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Feeding on Exudates and Leaves of Cassava Cultivars with Varying Cyanogenic Potentials: Implications for the Biology of *Typhlodromalus aripo*, a Key Biocontrol Agent of Cassava Green Mite in Africa

Nazer Famah Sourassou
Centre d'Excellence en Protection Durable des Cultures, Laboratoire des Sciences Agronomiques et Biologiques Appliquées, Institut Supérieur des Métiers de l'Agriculture, Université de Kara, Togo
Komi Agboka
Laboratoire de Recherche sur les Agroressources et la Santé Environnementale, Ecole Supérieure d'Agronomie, Université de Lomé, Togo
Koffi Negloh
Institut Togolais de Recherche Agronomque, Kara, Togo
Rachid Hanna
Center for Tropical Research, University of California, Los Angeles, USA
Atti Tchabi
Centre d'Excellence en Protection Durable des Cultures, Laboratoire des Sciences Agronomiques et Biologiques Appliquées, Institut Supérieur des Métiers de l'Agriculture, Université de Kara, Togo

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Abstract

The predatory mite *Typhlodromalus aripo*, a key biological control agent of the cassava green mite in Africa, is known to feed on cassava exudates and, in the absence of prey, directly on cassava leaves. While cassava cultivars differ greatly in cyanogenic potential (CNP), the consequences of feeding on exudates and leaves from cultivars with different CNP levels for *T. aripo*

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biology remain unknown. We conducted laboratory experiments to evaluate several life history parameters of *T. aripo* on exudates and leaf discs of three cassava cultivars – TME1 (low CNP), TMS91934 (moderate CNP), and TMS82/00661 (high CNP). *T. aripo* completed its development on exudates of all three cultivars, being faster with higher survival on exudate of TMS82/00661 (6.8 days, 68.2%) compared with TME1 (7.9 days, 53.8%) and TMS91934 (8.2 days, 56.8%). None of the exudates supported oviposition, although adult female survivorship was highest on TMS82/00661. *T. aripo* was unable to develop beyond the deutonymph stage on the leaf discs of all three cassava cultivars. However, juvenile and adult longevity were greater on TME1 compared with the two other cultivars. Exudates were free of cyanogenic glycosides with similar amino acid concentrations; however, sugar content was twice as high in exudates of TMS8200661 compared with the other cultivars. These findings highlight the importance of cassava exudate quality for predator persistence and biological control success.

Keywords: Phytoseiids, cassava, pest, exudate, nutritional value, cyanide, biological control

Introduction

Among natural enemies, predatory mites of the family *Phytoseiidae* are the most widely studied worldwide, including in Africa, due to their proven potential as biological control agents against key agricultural pests such as spider mites, thrips, and whiteflies (Gerson et al., 2003; McMurtry et al., 2013). There is substantial evidence that many predatory mites utilize plant-based foods such as pollen, nectar, and exudates, which allow them to persist during periods when their primary prey is scarce, therefore enhancing the biological control of target pest (Price et al., 1980; Overmeer, 1985; Bakker and Klein, 1992; Bruce-Oliver et al., 1996; Coll and Guershon, 2002; Nomikou et al., 2010; McMurtry et al., 2013; Samaras et al., 2021). In addition, several phytoseiid predators have been shown to extract nutrients directly from leaf tissues (Porres et al., 1975; Grafton-Cardwell and Ouyang, 1996; Magalhães and Bakker, 2002; Gnanvossou et al., 2005).

In cassava (*Manihot esculenta*), foliar exudates are produced along the petioles and midribs of young leaves (Klein, 1990). The quantity and quality of these exudates vary with cultivar, plant vigor, plant age, and time of day (Oduor, 1988; Klein, 1990). Previous studies have demonstrated the positive effects of cassava exudates on phytoseiid predators, including improved survival and development (van Rijn and Tanigoshi, 1999; Magalhães and Bakker, 2002; Toko et al., 1994). Cassava is also a major cyanogenic food crop (Cooke and Coursey, 1981). Cyanogenic glycosides occur in leaves and roots, with concentrations in leaves typically preceding those in roots (Cook

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and De La Cruz, 1982). These compounds release hydrogen cyanide upon hydrolysis and are well known for their toxicity to arthropods (Houk et al., 1989; Hansen et al., 1991).

The predatory mite *Typhlodromalus aripo* DeLeon is a successful biological control agent of the cassava green mite (*Mononychellus tanajoa* Bondar), a major pest of cassava in Sub-Saharan Africa (Yaninek and Hanna, 2003). Several ecological studies have been conducted to improve understanding of host plant–predator interactions involving cassava and *T. aripo* (Onzo et al., 2003; Gnanvossou et al., 2005; Hanna and Onzo, 2009; Onzo et al., 2012; Onzo et al., 2013; Onzo et al., 2014). This predator feeds on cassava exudates and, in the absence of prey, can also feed directly on cassava leaf (Bakker and Klein, 1992; Magalhães and Bakker, 2002; Gnanvossou et al., 2005). However, cassava cultivars differ considerably in their levels of cyanogenic glycosides, and it remains unclear whether feeding on exudates and leaves from cultivars with high cyanogenic potential (CNP) negatively influences the biology of *T. aripo*.

The objective of the present study was therefore to compare, under controlled laboratory conditions, several life history parameters of *T. aripo* when feeding on exudates and/or leaf discs of three cassava cultivars with different levels of CNP: TME1 (low CNP), TMS91934 (moderate CNP), and TMS82/00661 (high CNP (IITA, 1990).

Materials and methods

Predator and rearing technique

The predator, *T. aripo,* used in the experiment *was* collected from a cassava field near Sè, Cotonou, Benin (Gnanvossou et al., 2003), and reared in the laboratory of IITA, station of Benin at *25* ± 1ºC, and 70-90% RH and under 12h:12h light-dark cycle. The rearing followed Megévand et al. (1993). The petioles of cassava leaves infested with *M. tanajoa* are introduced into vials (Ø= 1 cm L= 3 cm) containing water and sealed with parafilm. The vials were placed on a black PCV tile (25 x 25 cm) laying on a foam pad (29 x 29 x 3.5 cm) in a plastic tray (37 x 37 x 56 cm) filled with water. Absorbent paper bands are stretched smoothly along the edges of the tile to provide a water source to the mites as well as to prevent them from escaping and avoid possible contamination by other arthropods.

Cassava cultivars and exudate production

The three cultivars (TME1, TMS91934, TMS82/00661) used in the study were obtained from the Plant Breeding Section of IITA-Ibadan station. The cassava cultivar AGRIC used in the experiments with exudates was obtained from the field of IITA-Benin. The cassava cultivars were grown in a greenhouse with temperature and relative humidity (RH) ranging between 29–

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32ºC and 65–72% respectively. Approximately 30 cassava cuttings (≈20 cm each) of each cultivar were singly planted in plastic pots (≈14 cm diameter at the base and 18 cm high) previously filled with about 40 kg of topsoil collected from IITA campus field. Plastic pots were then placed on an iron bench (350 x 180 x 76 cm) (L x W x H) arranged 65 cm apart. The plantation was done 4 weeks prior to the commencement of the experiments. Exudates were collected earlier in the morning (6-7 am) and used in the experiments. The excess exudate was kept in a refrigerator at 4 °C and used when necessary. Leaf discs were excised from clean leaves collected from these cassava plants and immediately used in the experiments.

Experimental conditions

All experiments were performed in the laboratory at 25±1ºC, 70-90% R.H. and 12L/12D photoperiod. Experimental units consisted of the leaf discs (2.5 cm) fitted to the bottom of the Petri dishes of the same size. Two opposite holes (2 mm diameter) were made in the sides of the dishes and covered with fine nylon mesh for aeration. The leaf discs were placed on a wet agar-agar solution in the dishes and were changed as soon as possible.

Development and survival on exudates of the three cassava cultivars

Approximately 300 mated females from the stock cultures were confined in the rearing arena for 24 h. After this period, females were removed, and the eggs laid were individually transferred to experimental units as described above. Thirty experimental units were established for each treatment.

For development on exudates, each experimental unit was assigned exudates from one of three cassava cultivars: TME1, TMS91934, or TMS82/00661. Leaf discs excised from the cassava cultivar Agric were used as the substrate in all experimental units. Each unit was supplied daily with a sufficient amount of exudate. Control treatment consisted of units provisioned with *M. tanajoa* (the prey). Experimental units were examined daily to determine the developmental stage reached, the duration of immature development, and survival to adulthood.

Development and survival on leaf discs of the three cassava cultivars

To assess development and immature longevity on leaf discs, individual eggs were placed directly onto leaf discs of one of three cassava cultivars: (a) TME1, (b) TMS91934, or (c) TMS82/00661. No additional food was provided. Leaf discs were excised from clean leaves of each cultivar and served both as substrate and food source for *T. aripo*. Control treatments consisted of individuals maintained on parafilm alone or parafilm supplied with water. Leaf discs were replaced as soon as deterioration was observed.

 ISSN: 1857-7881 (Print) e - ISSN 1857-7431

Experimental units were examined daily to record the development, and observations were continued until natural death in order to determine immature longevity.

Oviposition and adult survival on exudates of the three cassava cultivars

Approximately 200 mated females were selected from the culture and confined in the rearing arena for 24 h. After females were removed, newly laid eggs were reared until adulthood. Newly emerged females were then isolated and transferred individually into experimental units provisioned with the respective cassava exudates. For insemination, a single male was introduced into each unit for 24 h. Thereafter, experimental units were monitored daily to record oviposition and female survival. Oviposition was recorded for 10 consecutive days, while female survival was monitored for up to 20 days.

Adult survival on combined leaf discs and exudates of each cassava cultivar

In a separate experiment, females were maintained simultaneously on leaf discs and exudates of each cassava cultivar, following the same procedure as described above, and their survival was monitored daily for 20 days.

Adult longevity on leaf discs of the three cassava cultivars

To determine adult longevity on leaves, newly emerged females were individually placed on clean leaf discs excised from each cassava cultivar (TME1, TMS91934, and TMS82/00661). Leaf discs were replaced every 24–72 h to ensure freshness. Each experimental unit was examined daily until the female's natural death, and longevity was recorded.

Biochemical analysis of exudates and leaves from the three cassava cultivars

Biochemical analyses were conducted at the Biochemistry Laboratory of IITA, Ibadan. Exudates were collected from clean potted cassava plants grown in a greenhouse. Collections were made in the early morning (06:00–07:00 h) using sterile pipettes and transferred into 1-ml hermetic plastic tubes. Each tube was filled with at least 0.5 ml of exudate. Exudates were analyzed for sugar and amino acids, and cyanide.

For the analysis of cyanide in the leaves, 1g of clean leaves collected from each cultivar was introduced in a 15 ml plastic tube containing 10 ml of 1 M H_2SO_4 solution. Five tubes (5 replicates) were set up for each cultivar.

Statistical analysis

Differences among cassava cultivars in developmental time, fecundity, and longevity of *T. aripo* were tested using a single-factor analysis of variance (ANOVA) within the General Linear Model framework, followed by Student–Newman–Keuls (SNK) multiple range tests to separate means. The same

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approach was applied to compare sugar and amino acid concentrations in exudates, as well as cyanogenic glycoside concentrations in leaves of the three cassava cultivars. A chi-square test was used to assess the effect of treatment on juvenile survival (proportions of individuals reaching adulthood) and adult female survival (proportions of females surviving until the end of othe bservation period). All analyses were performed using SAS software (SAS Institute, 2005).

Results

Development of T. aripo on the exudates and leaves of the three cassava cultivars

T. aripo completed its development on exudates of all three cassava cultivars, but developmental rates differed significantly among cultivars. Development was fastest on exudate from TMS82/00661 (6.8 days), intermediate on TMS91934 (7.9 days), and slowest on TME1 (8.2 days), with no significant difference between the latter two. In all cases, development on exudates was significantly longer than on the prey *M. tanajoa* (5.2 days) (Table 1). Survival to adulthood was highest on TMS82/00661 exudate (68.2%), followed by TMS91934 (56.5%) and TME1 (53.8%). In contrast, *T. aripo* failed to complete development on cassava leaf discs, reaching the deutonymph stage. On parafilm and parafilm + water controls, development was even more limited, with individuals failing to progress beyond the larval stage (Table 1).

Juvenile and adult longevity on leaves of the three cassava cultivars

Juvenile longevity on leaf discs was significantly influenced by cassava cultivar ($F_{2,183.6} = 6.78$, $P < 0.002$), and a similar effect was observed for adult longevity ($F_{2,71.9} = 9.69$, $P < 0.0003$). Juveniles maintained on leaf discs of cultivar TME1 survived slightly longer (4.3 days) than those reared on leaf discs of TMS91934 (3.2 days) and TMS82/00661 (2.9 days) (Figure 1B). Similarly, adult females maintained on leaf discs of TME1 lived somewhat longer (3.5 days) compared to those on TMS91934 (2.57 days) and TMS92/00661 (2.10 days) (Figure 1A).

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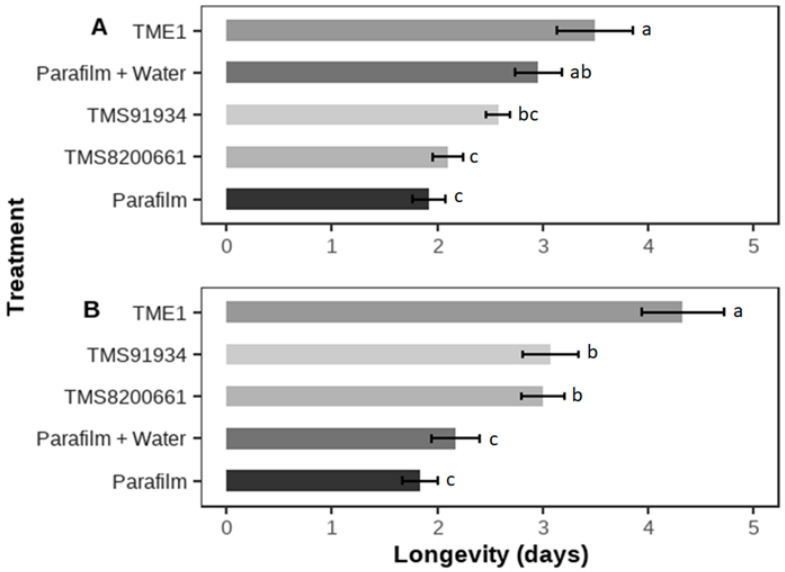

Figure 1: Juvenile (B) and adult (A) longevity on leaf discs of three cassava cultivrars; TME1 = low-cyanide cultivar; TMS91934 = moderate-cyanide cultivar; TMS82/00661 = high-cyanide cultivar

Oviposition and adult survivorship on exudates of the three cassava cultivars

None of the cassava exudates tested supported substantial oviposition of *T. aripo*. After 7 days, the mean total number of eggs per female was 0.27, 0.17, and 0.00 on exudates of TMS82/00661, TMS91934, and TME1, respectively (laid in the first two-day observation), compared with 8.5 eggs per female on the prey (CGM) (Table 2; Figure 2A).

Adult survival on exudates differed significantly among cultivars (df = 2; χ^2 = 7.38; *P* = 0.0241), being highest on exudates of TMS82/00661 (55.5%) but similar on TME1 (35.3%) and TMS91934 (38.8%). In contrast, when provided with prey (*M. tanajoa*), only 22.2% of females survived up to 20 days (Table 2; Fig. 2A). A similar pattern was observed (df = 2; χ^2 = 6.54; *P = 0.0379*) when females were maintained on both leaf discs and exudates of each cultivar: survival was greater on TMS82/00661 (47.0%) compared with TMS91934 (25.0%) and TME1 (18.7%) (Table 2; Figure 2B).

Composition of the exudates

No cyanide was detected in exudates of any of the three cassava cultivars. However, sugar concentration was significantly higher in exudates of TMS82/00661 (1491.8 g/ml) compared with TME1 (737.9 g/ml) and TMS91934 (671.1 g/ml) (Table 3). In contrast, amino acid concentrations did not differ significantly among cultivars, with values of 171.4 ppm, 171.3 ppm, and 177.6 ppm for TMS82/00661, TME1, and TMS91934, respectively (Table 3).

 ISSN: 1857-7881 (Print) e - ISSN 1857-7431

Table 1: Development of *Typhlodromalus aripo* on the exudates and leaf discs of three cassava cultivars of different cyanogenic potentials

	N	Stage reached	Egg (days)	Larva (days)	Protonymph (days)	Deutonymph (days)	Egg to Adult (days)	Survival to Adult (%)
Exudates								
TME1	30	Adult	1.71 ± 0.12 a	1.50 ± 0.14 a	1.93 ± 0.19 a	3.00 ± 0.33 a	7.93 ± 0.51 ab	53.84
TMS91934	30	Adult	1.84 ± 0.10 a	1.31 ± 0.13 a	2.07 ± 0.13 a	2.92 ± 0.26 a	8.23 ± 0.49 a	56.52
TMS82/00661	30	Adult	1.73 ± 0.11 a	1.27 ± 0.12 a	1.80 ± 0.10 ab	2.06 ± 0.24 b	6.80 ± 0.26 b	68.20
Prey (M. tanajoa)	30	Adult	1.54 ± 0.10 a	1.25 ± 0.09 a	1.41 ± 0.12 b	1.04 ± 0.04 c	5.21 ± 0.14 c	82.75
Leaf Discs								
TME1	30	Deutonymph	-	-	-	-	-	-
TMS91934	30	Deutonymph	-	-	-	-	-	-
TMS82/00661	30	Deutonymph	-	-	-	-	-	-
Parafilm + Water	30	Larva	-	-	-	-	-	-
Parafilm	30	Larva	-	-	-	-	-	-

Means followed by the same letter in each column are not significantly different (SNK; P > 0.05); TME1, low-cyanide cultivar; TMS91934, moderate-cyanide cultivar; TMS82/00661, high-cyanide cultivar

Table 2: Mean fecundity (±SE) over 7 days, and survival over 20 days of female *T. aripo* reared on exudates alone or combination leaf+exudate of three cassava cultivars of different cyanogenic potentials

	N	Fecundity	Survival (%) Exudates	Leaf Discs + Exudates
TME1	20	0 b	33.3	25.0
TMS91934	20	0.17 ± 0.1 b	38.8	18.7
TMS82/0661	20	0.27 ± 0.1 b	53.3	47.0
M. tanajoa (prey)	20	8.50 ± 0.5 a	22.2	-

N = number of females; means followed by the same letter in each column are not significantly different (SNK, P > 0.05)

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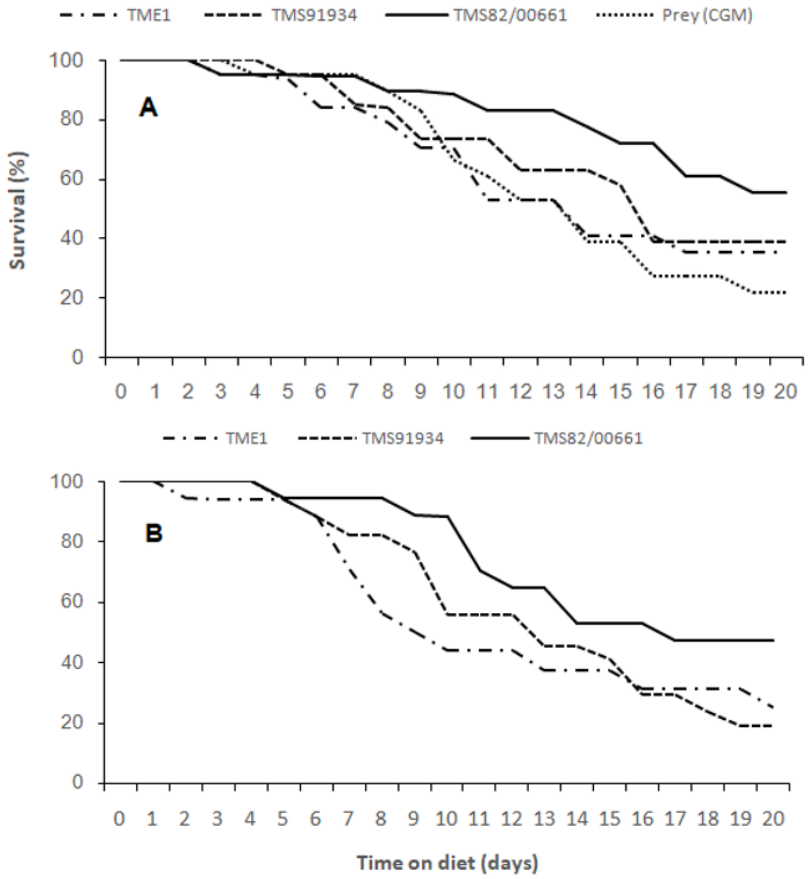

Figure 2: Survivorship of adult females on exudates alone (A) or on combination of 'leaf +exudate' of three cassava cultivars. TME1, low-cyanide cultivar; TMS91934; moderate cyanide cultivar; TMS82/00661, high-cyanide cultivar

Table 3: Determined concentrations of amino acids and sugar in the exudates, and of cyanide in the exudates and leaves of three cassava cultivars

	HCN (mg/100g)	Sugar (mg/ml)	Amino acids (ppm)
Exudates			
TME1	0	737.9 ± 9.8 b	173.1 ± 1.8 a
TMS91934	0	671.7 ± 10.9 b	177.6 ± 3.8 a
TMS82/00661	0	1491.8 ± 16.7 a	171.4 ± 2.1 a
Leaves			
TME1	8.25 ± 1.65 c		
TMS91934	18.03 ± 1.93 b		
TMS82/00661	27.13 ± 4.06 a		

Means followed by the same letter in each column are not significantly different (SNK test, $P > 0.05$). TME1, low-cyanide cultivar; TMS91934; moderate-cyanide cultivar; TMS82/00661, high-cyanide cultivar

 ISSN: 1857-7881 (Print) e - ISSN 1857-7431

Discussion

The role of plant-derived food supplements in plant–herbivore–predator interactions is central both to basic ecology and to applied biological control. In this study, we evaluated how leaf exudates and leaves from three cassava cultivars differing in cyanogenic potential affected the development, reproduction, and survival of *T. aripo*, an important predator of the cassava green mite (*M. tanajoa*).

Our results demonstrate that *T. aripo* successfully completed development on exudates from all three cassava cultivars. This is consistent with the biochemical analyses, which revealed the absence of cyanide in cassava exudates, corroborating previous findings that cassava exudates are free of cyanide (Pereira and Splittstoesser, 1987). Of particular interest were the cultivar-specific differences in developmental time. Exudate from the high-cyanide cultivar TMS82/00661 supported the fastest development and highest juvenile survival. Because amino acid concentrations did not differ significantly among cultivars, these differences are likely linked to the higher sugar content in TMS82/00661 exudate. Comparable effects of sugars on phytoseiid development and survival have been reported: for example, *Euseius hibisci* developed faster when honeydew of *Planococcus citri* was included in its diet (McMurtry and Scriven, 1964). However, other studies have shown that sugar alone is not always sufficient to sustain development beyond immature stages (El-Banhawy, 1975; Ferragut et al., 1987; James, 1989).

Although amino acids were detected in the exudates of all three cultivars, none of the exudates supported sustained oviposition in *T. aripo*. This agrees with previous studies showing that cassava exudates are not suitable for the reproduction of phytoseiids (Bakker and Klein, 1990; Toko et al., 1994). The brief oviposition observed may reflect residual effects of previous feeding, suggesting that either amino acid concentrations were too low or that specific amino acids required for oogenesis were absent. In contrast, adult survival was positively affected by exudate quality. The highest adult survival was again observed on TMS82/00661, supporting the hypothesis that sugar content is the main driver of prolonged survival, as sugars, sucrose, honey, and honeydew are known to extend phytoseiid longevity (Chant and Fleschner, 1960; McMurtry and Scriven, 1966; Ferragut et al., 1987; James, 1989). Semi-field studies have also shown that sugar-rich food sources, such as honey applied to cassava leaves, enhance predator survival and reduce dispersal (Bakker and Klein, 1992).

Juvenile and adult longevity on cassava leaf discs also varied among cultivars, possibly due to differences in cyanogenic potential. Enzymatic hydrolysis during tissue disruption can release hydrogen cyanide, which is toxic. Feeding activity along the cut edges of leaf discs may have exposed *T. aripo* to variable cyanide levels among cultivars. Previous work has shown

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that *T. aripo* can survive by feeding on cassava leaves in the absence of prey (Magalhães and Bakker, 2002, Gnanvossou et al., 2005). However, survival on combined "leaf discs + exudate" treatments was similar to survival on exudates alone, suggesting that in the presence of exudates, direct leaf feeding is unlikely to be significant.

From an applied perspective, our results confirm that cassava exudates represent an important alternative food source for *T. aripo* during periods of prey scarcity, but their value is strongly cultivar-dependent. Exudates rich in sugars, such as those of TMS82/00661, enhance predator survival and development, which may contribute to greater persistence and effectiveness of *T. aripo* in the field. In contrast, leaf feeding by the predator appears to have limited ecological relevance.

In conclusion, differences in cyanogenic potential among cassava cultivars do not constrain the value of cassava exudates as supplemental food for *T. aripo*. Instead, sugar richness of exudates is the key factor influencing predator performance. These findings reinforce the importance of considering cultivar choice in integrated pest management programs, as cultivars that produce higher-quality exudates may enhance the efficacy of *T. aripo* as a biological control agent of cassava green mite.

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