



Plant feeding by a predatory mite inhabiting cassava

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Abstract. Plant feeding by arthropod predators may strongly affect the dynamics of bi- and tri-trophic interactions. We tested whether a predatory mite, *Typhlodromalus aripo*, feeds upon its host plant, cassava. This predator species is an effective biological control agent of *Monoychellus tanajoa* (the cassava green mite or CGM) a herbivorous mite specific to cassava. We developed a technique to detect plant feeding, based on the use of a systemic insecticide. We found that *T. aripo* feeds upon plant-borne material, while other predatory mite species, *Neoseiulus idaeus* and *Phytoseiulus persimilis*, do not. Subsequently, we measured survival of juveniles and adult females of *T. aripo* and *N. idaeus*, both cassava-inhabiting predator species, on cassava leaf discs. Survival of *T. aripo* was higher than that of *N. idaeus*. Thus, *T. aripo* was able to withstand longer periods of prey scarcity. Because CGM populations fluctuate yearly and are heterogeneously distributed within plants, plant feeding may facilitate the persistence of populations of *T. aripo* in cassava fields and its control of CGM outbreaks.

Key words: plant feeding, alternative food sources, omnivory, *Typhlodromalus aripo*, cassava green mite

Introduction

Many predatory arthropods utilize plant-borne material, such as pollen, nectar, exudates or leaf tissue, in addition to their primary diet (Price *et al.*, 1980; Overmeer, 1985; Coll and Guershon, 2002). Plant feeding by predators may alter the dynamics of predator–prey interactions, for example by allowing persistence of predator populations in absence of prey (Bakker and Klein, 1992), by increasing predator numbers or by decreasing their predation rate (Eubanks and Denno, 1999; Lalonde *et al.*, 1999; Van Rijn and Tanigoshi, 1999; Van Rijn *et al.*, 2002). Moreover, attraction and arrestment

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of predators by means of plant-provided alternative food sources may affect plant fitness (Bentley, 1977; Heil *et al.*, 2001; Van Rijn *et al.*, 2002).

We tested the occurrence of plant feeding in *Typhlodromalus aripo* DeLeon, a predatory mite species inhabiting cassava. Cassava is a subsistence crop in several regions in the tropics. It is attacked by a few herbivores, among which is the cassava green mite (CGM), *Mononychellus tanajoa* Bondar. In absence of predators, CGM populations may cause severe damage to cassava plants (Yaninek *et al.*, 1989). *T. aripo* is the most effective predator against CGM. It was first reported by Bakker and Klein (1992) from the apices of cassava. In plants with *T. aripo*, CGM is generally absent from the apices (Bakker, 1993), but it occurs lower in the plant. Since *T. aripo* migrates to the lower strata at night (Onzo *et al.*, 2002), it could feed upon CGM during these migrations. Moreover, CGM migrates to the upper strata during the day, both in presence and absence of leaf-dwelling predators (Magalhães *et al.*, 2002). Thus, *T. aripo* could feed on CGM that migrates to the apex. However, electrophoresis data show that a large proportion of *T. aripo* collected in the field do not contain CGM in their gut (Bakker, 1993). The upper strata of cassava plants harbour few prey species. Apart from CGM, some species of thrips and of whiteflies are found, but *T. aripo* feeds poorly on these prey (Bakker, 1993). Therefore, we hypothesize that *T. aripo* feeds on plant-borne material from cassava. Testing this hypothesis is the aim of the present paper.

Materials and Methods

Experiments were done in Cruz das Almas (Brazil) and in Amsterdam (The Netherlands). We present the cultures in the two locations separately and the experimental procedure together.

Cultures

Brazil. Cassava (variety: Cigana Preta) was grown in a greenhouse at the Empresa Brasileira de Pesquisa em Agropecuária (EMBRAPA). Plants were planted as stakes (circa 20 cm) in 2.5-l plastic pots (surface: 20 cm²), and watered every other day. CGM was reared on young potted plants in another greenhouse. Clean plants were infested by placing CGM-infested leaves at the base of one or more petioles. Every month, cultures were supplemented with CGM individuals collected from several fields around the station.

Typhlodromalus aripo and *Neoseiulus idaeus* Denmark and Muma were reared in an acclimatized room at 24 ± 2°C, and 70–90% RH. Each rearing

unit consisted of a PVC arena (20 × 20 cm) on top of a sponge, surrounded by wet tissue and placed in the middle of a 30 × 30 × 10 cm plastic tray with water on the bottom. This set-up prevented escapes and enhanced humidity (Mégevand *et al.*, 1993). Predatory mites were fed three times a week by introducing two CGM-infested leaves in the rearing trays. Every month, predator cultures were supplemented with specimen collected in the field.

Amsterdam. Cassava (variety: CMC 40) was grown in a greenhouse at 25°C, 70% RH and 16L/8D photoperiod at the University of Amsterdam. Plants were planted as stakes (circa 20 cm) in 1-l pots (surface: 15 cm²) with soil and a 28N, 14K, 14P fertilizer. CGM was reared on intact plants in a separate greenhouse compartment. Clean plants were infested by placing CGM-infested leaves at the base of one or more leaf petioles. *Typhlodromalus aripo* (from Benin, West-Africa) and *Phytoseiulus persimilis* Athias-Henriot (from Sicily, Italy) were reared in a climate room, under the same conditions as those in the greenhouse compartments. The rearing procedure for *T. aripo* was the same as the one followed in Brazil. Every three months, cultures were renewed with specimen that had been collected in the field. *P. persimilis* was reared on bean leaves infested with *Tetranychus urticae* Koch placed on top of inverted pots. Each rearing unit consisted of two pots placed on a tray with water and covered with a 40 × 40 × 60 cm Plexiglas box. Infested leaves were added thrice a week.

Experimental procedure

To detect plant feeding in *T. aripo*, we developed a technique based on the use of a systemic insecticide. Replicates differed in a few technical details (cf. Table 1), but the basic principle was maintained across all trials.

Table 1. Experimental details

Parameters	Trial			
	Brazil	Amsterdam 1	Amsterdam 2	Amsterdam 3
Mites/treatment	10	20	20	20
Temperature (°C)	24 ± 2	25 ± 5	25	25
Relative Humidity (%)	70–90	60–80	70	70
Insecticide concentration (g/l)	2	5	1	1
Substrate for leaf-discs	Cotton wool	Agar	Cotton wool	Cotton wool

For each replicate, we selected 4 three-week-old plants from the same variety (Table 1). We placed a systemic insecticide (Temik 10G[®], active ingredient: aldicarb) on the pots of two of them at rates of 1–5 g/l (Table 1) and left the other two pots untreated. We watered the two sets of plants every other day during 15 days, enough time for the insecticide to be translocated from roots to leaves (Ridgway *et al.*, 1967; Chamberlin *et al.*, 1992), and not enough for it to be lost (Arienzo *et al.*, 1991; Chamberlin *et al.*, 1992). Then, we cut leaf discs (diam. 2 cm) from the two types of plants and placed them on a substrate that would keep them fresh (Table 1). We placed one *T. aripo* per leaf disc and assessed mortality 24 h later. Under the condition that bio-availability of the insecticide was restricted to inside the leaf tissue, any increase in mortality in insecticide leaf discs compared to control leaf discs would be the result of intake of pesticide-contaminated plant material by active feeding. To test if the only possible route of pesticide uptake was through feeding, additional treatments were included in the experimental design.

To test for contamination of the leaf surface, bio-assays with two additional species of predatory mites were included as a negative control. The species used, *N. idaeus* and *P. persimilis*, are relatively specialized on one prey type (McMurtry and Croft, 1997), thus expected not to feed on plant material. Mortality of these species on insecticide leaf discs invalidates the test design because it might indicate that the bio-availability of insecticide was not restricted to the leaf tissue (it may also result from these species feeding on the plant, but this explanation cannot be distinguished from the previous one).

Alternatively, a negative result (i.e., no mortality) in *N. idaeus* or *P. persimilis* versus a positive result with the test species *T. aripo* could also be caused by differences in susceptibility to the pesticide. To test the susceptibility of these species, we performed slide-dip tests (Busvine, 1971): mites were glued by their backs to a double-sided sticky tape on a microscope slide, then dipped for 15 s in solutions with different concentrations of the active substance. Twenty-four hours later, mortality (i.e., the percentage of mites not moving their legs when dabbed with a brush) was assessed, and compared with that of mites on a control slide that had been dipped in water (control).

Mortality of the individuals tested could also result from contamination of the substrate supporting the leaf discs. To test if this was the case, we removed insecticide leaf discs after the test and placed control leaf discs on the same substrate. On these leaf discs, we placed individuals from the species that showed high mortality on insecticide leaf discs. One day later, we assessed mortality. Occurrence of mortality would indicate contamination of the substrate. Finally, to test whether our method was adequate to induce

mortality in leaf-feeding mites, we assessed mortality of CGM on insecticide versus control leaf discs.

To test whether plant feeding affected the survival of predatory mites that inhabit cassava (*T. aripo* and *N. idaeus*), we measured survival of juveniles and females of these species on cassava leaf discs without prey. Egg cohorts of *T. aripo* and *N. idaeus* were produced by well-fed females placed on CGM-infested cassava leaflets for 24 h. Subsequently, eggs were placed individually on cassava leaf discs (diam. 2 cm). As soon as the eggs hatched, leaf discs were replaced every day until the individuals died. Individuals that escaped the set-up were used as censored data in the analysis. Sample sizes for total data: *N. idaeus* – 60, *T. aripo* – 41; uncensored data: *N. idaeus* – 22, *T. aripo* – 19. To measure survival of adult females without prey, we did cohorts of both species until the deutonymph stage, then transferred each female individually to a leaf disc with conspecific males and CGM. As soon as the female had oviposited its first egg, she was moved to a clean leaf disc and followed the same treatment as the juveniles. Sample sizes for total data: *N. idaeus* – 52, *T. aripo* – 70; uncensored data: *N. idaeus* – 31, *T. aripo* – 40. Survival curves were constructed using the Kaplan–Meier method. Differences between curves were analysed with the Gehan’s Wilcoxon test (Hosmer and Lemeshow, 1998).

Results

Nearly all *T. aripo* died 24 h after being placed on insecticide leaf discs (Table 2). No mortality was observed on control discs. The positive reference treatment (CGM) showed a similar mortality pattern. On leaf discs placed on the same substrate where insecticide leaf discs had been, no mortality was

Table 2. Mortality (mean \pm S.E) of CGM, *T. aripo*, *N. idaeus* and *P. persimilis* on leaf discs from plants with and without systemic insecticide. ‘Substrate control’ refers to mortality assessed on leaf discs placed on the same substrate where the insecticide leaf discs had been placed

Treatment	Species			
	CGM (<i>N</i> = 70)	<i>T. aripo</i> (<i>N</i> = 70)	<i>N. idaeus</i> (<i>N</i> = 10)	<i>P. persimilis</i> (<i>N</i> = 60)
Insecticide	1	0.97 \pm 0.013	0	0.14 \pm 0.039
Control	0.02 \pm 0.017	0	0	0
Substrate control	0	0		

Table 3. Slide-dip test in (a) Brazil and (b) Amsterdam. Indicated are the fractions of mites that died upon exposure to each concentration of the insecticide. N per insecticide concentration = 10, except for 0.001 g/l and control in (b), where $N = 20$ initially, to compensate for a few individuals that escaped from the sticky tape

Location	Concentration (g/l)	<i>T. aripo</i>	<i>N. idaeus</i>
(a) Brazil	1	1	1
	0.2	1	1
	0.1	1	0.7
	0	0	0
		<i>T. aripo</i>	<i>P. persimilis</i>
(b) Amsterdam	1	1	1
	0.1	1	0.9
	0.01	0.2	0.5
	0.001	0.2	0.16
	0	0.11	0.13

observed. This indicated that the insecticide was not available from the substrate. No *N. idaeus* and only few *P. persimilis* died when placed on insecticide leaf discs, and none died on control leaf discs. The slide-dip tests (Table 3) yielded only small differences among the phytoseiid species at very low insecticide concentrations. Thus, relative to the level of pesticide expected in the plant (Andrawes *et al.*, 1971, 1973), similar mortality levels on insect-

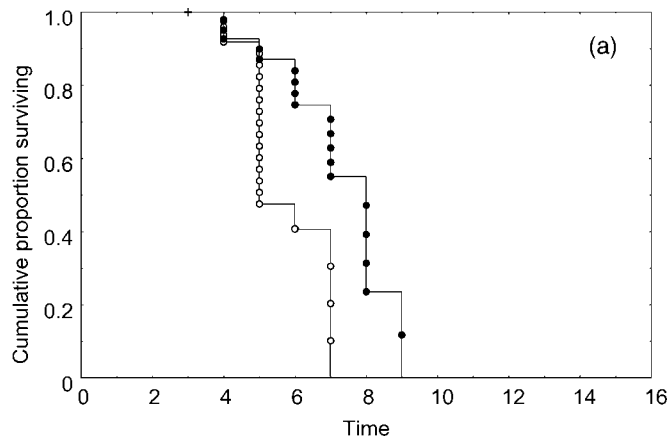


Figure 1. Longevity of *T. aripo* (black dots) and of *N. idaeus* (white dots) on cassava leaf discs: (a) juveniles, (b) adult females.

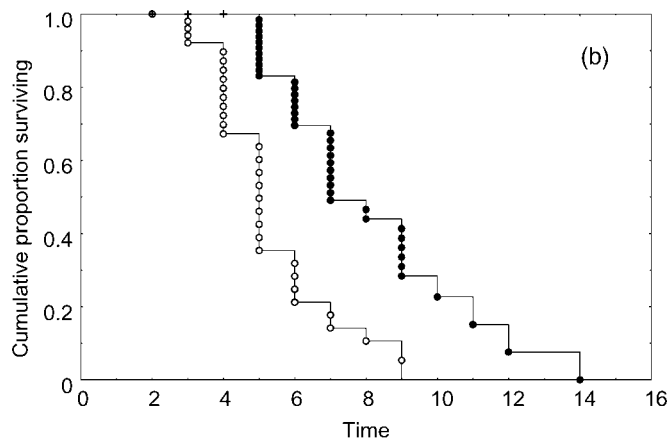


Figure 1. (Continued.)

icide leaf discs could be expected among the species used. Together, these results show that *T. aripo* feeds on the plant while *N. idaeus* and *P. persimilis* do not.

When placed on clean cassava leaf discs, *T. aripo* juveniles survived longer than *N. idaeus* juveniles ($p = 0.004$, Figure 1a). Similarly, survival of *T. aripo* adult females was higher than that of *N. idaeus* adult females ($p < 0.001$, Figure 1b).

Discussion

Our results show that *T. aripo* feeds upon cassava leaves, whereas *P. persimilis* and *N. idaeus* do not. Similar results were reported by Porres *et al.* (1975), where one out of four predatory mite species tested appeared to feed on green plant tissue, and by Soares *et al.* (1996).

Among the most widely used methods to detect plant feeding by arthropods are direct observations (Al-Wahaibi and Walker, 2000; Messchendorp *et al.*, 2000; Pedrosa-Macedo, 2000; Montserrat, 2001) and measuring feeding damage (Meyer, 1993; Agrawal *et al.*, 1999; Greenberg *et al.*, 2000). However, these methods are not universally applicable, since direct observations are only possible with relatively big arthropods and plant feeding does not necessarily entail visible damage (Montserrat, 2001). Many studies compare life histories of arthropods on plant tissue and on an artificial substrate as a test for plant feeding (e.g., Ruberson *et al.*, 1986; Eubanks and Denno, 1999; Gillespie and McGregor, 2000). While this method clearly shows the effect of plants on the life history of predatory arthropods, it does not necessarily demonstrate that this effect is due to feeding. In fact, many

characteristics of the leaf substrate (microclimate, leaf topography) may affect the life history of predatory arthropods (Kareiva and Sahakian, 1990; van Lenteren *et al.*, 1995). Therefore, differences in life-history traits of arthropods placed on leaf versus plastic substrates may be interpreted in several ways. In some studies, plant tissues have been labelled, by either radiolabelling (Porres *et al.*, 1975; Ostrom *et al.*, 1997; Armer *et al.*, 1998) or by staining (Armer *et al.*, 1998). The analogous use of a systemic insecticide to detect plant feeding simplifies this methodology.

Using this new method allowed us to show that *T. aripo* takes up nutrients from cassava leaves, but the specificity of this predator–plant association is as yet unclear. It seems unlikely that *T. aripo* has taken up nutrients from cassava exudates because *N. idaeus*, known to feed upon cassava exudate (Tanigoshi *et al.*, 1993; Mégevand and Tanigoshi, 1995), did not die in our test. Moreover, Temik is not available from the leaf surface (Ingram *et al.*, 1997). Thus, *T. aripo* has probably fed upon plant-borne material and not upon microorganisms from the phyllosphere. Since cassava leaves contain cyanide (Haque and Bradbury, 2002), *T. aripo* must have developed adaptations to overcome this plant defence. This suggests that the interaction predator–plant is specific, but this hypothesis needs further testing. Moreover, *T. aripo* occurs on the upper strata of cassava plants. Due to the apical dominance of cassava, nutrient density in the apices is expected to be high. Thus, the within-plant distribution of *T. aripo* may be related to the within-plant availability of nutrients.

Typhlodromalus aripo survived longer than *N. idaeus* on cassava leaf discs. Probably, the nutrients that *T. aripo* took from cassava leaves contributed to this higher survival. However, differences in survival may also be related to differences in metabolic rates between species. In any case, both juveniles and adults of *T. aripo* are able to survive long periods without prey. CGM populations are heterogeneously distributed in space and time (Noronha and Silva, 1998). Moreover, predatory mites are passive dispersers, thus prone to land on plants without prey. Since the dispersing stage of predatory mites is the young female (Kennedy and Smitley, 1985), this stage (and the eggs it carries) is likely to undergo periods of prey scarcity. Feeding on the plant may allow for the persistence of *T. aripo* populations in absence of prey and contribute to the success of *T. aripo* as a biological control agent of CGM.

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