf primordia and the youngest, still folded leaves, can be considered as domatia, with hairy or glabrous expressions, depending on cassava genotype. *Typhlodromalus aripo* occurs in greater abundance on hairy compared with glabrous genotypes (Hanna *et al.*, 2000; Zundel, 2006). Because populations of the pest mite peak in the dry season, the present study aimed to identify options to sustain the predators' presence during the dry season, with the ultimate aim of enhancing the biological control of *M. tanajoa* on cassava.

The present study, comprising a field experiment and a controlled climate experiment, investigated whether humid macro-habitats combined with hairy cassava genotypes (microhabitats) can mitigate the effects of low RH on *T. aripo*. In addition, a discriminant and regression analysis was performed on field data to determine the factors that are likely to affect the presence of *T. aripo* in the dry season. The present study is based on three hypotheses: (i) habitat type affects persistence of *T. aripo* during dry season; (ii) disappearance of *T. aripo* in the dry season and its reappearance in the beginning of the rainy season depend on RH in the habitat; and (iii) morphological features of the host plant (micro-level) mitigate adverse climatic conditions in the habitat (macro-level), and thus affect the persistence of *T. aripo* on the plant through the dry season.

Materials and methods

Field study

Field selection and planting. To test whether a habitat with high RH together with hairy cassava host-plant genotypes can increase the persistence of *T. aripo* during the dry season, a field experiment was conducted from July 2003 to July 2004 in a watershed near Bamenda (800 m a.s.l.); 06°07′59″N, 10°06′20″E) in the North-West Province of Cameroon. The climate of this area is marked by a sub-humid and cool climate. The topography of the site is representative of the province and is characterized by a fragmented landscape of hills and valleys. The vegetation can be classified in three predominant land cover types (Di Gregorio & Jansen, 1998). The first comprises of closed grassland with sparse shrubs and agricultural fields, with a cover height of 0.03–3 m and broad leaf, semi-deciduous vegetation on a high-gradient hill slope (referred to as grassland hills). These grassland hills are increasingly cultivated with cassava. The second encompasses cultivated areas with multiple herbaceous and fruit tree crops on scattered small fields in a rainfed, fallow-practicing agricultural system, located on gently undulating, low-gradient slopes (referred to as multiple cropping areas). The third land cover type has closed forest with a cover height of more than 14 m, with broad leaf evergreen vegetation, located on the valley floor in a fragmented landscape pattern (referred to as riparian forest). Within a radius of approximately 300 m, two to four plots in each of the three typical land cover types were selected. The four plots in the grassland hills were at an average distance of 200 m from the hill-base and were 50–300 m apart, whereas the three riparian forest fields were scattered across the valley floor about 400 m apart. The two cultivated plots at the hill-base were within 20 m of each other. Each plot measured 48 × 10 m and was surrounded by vegetation that is typical for the habitat type of the plot. All plots were located 810–920 m a.s.l. In each plot, three cassava genotypes, TMS 92/0326 (hairy apices), TMS 92/0427 (semi-hairy apices) and a local cultivar (glabrous apices), were planted, providing a range of suitability to the predatory mite *T. aripo*. Seventy-two plants of each genotype were planted with a planting distance of 1 × 1 m in randomly assigned sub-plots of 6·12 m within each experimental plot (12 × 18 m).

In a preliminary habitat climate analysis, mean temperatures were higher in the grassland hill site plots than in riparian forest and multiple cropping area plots, whereas mean temperatures in the latter were not different from plots in the riparian forest site. Similarly, mean RH was lower in the grassland hill site plots than in the riparian forest and the multiple cropping area plots, whereas mean RH in the multiple cropping area plots was similar to the riparian forest site plots.

Climatic differences between habitat types were particularly pronounced during the dry season months (November to February) and tended towards convergence during the course of the rainy season (March to October).

Origin and introduction of predatory mites. The population of *T. aripo* (Bam population originating from Bambuì in Minas Gerais State in Brazil, with a climate similar to our study area) used in the present study was provided by the International Institute of Tropical Agriculture (IITA) in Cotonou, Republic of Benin. The Bam strain of *T. aripo* had been maintained in the laboratory on detached cassava leaves at $25 \pm 1\,°C$ and $80 \pm 10\%$ RH for 4 years. The predators were multiplied for at least three generations on cassava plants in a screenhouse prior to packing and shipping to Cameroon. Packing was carried out according to the technique described by Mégevand (1997). At the time when *T. aripo* was released (less than 96 h after packing), mortality in the shipping container was approximately 10%. Ten sample plants were randomly selected from the 72 plants of each genotype in a field, inspected for *T. aripo*, and tagged before release.

The predators were introduced twice within 8 weeks to ensure establishment of *T. aripo* before the dry season. At the first introduction (18 October 2003), the predators were released on all plants in each plot by transferring five active predators with camel-hair brushes from the pipette tips to the plants. Subsequent monitoring on the released plants showed that they had established on 3–48% of the sample plants. For the second release (28 November 2003), pipette tips containing 25 *T. aripo* females each were attached with scotch band to the stems of the sample plants only, close to the apex. A few days after the second release, *T. aripo* was present on 45–97% of the sample plants.

Mite and cassava plant monitoring. Release plants were monitored throughout the duration of the experiment at weekly intervals for the presence/absence of *T. aripo* in the cassava apex in a nondestructive manner using ×4 head lenses. In addition, *M. tanajoa* and indigenous phytoseiid mite densities were estimated from monthly counts of their mobile stages on the first fully-developed leaf of the terminal branch (Yaninek *et al.*, 1989). Indigenous phytoseiids were also counted on the eighth fully-developed leaf. Samples of local phytoseiids were kept in ethanol for later identification to species. On each sample plant, plant growth parameters were recorded at monthly intervals: plant height (cm), stay-green index (scored from 1 = full canopy with turgid and green leaves to 5 = complete defoliation of stem), apex retention index (scored from 1 = first five leaves present to 5 = none of the first five leaves present and dieback of apex), apex diameter (mm) and apex hairiness (scored from 1 = glabrous to 3 = very hairy). Mite and plant sampling started on 29 December 2003 (i.e. 1 month after the second predator release) and ended on 29 July 2004.

Climate monitoring. In each field, climate data were recorded at canopy height throughout the experiment using self-contained loggers (HOBO H8 Pro, Onset Corporation, Pocasset, Massachusetts). The position of the loggers was increased as plant height increased. Temperature and RH were measured with internal sensors (temperature accuracy: $\pm 0.2\,°C$; RH accuracy: $\pm 3\%$) at 12-min intervals.

Growth chamber experiment

An experiment was conducted in a controlled environment chamber at IITA in Cotonou, Benin, to test whether morphological features of the host plant mitigate adverse climatic conditions in the habitat and thereby affect the presence of *T. aripo* on the plant in the dry season. Specifically, the effects of cassava apex morphology (i.e. amount of hairiness) and its potential interaction with RH on *T. aripo* egg hatch were determined. Two assumptions were tested: (i) plant substrate and RH 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 protect *T. aripo* eggs from unfavourable RH more than glabrous apices. The trial was designed as a two-factor experiment with three RH levels and four substrates. In a first experiment, two RH levels (55% and 85%) and four substrate levels were tested with three replications and, in a second experiment, three RH levels (33%, 55% and 85%) and four substrate levels were included with three replications. Survival of *T. aripo* eggs was measured as the proportion of eggs that hatched.

For this experiment, the Bam population of *T. aripo* was collected from a field in the mid-altitudes of Cameroon (1294 m a.s.l.) in May 2004 (released in November 2003), and was thereafter maintained in the laboratory on detached cassava leaves at $25 \pm 1\,°C$ and $80 \pm 10\%$ RH, under an LD 12 : 12 h photoperiod, and fed with *M. tanajoa* (all stages) and maize pollen. Cohorts of eggs of the same age were used. In phytoseiids, 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 & Chapman, 1980; Gaede, 1992). 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 LRH_{50} (i.e. RH at which 50% of eggs fail to hatch) of *T. aripo* eggs maintained on glass slides was 67% at room temperature. Humidity was controlled with oversaturated salt slurries (Winston & Bates, 1963) in round Perspex containers with lid (diameter 185 mm, height 80 mm) containing 70 mL of KCl slurry for maintaining 85% RH, 50 mL of $Mg(NO_3)_2 * 6\ H_2O$ slurry for 55% RH and 50 mL of $MgCl_2 * 6\ H_2O$ slurry for 33% RH.

For this experiment, 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 cassava genotypes of the field experiment in Cameroon could not be used as they were not available in Benin. The apices and leaves were selected from 5-week-old cassava plants grown in pots in a screenhouse free of mites. When preparing the apices and leaves, the unfolded leaves

around the apex were removed and the stem was cut approximately 3 cm 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 approximately 3 cm below the leaf blade and the mid-lobe was cut approximately 3 cm from the petiole. To keep plant apices and leaves fresh for the duration of the experiment, each apex or leaf was prepared with its stem or petiole base inserted in a glass screw cap vial (12 mm diameter × 45 mm height), filled with water and sealed with parafilm around the stem or petiole. The mini-Petri dishes had two opposite aeration holes of 2 mm in 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 h old. The mini-Petri dishes were placed above the slurry, on polyethylene racks (diameter 168 mm, height 20 mm) with a grid size of 2 mm, whereas the vials were placed upright with their base in the slurry. The humidity control containers were kept in the growth chamber at 22 °C (mean dry season temperature in the area of the field experiment in the North-West Province of Cameroon), under an LD 12 : 12 h photoperiod. Temperature and RH were monitored with HOBO H8 Pro loggers (Onset Corporation) inside the containers. After 72 h, the shrivelled (dead) eggs, the viable eggs and the hatched larvae were counted. The containers remained tightly closed for the entire duration of the experiment.

Statistical analysis

Effects of habitat type and host-plant genotype on T. aripo *densities.* The analyses proceeded in two steps. First, a generalized linear mixed model (function lmer from library lme4; R Development Core Team, 2005) was performed with the proportion of plants having *T. aripo* as the dependent variable. The independent (explanatory) variables were habitat type and host-plant genotype as fixed factors, week as time variable and field as random factor. Separate intercepts were estimated for each field. A logit link function and a binomial error distribution were used. The full model contained all interactions up to the three-way interaction habitat type × host-plant genotype × time. The model was reduced stepwise backwards based on the Bayesian information criterion (Schwarz, 1978). The resulting most parsimonious model might still contain too many significant parameters because the generalized linear model does not take into account serial autocorrelation generated by the weekly measurements. If autocorrelations are not corrected for, significance tests are less meaningful due to pseudoreplication. Thus, in a second step, the parameters and their variance of the most parsimonious model of step one were estimated by a generalized estimation equation (GEE; function gee from library gee; R Development Core Team, 2005). Nonsignificant terms were removed stepwise from the model. Pairwise comparisons between the different levels of habitat and plant genotype were conducted by robust *z*-tests. The error probability level was adjusted to $\alpha = 0.0085$ according to Dunn-Šidák (Ury, 1976) to correct for multiple tests. The analyses were conducted separately over the periods of the

dry season (29 December to 8 March) and the rainy season (15 March to 29 July).

Identification of factors affecting the persistence of T. aripo. The analytical procedure was divided into two steps to identify the variables that have an effect on the presence of *T. aripo* in the apices of cassava plants. First, a linear discriminant analysis was performed, which separated the plants where *T. aripo* was present from those where it was absent. This way, potential explanatory variables were pre-selected. Second, a generalized least square linear regression was performed to model the presence of *T. aripo* by the selected set of explanatory variables at the same time as correcting for autocorrelations present in the data due to their time series nature. Several discriminator variables were entered into the discriminant model: number of *M. tanajoa* mobiles on the first fully-expanded leaf, plant height, stay-green index, apex retention index, apex diameter, apex hairiness, weekly mean temperature, and weekly mean RH. Data collected at monthly intervals (*M. tanajoa* densities, plant characteristics) were interpolated to obtain values for each week. Between two sampling dates, the growth of *M. tanajoa* densities and plant characteristics was assumed to be linear. To adjust for the different scales of measurements, all variables were scaled to zero mean and a standard deviation of one. Riparian forest data were excluded from the analysis because a strong interaction with indigenous phytoseiids was suspected. Such an interaction may confound the relationships between the presence of *T. aripo*, prey densities, plant parameters and climate characteristics. Backward selection based on the Akaike Information Criterion (AIC) was applied to find the most appropriate model to predict the presence of *T. aripo*. The discriminant factor analysis was performed: (i) on the dry season data subset (29 December to 8 March) and (ii) on the wet season data subset (15 March to 29 July). In a second step, the relationship between the presence of *T. aripo* and the variables identified in the discriminant analysis by a generalized least squares regression allowing for autocorrelations (function gls from library nlme; R Development Core Team, 2005) was modelled. An autocorrelation process of the first order was assumed. This assumption was evaluated for each variable based on 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, a two-way analysis of variance (ANOVA) (function lm; R Development Core Team, 2005) was used to test for the effects of RH and substrate (independent variables) on the proportions of eggs hatched (dependent variable). Because residuals were not normally distributed, the proportions of eggs hatched were arcsine transformed. Because interactions occurred, each humidity level was examined separately by 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

Effect of habitat type and host-plant genotype on the presence of T. aripo. When mite monitoring started (29 December 2003), the percentage of plants with *T. aripo* was low in the dry grassland hill (20–30%) and in the humid riparian forest (7–39%) habitat. In the humid 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 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 humid multiple cropping habitat type, where it persisted until 1 March 2004 (Fig. 1). After backward selection from the full generalized

linear model, all main effects and the interaction between genotype and habitat remained in the model (Table 1). In the GEE, only the three main effects were significant (Table 2). The proportions of plants with *T. aripo* during the dry season were higher in the humid multiple cropping habitat than in the humid riparian forest, whereas proportions of plants with *T. aripo* were similar in the dry grassland hill and the humid riparian forest. Moreover, the proportions of plants with *T. aripo* were higher in the humid multiple cropping habitat than in the dry grassland hill. With regard to the host-plant genotypes, the proportions of plants with *T. aripo* were higher in all habitats in the hairy genotype TMS 92/0326 than in the glabrous local genotype, whereas there was no difference in proportions of plants with *T. aripo* between the semi-hairy genotype TMS 92/0427 and the glabrous local genotype (Table 2). Furthermore, the hairy TMS 92/0326 had higher proportions of plants with *T. aripo* than the semi-hairy TMS 92/0427.

Although *T. aripo* began to reappear in the apices of TMS 92/0326 in the humid multiple cropping habitat on 22 March, which was 3 weeks after its disappearance, its reappearance was delayed for another 8 weeks (until 17 May) on plants of TMS 92/0427 and on the local genotype. In the humid riparian forest, the predators reappeared first on 17 May, on plants of TMS 92/0326, and 4 weeks later, on 18 June, on TMS 92/0427. By contrast, *T. aripo* did not reappear on the local genotype during the time period of this experiment in the humid riparian forest habitat. In the dry grassland hill habitat, the predators simultaneously reappeared on plants of TMS 92/0326 (hairy) and TMS 92/0427 (semi-hairy) on 24 June, but did not reappear on plants of the local (glabrous) genotype. *Typhlodromalus aripo* colonized all sample plants of TMS 92/0326 in the humid multiple cropping habitat within 7 weeks (10 May) after its first reappearance. Plants of TMS 92/0427 reached 100% coverage on 7 June, which was 3 weeks after first *T. aripo* reappearance on this genotype, and it recolonized 70–80% of all sample plants of the local genotype within 5 weeks after its first reappearance on this genotype (i.e. before 24 June). Although it lasted 5 weeks (until 24 June) from its first reappearance to a percentage of plants with *T. aripo* of 40–50% in the humid riparian forest habitat on plants of TMS 92/0326, recolonization remained on a very low level in the humid riparian forest on plants of TMS 92/0427 (3–13%). In the dry grassland habitat, plants of TMS 92/0326 and TMS 92/0427 with *T. aripo* never exceeded 30% and 20%, respectively, during throughout our observations (Fig. 1).

In the rainy season, the full generalized linear model (containing the main effects of habitat, genotype and week, all their two way-interactions and the three-way interaction) could not be simplified (Table 3). The GEE-algorithm did not converge for this model. Because the *P*-value for the three-way interaction was very low (6×10^{-9}), we accepted the significance of this three-way interaction despite the lmer-model being weakened by pseudoreplication. This decision is supported by Fig. 1, which suggests a three way-interaction in the rainy season.

Identification of factors affecting the presence of T. aripo. The discriminant analysis of the dry season subset
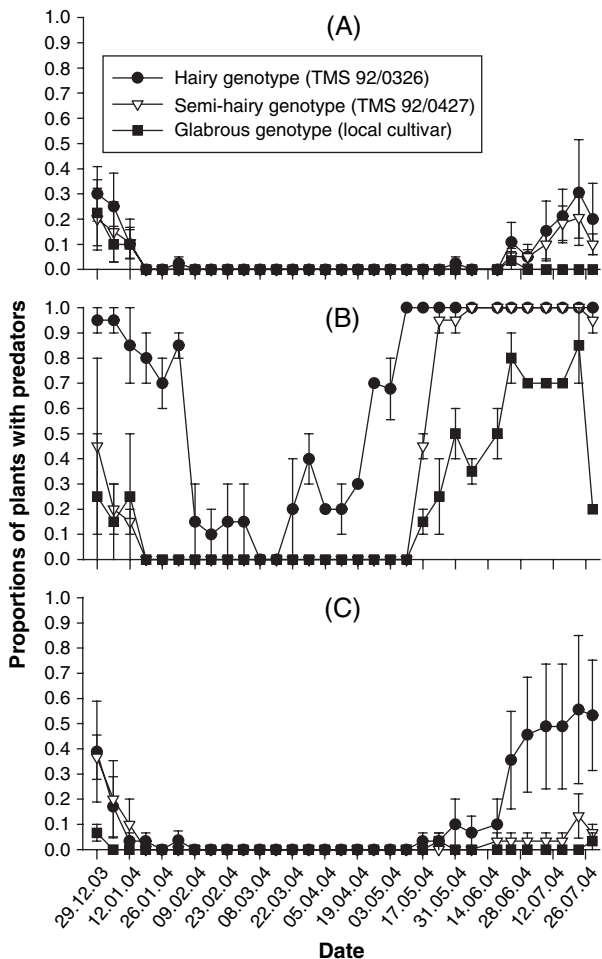

Figure 1 Proportions of plants with *Typhlodromalus aripo* on three cassava genotypes (hairy: TMS 92/0326; semi-hairy: TMS 92/0427; glabrous: local genotype) on cassava fields: (A) in the grassland hills; (B) on multiple cropping areas; and (C) in the riparian forest. Data points are mean proportions of plants with *T. aripo*. Vertical bars indicate the SEM.

Table 1 Stepwise backwards selection from the full generalized linear model (ModFull) with proportions of plants with *Typhlodromalus aripo* as dependent variable (*Y*) and habitat (*h*), genotype (*g*) and time (*t*) as explaining variables for the dry season

Model name	Model equation	d.f.	BIC	χ^2	*P*
ModFull	$Y = h+g+t+h^*g+h^*t+g^*t+h^*g^*t$	19	298		
Mod1	$Y = h+g+t+h^*g+h^*t+g^*t$	15	277		
ModFull versus Mod1	$-h^*g^*t$	−4		2.12	0.7137
Mod2	$Y = h+g+t+h^*g+h^*t$	13	275		
Mod1 versus Mod2	$-g^*t$	−2		9.65	0.0080
Mod3	$Y = h+g+t+h^*g$	11	267		
Mod2 versus Mod3	$-h^*t$	−2		12.65	0.0131
Mod4	$Y = g+h+t$	7	333		
Mod3 versus Mod4	$-h^*g$	−4		101.68	<0.0001

For each model, the Bayesian information criteria (BIC) and, for each step, the likelihood ratio test statistics are shown.
d.f., degrees of freedom.

identified stay-green, apex retention, apex diameter, apex hairiness, weekly temperature and weekly mean RH as variables influencing the presence of *T. aripo* (Table 4). The number of *M. tanajoa* mobiles on the first fully-expanded leaf and plant height were not selected by the model as potentially influential variables. Accounting for autocorrelations, the influence of stay-green, apex retention, apex diameter, apex hairiness and weekly mean RH on the presence of *T. aripo* remained significant (Table 4). In the rainy season subset, the number of *M. tanajoa* on the first fully-expanded leaf, plant height, stay-green, apex diameter, apex hairiness and weekly mean temperature became potentially influential. Only plant height and apex diameter were retained as variables that influenced the presence of *T. aripo* in the cassava apex after accounting for autocorrelations.

Growth chamber experiment

Typhlodromalus aripo egg hatch rates increased with increasing RH (Fig. 2). At the lowest RH level of 33%, almost all eggs failed to hatch. At the intermediate RH level of 55%, egg hatch exceeded 50% on plant substrates (apices of cv. 'Agric', apices of cv. 'Amala', cassava leaves), but almost all eggs failed to hatch when placed on mini-Petri dish surface. Eggs hatched

with rates of almost 100% at the highest RH level (85%). The interaction between RH and substrate was highly significant ($F_{6,288} = 49.75$, $P < 0.0001$) but substrate affected egg hatch only at 55% RH ($F_{3,92} = 84.86$, $P < 0.0001$). In the post-hoc contrast test, there was a significant difference in egg hatch between plant tissue (i.e. apices of cv. 'Agric', apices of cv. 'Amala', cassava leaves) and mini-Petri dish ($P = 0.05$).

Discussion

Field study

Effects of habitat type and host-plant genotype on the presence of T. aripo. The field trial data showed a clear seasonal pattern in *T. aripo* dynamics (Fig. 1): the densities of the predator declined to zero during the dry season and increased gradually, starting shortly after the beginning of the rainy season. These patterns are similar to those observed over 7 years of monthly monitoring at one location in Benin (Hanna *et al.*, 2005).

In the dry season, the nonsignificant interaction terms with time and the significant main effect of time indicate that proportions of plants with *T. aripo* declined at the same rate in

Table 2 Pairwise comparison of the proportions of plants with *Typhlodromalus aripo* between habitat and genotype levels according to the generalized estimation equation estimates

Coefficients	Estimate	Estimate SE	*P*
Intercept	0.989	0.773	0.0002
Dry grassland hill (compared with riparian forest)	0.484	0.634	0.9092
Humid multiple cropping area (compared with riparian forest)	0.898	0.643	0.0002
Dry grassland hill (compared with humid multiple cropping area)	0.904	0.651	0.0003
Hairy TMS 92/0326 (compared with glabrous local)	0.881	0.664	0.0034
Semi-hairy TMS 92/0427 (compared with glabrous local)	0.680	0.685	0.3332
Hairy TMS 92/0326 (compared with semi-hairy TMS 92/0427)	0.223	0.635	0.0248
Time	0.350	0.519	<0.0001

The coefficients are significant if $P < 0.0085$ (Dunn-Šidák method).

Table 3 Stepwise backwards selection from the full generalized linear model (ModFull) with proportions of plants with *Typhlodromalus aripo* as dependent variable (*Y*) and habitat (*h*), genotype (*g*) and time (*t*) as explanatory variables for the rainy season

Model name	Model equation	d.f.	BIC	χ^2	*P*
ModFull	$Y = h+g+t+h^*g+h^*t+g^*t+h^*g^*t$	19	485.96		
Mod1	$Y = h+g+t+h^*g+h^*t+g^*t$	15	504.84		
ModFull versus Mod1	$-h^*g^*t$	-4		44.05	<0.0001

For each model, the Bayesian information criteria (BIC) and, for each step, the likelihood ratio test statistics are given.
d.f., degrees of freedom.

the different habitat–genotype combinations. The multiple cropping habitat was more favourable for *T. aripo* than the grassland hill and the riparian forest, irrespective of the host-plant genotype. The hairy genotype TMS 92/0326 was more frequently colonized by *T. aripo* than the semi-hairy TMS 92/0427 and the glabrous local genotype, irrespective of habitat type. In the rainy season, the rate of *T. aripo* reappearance was different in the various habitat–genotype combinations, as indicated by the significant interaction between habitat, genotype and time.

The most favourable conditions for the survival of *T. aripo* in the dry season and the presence of *T. aripo* in the rainy season were provided by hairy host-plant genotypes grown in humid multiple cropping areas (Fig. 1). In the relatively drier and more exposed grassland hill habitat, the abundance of *T. aripo* was low throughout the experiment. However, even under these adverse conditions, the hairy genotype TMS 92/0326 could sustain the predators better than the semi-hairy genotype TMS 92/0427 and the glabrous local genotype. This is in line with the observations of Ferro and Southwick (1984), Holtzer *et al.* (1988) and Cunningham (1998), who showed that the climate of the leaf boundary layer (which was assumed to be affected by the genotype) is of more immediate relevance to phytoseiids than the ambient climate. It is unexpected, however, that this effect still worked under conditions where cas-

sava plants were affected by eroded, infertile and dry soils, which were prevailing in this habitat type. These conditions are likely to reduce photosynthetic activity in the dry season and thus may limit the mitigating capacity of the leaf boundary layer. Access to water or high RH spells for the uptake of water vapour from the air is crucial for mite survival under dry conditions, as shown by Gaede (1992) for phytoseiids and by DeBoer *et al.* (1998) for house dust mites. The fact that *T. aripo* never returned to the glabrous genotype, which was present in the immediate neighbourhood of the other two genotypes, points to an effect of 'hairiness' with respect to *T. aripo* colonizing the apex of a plant.

The abundance of *T. aripo* in the riparian habitat is an intriguing example of the complexity of biotic and abiotic interactions driving the dynamics of this acarine predator–prey system on cassava. By contrast to what was expected, the riparian forest habitat was not suitable for *T. aripo*, despite its humid conditions. It is suspected that the poor persistence and reappearance of *T. aripo* in the riparian habitat was due to the negative effects of intraguild predation on *T. aripo* by indigenous phytoseiid mites. Indigenous phytoseiids were numerous (1.5 phytoseiids per sample leaf) in the riparian forest sites compared with the multiple cropping area and the grassland hill sites (0.1 phytoseiids per sample leaf) in December 2003.

Table 4 *t*- and *P*-values of the discriminant (smallest model) and generalized least square regression (corrected for autocorrelation) for the variables that were identified to possibly have an influence on *Typhlodromalus aripo* presence in the cassava apex

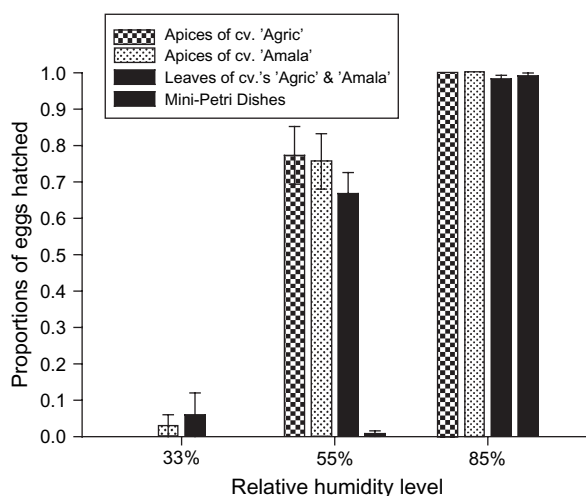|	Discriminant analysis (smallest model)				Generalized least square regression			
	Coefficients	SE	*t*	*P*	Coefficients	SE	*t*	*P*
Dry season					Autocorrelation = −0.84			
Stay-green	−0.0265	0.0104	−2.64	0.0083	−88.37	5.61	−15.75	0.0001
Apex retention	−0.0350	0.0111	−3.09	0.0021	90.28	12.34	7.32	0.0019
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 relative humidity	0.0649	0.0112	5.89	<0.0001	1.12	0.22	5.22	0.0064
Rainy season					Autocorrelation = −0.16			
Mononychellus tanajoa	−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

Figure 2 Egg hatch of *Typhlodromalus aripo* on four substrates under three humidity regimes. Columns are mean proportions of eggs hatched. Vertical bars indicate the SEM.

Indigenous phytoseiid guild in the riparian forest sites was largely dominated by two species: *Ueckermannseius* (syn. *Typhlodromalus) saltus* (Denmark & Matthysse) and *Euseius fustis* (Pritchard & Baker), which occurred at 78% and 22%, respectively. Although intraguild interactions between *U. saltus* and *T. aripo* are unknown, there is abundant evidence from laboratory experiments that *E. fustis* can act as an intraguild predator on *T. aripo*. Normally, the two species are spatially separated: *T. aripo* resides in the cassava apex during the day and forages on the upper 20% of the cassava foliage during the night hours (Onzo *et al.*, 2004). *Euseius fustis* inhabits largely the middle part of the canopy (Zannou *et al.*, 2005). Evidence from screenhouse experiments show that, under shady conditions, *T. aripo* does not exclusively stay in the apex during daylight hours, but also dwells and oviposits on the leaves (Onzo *et al.*, 2003). Such behaviour increases the likelihood of encounters between *T. aripo* and indigenous phytoseiids inhabiting the same leaves and thereby increases predation on *T. aripo* by *E. fustis* and possibly by *U. saltus*. In field observations without shade, there was no evidence of intraguild predation by *E. fustis* on *T. aripo* (Onzo *et al.*, 2003; Zannou *et al.*, 2007). The fact that the hairy genotype was more frequently colonized by *T. aripo* than the semi-hairy and the glabrous genotype suggests a protective effect of apex hairiness on the presence of *T. aripo* in this environment. Because prey densities in the riparian forest sites were not different from prey densities in the multiple cropping areas (data not shown), where *T. aripo* persisted at high levels, it is unlikely that scarcity of food caused the low predator densities in the riparian forest sites.

The fact that the semi-hairy genotype TMS 92/0427 did not host *T. aripo* more frequently than the glabrous local genotype, and less frequently than the hairy genotype TMS 92/0326 in the dry season, supports the idea that slight hairiness alone is not enough to 'protect' the predators in the dry season. It is assumed that, in addition to considerable hairiness, drought resistance (i.e. plants remaining vigorous through the dry season) is required.

The variable time pattern of *T. aripo* reappearance on the host plant after the onset of the rains may be due to different types of dry season refuges: reappearance may have occurred earlier if the predators survived in low densities in the apex, and it may have occurred later if the apices were recolonized from other plants (Zundel *et al.*, 2007). Another reason may be the different sizes of the start populations in the different habitat–genotype combinations at the beginning of the rainy season. Figure 1 indicates that the most favourable habitat for *T. aripo* in the rainy season was the humid multiple cropping area, too. Furthermore, it was difficult for the predatory mite to re-establish in a dry grassland hill or a humid riparian forest habitat. Also in the wet season, in all habitats, most of the predatory mites were found on the hairy host-plant genotype TMS 92/0326 (Fig. 1).

Identification of factors affecting the presence of T. aripo. The predators' presence in the dry season was affected by more variables than its presence in the rainy season. Whereas *T. aripo* was negatively affected by poor stay-green, low apex retention, small apex diameter, low apex hairiness and low RH during the dry season, the predators were negatively affected only by low plant height and small apex diameter during the rainy season. Mean RH was high during the latter and, as such, was not a limiting factor. Plant vigour, as represented by one or more indices such as apex diameter, stay-green index, apex retention and plant height, played an important role with respect to the presence of *T. aripo* during both the rainy and dry seasons. Apex hairiness played a crucial role during the dry season, but had little effect on the presence of *T. aripo* during the rainy season, probably because apex hairiness is a trait of the cassava genotype and is presumably not affected by environmental conditions. In an experiment with three hairy and three glabrous cultivars, Hanna *et al.* (2000) also found that apex hairiness is essential for the persistence of *T. aripo* mainly during the dry season. Apparently, the type of protection offered by hairy apices is only required (or more effective) in the dry season. Taken together, our data show that the presence of *T. aripo* is affected by a strictly habitat type effect (RH), a strictly plant type effect (apex hairiness) and a combination of both habitat type and plant genotype effect (resulting in plant vigour). Surprisingly, although plant variables affected the presence of *T. aripo*, prey abundance did not play a role with respect to the presence of *T. aripo* in our analysis. This may be due to the predator's ability to survive on alternative food sources such as cassava extra-floral exudates and maize pollen (Yaninek & Hanna, 2003; Gnanvossou *et al.*, 2005). Several studies in various acarine predator–prey systems on plants also showed that prey densities were less important for predator presence than host-plant characteristics (Karban *et al.*, 1995; Nyrop *et al.*, 1998; Duso & Vettorazzo, 1999; Hanna *et al.*, 2000).

Growth chamber experiment

In this experiment, the effects of cassava apex morphology (i.e. level of hairiness) and RH on *T. aripo* egg hatch were

further explored independently from other habitat effects. Substrate and RH interacted only at intermediate RH levels (55%), where a clear advantage for egg survival became evident if the eggs were placed on a plant substrate compared with an artificial solid substrate (mini-Petri dish). However, egg survival was not affected by the type of substrate. By contrast, egg survival was very high at high RH (85%) and very low to zero under dry conditions (RH of 33%), irrespective of plant tissue or mini-Petri dish. The crucial role of the plant substrate under critical humidity conditions (55%) may be due to the effect of plant transpiration in mitigating the low RH level of the microclimate close to the boundary layer in which the predatory mites are dwelling. The growth chamber experiment did not support the expectation that hairy apices are more favourable to *T. aripo* egg survival than glabrous apices at any of the RH levels tested.

The results of the growth chamber experiment, however, support the findings of the field study in two aspects: both trials confirmed that the environment (growth chamber experiment: RH 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 predatory mites. There are two aspects, however, where the results of the two experiments diverged: first, the interacting effect of environment and host-plant characteristics, which was found in the growth chamber experiment, did not manifest itself in the field trial. This can be explained by the fact that climatic conditions in the field did not reach the extremes (low RH, high RH) of the growth chamber. Second, in the field study, hairy cassava host-plant genotypes played a more important role for *T. aripo* presence than can be assumed from the results of the growth chamber experiment. Cassava genotypes with hairy apices also promoted higher abundances of *T. aripo* compared with genotypes with glabrous apices in another field experiment (Hanna *et al.*, 2000). It is assumed that hairs are more important under field conditions than in the controlled environment of a growth chamber. In the field, hairs probably protected the predators from negative effects of wind or predation, or they may have provided alternative food by trapping pollen (O'Dowd & Willson, 1991; Karban, *et al.* 1995; Bottrell *et al.*, 1998; Sabelis *et al.*, 1999; Cortesero *et al.*, 2000; Roda *et al.*, 2000; Norton *et al.*, 2001). These effects of apex hairiness, however, were irrelevant in the growth chamber experiment. Other potentially beneficial mechanisms displayed by the hairy genotype TMS 92/0326 in the field, but not under the controlled conditions of the growth chamber, are still climate-related, but not 'hair-related' (i.e. the plant canopy mediating the diurnal climate dynamics, and plant vigour affecting microclimate). Plant morphology, in particular plant height, plant canopy and foliar density, reportedly play a role in the conservation of phytoseiid mites (Nyrop *et al.*, 1998; Pratt *et al.*, 2002). Heinz and Parrella (1994) and Rutledge *et al.* (2003) also 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.

It is well recognized that not one single factor among prey abundance, intraguild competition, macro-predators, host-plant quality and (micro) climate is determining phytoseiid dynamics. Rather, it is their interacting effects, expressed differently in each agricultural system (Agrawal *et al.*, 2000), that are essential for the fate of predatory mite populations. 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 RH (Grostal & O'Dowd, 1994); and on plant substrate interacting with RH (van Dinh *et al.*, 1988). To our knowledge, the present study is the first to investigate the interaction between genotype/hairiness and habitat climate and its effects on phytoseiids in the field and in the growth chamber.

Implications for the control of M. tanajoa

In areas with cool temperatures and pronounced dry seasons, the establishment of *T. aripo* to control the herbivorous mite *M. tanajoa* is a challenge. It becomes all the more important to know which small scale agro-ecological conditions are favourable to the predatory mite and, if possible, to create them. We found that, among the tested combinations of habitats and host-plant genotypes, the humid multiple cropping areas planted with the hairy cassava genotype TMS 92/0326 were most suitable for *T. aripo*. However, the agronomic acceptability of the tested hairy genotype TMS 92/0326 is not ideal for the sub-humid and cool climate of the study area. Although taste and cooking properties are appreciated by farmers, yields are probably too low to make it a competitive cultivar. Also, this genotype showed a slight susceptibility to the African cassava mosaic virus. The value of the present study lies in the exploration of the potential of a hairy genotype to facilitate *T. aripo* establishment and to increase its presence. The results obtained imply that cassava breeding includes hairiness in the desired traits. Until high yielding, hairy and drought resistant cultivars be available, the effectiveness of *T. aripo* can be increased by using small plant numbers of TMS 92/0326 to create reservoirs that are favourable to the predatory mites.

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