

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

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Doi: 10.19044/esipreprint.9.2025.p649

Approved: 24 September 2025

Posted: 26 September 2025

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OPEN ACCESS

Cite As:

Sourassou, N.F., Agboka, K., Negloh, K., Hanna, R. & Tchabi, A. (2025). *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*. ESI Preprints. <https://doi.org/10.19044/esipreprint.9.2025.p649>

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* 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 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; Bakker and Klein, 1992; Overmeer, 1985; Coll and Guershon, 2002; Nomikou et al., 2010; McMurtry et al., 2013; Konstantinos Samaras, 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 (Magalhães and Bakker, 2002; Toko et al., 1994). Cassava is also a major cyanogenic food crop (Cooke and Coursey, 1981). Cyanogenic glycosides are present in both leaves and roots,

with concentrations in leaves generally preceding those in roots (Cook and De La Cruz, 1982). Upon hydrolysis, these compounds release hydrogen cyanide, which is well known for its toxicity to arthropods (Houk et al., 1989; Hansen et al., 1991).

The predatory mite *Typhlodromalus aripo* DeLeon is an effective biological control agent of the cassava green mite (*Mononychellus tanajoa* Bondar), a major pest of cassava in Sub-Saharan Africa (Yaninek and Hanna, 2005). Numerous ecological studies have examined 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 leaves (Bakker and Klein, 1992; Magalhães and Bakker, 2002; Gnanvossou et al., 2005). However, cassava cultivars vary considerably in their cyanogenic glycoside content, and it remains unclear whether feeding on exudates and leaves from high cyanogenic potential (CNP) cultivars adversely affects 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 from three cassava cultivars differing in cyanogenic potential (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, Benin station, at 25±1°C, 70-90% RH, and under a 12h:12h light-dark cycle. The rearing technique followed Megévand et al. (1993). Cassava leaf petioles infested with *M. tanajoa* were introduced into vials (Ø = 1 cm L = 3 cm) containing water and sealed with parafilm. The vials were placed on a black PVC tile (25 x 25 cm) resting on a foam pad (29 x 29 x 3.5 cm) inside a plastic tray (37 x 37 x 56 cm) filled with water. Absorbent paper bands were stretched smoothly along the edges of the tile, to supply water to the mites, prevent them from escaping, and avoid the risk of contamination by other arthropods.

Cassava cultivars and exudate production

The three cultivars (TME1, TMS91934, and TMS82/00661) used in the study were obtained from the Plant Breeding Section of IITA-Ibadan station. The cultivar AGRIC used in the exudate experiments was obtained from the IITA-Benin fields. All cultivars were grown in a greenhouse under

a temperature range between 29–32 °C and a relative humidity (RH) of 65–72% respectively. Approximately 30 cuttings (\approx 20 cm each) of each cultivar were individually planted in plastic pots (\approx 14 cm in diameter at the base and 18 cm in height) filled with about 40 kg of topsoil collected from the IITA campus field. The pots were placed on an iron bench (350 x 180 x 76 cm; L x W x H), arranged with 65 cm spacing. Planting was carried out four weeks prior to the start of the experiments. Exudates were collected early in the morning (06:00-07:00 h) and used fresh in the experiments. Excess exudate was stored 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 $25\pm 1^\circ\text{C}$, 70-90% RH, and under a 112h:12h light-dark cycle. Experimental units consisted of cassava leaf discs (2.5 cm in diameter) fitted to the bottom of Petri dishes of the same size. Two opposite holes (2 mm in diameter) were made in the sides of the dishes and covered with fine nylon mesh to allow aeration. The leaf discs were placed on a layer of wet agar-agar solution within the dishes and were replaced as needed.

Development and survival on exudates of the three cassava cultivars

Approximately 300 mated females from the stock culture 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 provisioned with exudate 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, and fresh exudate was supplied daily in sufficient quantity. Control treatment consisted of units provisioned with *M. tanajoa* (the prey). Experimental units were examined daily to record the developmental stage, 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. No additional food was provided. Leaf discs excised from clean leaves of each cultivar served both as substrate and food source for *T. aripo*. Control treatments consisted of individuals maintained either on parafilm

alone or on parafilm supplied with water. Leaf discs were replaced as soon as deterioration was observed. Experimental units were examined daily to record the development, and observations 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 removal of the females, the newly laid eggs were reared until adulthood. Newly emerged females were then isolated and transferred individually to experimental units provisioned with exudates from the respective cassava. 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 assessed 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 the exudate of each cassava cultivar, following the procedure described above. Their survival was monitored 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 as soon as deterioration was observed. 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 performed early in the morning (06:00–07:00 h) using sterile pipettes and transferred into 1-ml hermetic plastic tubes, each containing at least 0.5 ml of exudate. Exudates were analyzed for sugar and amino acids, and cyanide content.

For the analysis of cyanide in the leaves, 1g of clean leaf material from each cultivar was placed in a 15-ml plastic tube containing 10 ml of 1 M H₂SO₄ solution. Five tubes (5 replicates) were prepared 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 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. Chi-square test was applied to assess the effect of treatment on juvenile survival (proportions of individuals reaching adulthood) and adult females' survival (proportions of females surviving until the end of the observation 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 from 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 only 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).

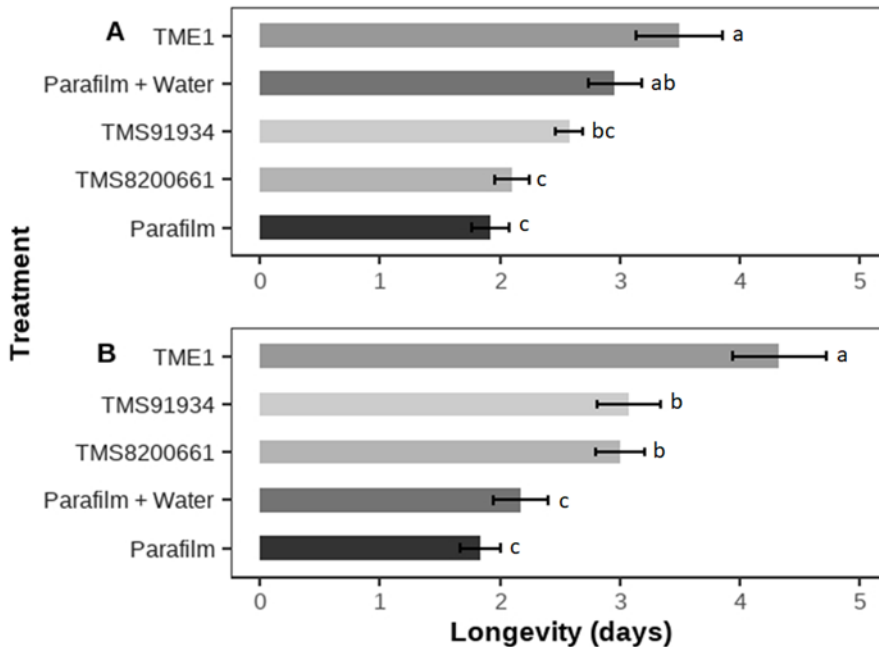


Figure 1: Juvenile (B) and adult (A) longevity on leaf discs of three cassava cultivars; TME1 = low-cyanide cultivar; TMS91934 = moderate-cyanide cultivar; TMS82/00661 = high-cyanide cultivar

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 (with eggs laid during the first two-day observation), compared with 8.5 eggs per female on the prey (*M. tanajoa*) (Table 2; Figure 2A).

Adult survival on exudates differed significantly among cultivars ($df = 2$; $\chi^2 = 7.38$; $P = 0.0241$), being highest on TMS82/00661 exudate (55.5%) and 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 ($df = 2$; $\chi^2 = 6.54$; $P = 0.0379$) 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 the exudates of any of the three cassava cultivars. However, sugar concentration was significantly higher in exudate 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).

Discussion

Plant-derived food supplements play a central role in plant–herbivore–predator interactions, both in basic ecology and in applied biological control. In this study, we evaluated how exudate and leaves from three cassava cultivars differing in cyanogenic potential influenced the development, reproduction, and survival of *T. aripo*, a key biological control agent 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 (Splittstoesser and Pereira, 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 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.

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

Treatment Substrate	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 (<i>M. tanajoa</i>)	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 (\pm 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

Treatment	N	Fecundity	Survival Exudates (%)	Survival 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
<i>M. tanajoa</i> (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, $P > 0.05$).

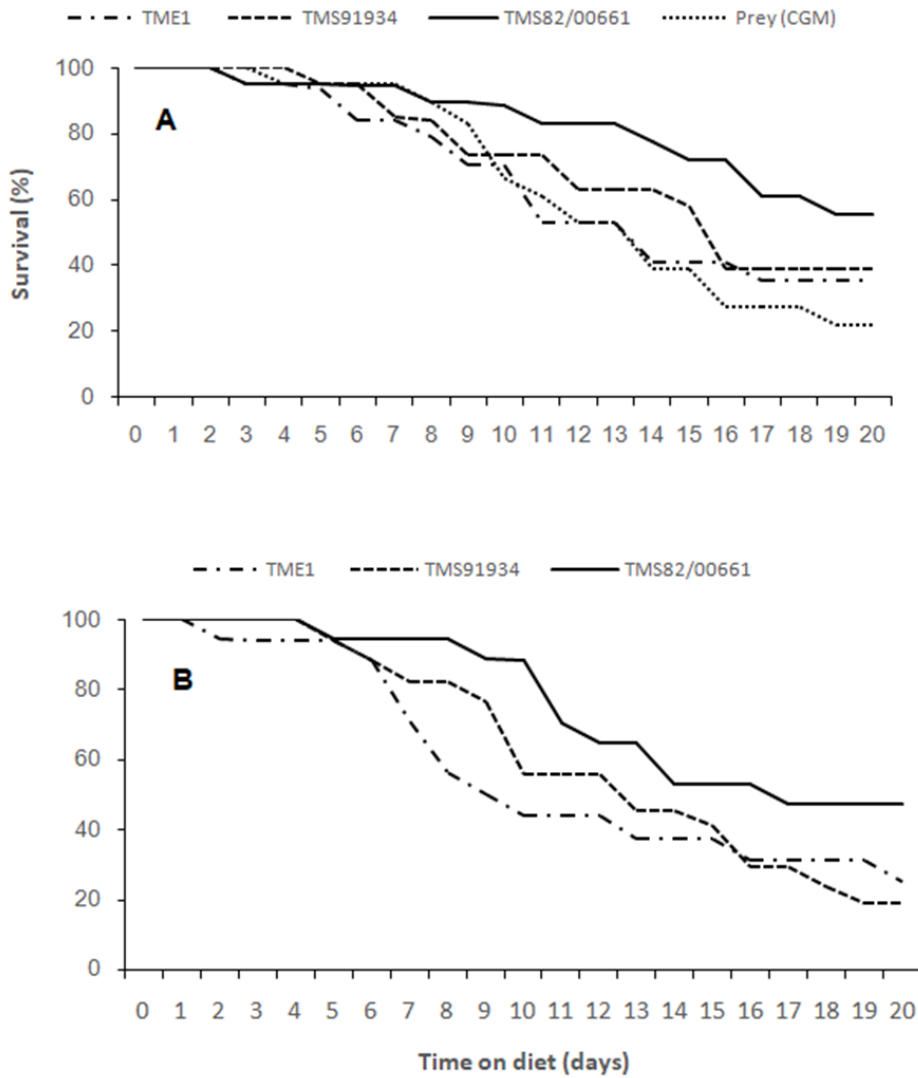


Figure 2: Survivorship of adult females on exudates alone (A) or on combination of ‘leaf +exudate’ of three cassava cultivars. TME1, low-cyanide cultivar; TMS91934; moderate-cyanide cultivar; TMS82/00661, high-cyanide cultivar

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

Cultivar	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

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, the 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.

Acknowledgments: We thank R. Houndafoche, P. Sovimi, for their assistance in maintaining the predator colonies and conducting experiments. This research was supported by the International Institute of Tropical Agriculture (IITA).

Conflict of Interest: The authors reported no conflict of interest.

Data Availability: All data are included in the content of the paper.

Funding Statement: The authors did not obtain any funding for this research.

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