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Tomato leaf miner: oviposition pattern and larval survival on three tomato cultivars

Minador de la hoja del tomate: patrón de oviposición y supervivencia larval en tres cultivares de tomate

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ABSTRACT: Understanding the behaviour and biological parameters of insect pests helps enhance the benefits of resistant cultivars within integrate management programs. In semi-controlled conditions, the non-preference effect measured by oviposition pattern, as well as antibiosis effect measured by larval survival of the pest *Tuta absoluta* (Meyrick) were assessed on three tomato cultivars, 'Vyta' from Cuba and 'Santa Clara' and 'TOM 687' from Brazil. Adult females laid eggs on plants during 96 h, and the larvae were allowed to feed on the tomato leaves for ten days. The number of eggs and active larvae on each plant stratum (i.e., upper, middle, and lower) were counted in the treatments with combined or non-combined tomato cultivars. Based on results, *T. absoluta* preferred the upper and middle strata of the plants to lay the highest number of eggs, mainly when the cultivars were combined. Also, higher numbers of active larvae used those strata for feeding. Cuban cultivar 'Vyta' had a similar response to Brazilian cultivar 'TOM 687' in relation to the parameters evaluated. However, this cultivar was less preferred by TLM females for oviposition when it was in combination with 'Santa Clara' and 'TOM 687'. Cultivar combination influenced only 'TOM 687' and 'Santa Clara', which suggests that 'Vyta' has characteristics that confer it some level of resistance against this important pest. This insect behaviour is an indicator to be taken into account when sampling *T. absoluta*. Tomato cultivar 'Vyta' could be considered an alternative to mitigate the impact of *T. absoluta* damages in Cuba.

Keywords: Insect behaviour, Integrated pest management, plant resistance, *Tuta absoluta*, tomato cultivars.

RESUMEN: Entender el comportamiento y los parámetros biológicos de insectos plagas ayuda a mejorar los beneficios de cultivares resistentes en programas de manejo integrado. En condiciones semicontroladas, se evaluó el efecto de no preferencia medido por el patrón de oviposición y el efecto de antibiosis medido por la supervivencia larval de *Tuta absoluta* (Meyrick) en tres cultivares de tomate, 'Vyta' de Cuba y 'Santa Clara' y 'TOM 687' de Brasil. Durante 96 h las hembras ovipositaron sobre las plantas y las larvas se alimentaron de las hojas, otros diez días. Se contó el número de huevos y larvas activas en los estratos superior, medio e inferior de las plantas para cultivares combinados y no combinados. *T. absoluta* coloca el mayor número de huevos en los estratos superior y medio de las plantas, principalmente, cuando están combinados. El mayor número de larvas activas utilizan esos estratos para alimentarse. El cultivar cubano 'Vyta' tuvo una respuesta similar al cultivar brasileño 'TOM 687' en relación con los parámetros evaluados. Sin embargo, fue menos preferido por las hembras del insecto para la oviposición en las combinaciones con 'Santa Clara' y 'TOM 687'. La combinación de cultivares sólo tuvo influencia para 'TOM 687' y 'Santa Clara', lo que sugiere que 'Vyta' tiene características que le confieren algún nivel de resistencia contra *T. absoluta*. Este comportamiento del insecto constituye un indicador a considerar en el método de muestreo. El cultivar 'Vyta' podría considerarse como una alternativa para mitigar el impacto de los daños de *T. absoluta,* en Cuba.

Palabras clave: Comportamiento insectil, manejo integrado de plagas, plantas resistentes, *Tuta absoluta*, cultivares de tomate.

INTRODUCTION

Tomato leaf miner (*Tuta absoluta* (Meyrick) (TLM)) is a devastating pest that can decrease fruit quality and cause up to 100% losses in Solanaceous crops in absence of control methods (1, 2). The pest originated in South America and, after a rapid invasion, became a major threat to tomato production in Europe, Africa and Asia (3, 2). Its presence was reported in Panama and Costa Rica (4), and Caribbean countries such as Cuba and Dominican Republic are at high risk of being invaded, due to their proximity to infested areas, mainly after its first report in Haiti in 2019 (5).

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In countries where the pest is present, the adopted integrated pest management (IPM) includes biological control augmentative or conservative, sex pheromone traps and use of selective insecticides (2, 6). However, the indiscriminate use of chemical pesticides may fail to successfully control the pest by inducing insect resistance (2) and reducing the populations of natural enemies associated with the crops, and it also causes higher levels of residues on harvested tomato fruits (1). Due to this problem, the development of tomato cultivars resistant to TLM was promoted in South America (7).

Solanum species such as *S. peruvianum, S. hirsutum, S. galapagense, S. cheesmaniae* and *S. pimpinellifolium*, among others, constitute a genetic background for breeding resistant tomato cultivars to TLM and other pests (8, 9, 10). Currently, the most used *Solanum* species to develop resistant tomato cultivars are *S. pennellii* Correll and *S. habrochaites* Knapp & Spooner (11). Higher plants are capable to synthetize secondary metabolites to induce toxic metabolic effects, or of non-preference effects, to different harmful organisms (12). These compounds (toxic or repellent chemical substances) are synthetized on specialized plant structures (e.g., glandular trichomes in tomato) and help protect them against several arthropod pests (13). The mechanisms of resistance detected in *Solanum* species are antixenosis (non-preference effects) and antibiosis (chemical compounds effects) associated with glandular or non-glandular trichomes (14). These mechanisms reduce egg laying (i.e., female fertility) and larval feeding on TLM (2, 15) and increase adult longevity of the adults by the effect of methyl ketone 2-tridecanone present in the glandular trichomes (15).

The tomato cultivars may confer resistance against TLM by affecting its development time, survival and reproduction, among other biological parameters (15). For example, longer duration of larval and pupal stages, reduction of larval viability lower pupal weight and lower female fecundity of females in different lineages of cultivars belonging to *Solanum lycopersicon* L. have been found to indicate resistance to TLM under laboratory conditions (16, 17).

Moreover, the acyl sugar (AS) content present in tomato leaves is another factor related to resistance to arthropods. High AS contents confer resistance of cultivars to TLM and other pests. The use of hybrid lines obtained from at least one parent with high content of AS is enough to obtain hybrids resistant to a broad spectrum of crop pests (11). Another defense mechanism to TLM documented in tomato plants is the induced resistance generated by the larval feeding, which activates the metabolic pathway of jasmonic acid (JA) and, in turn, could make tomato less attractive to other pests associated with the crop and TLM more attractive to their natural enemies (2).

In summary, knowledge about tomato genotypes and their resistance properties against TLM is a strength to be used in integrated pest management (IPM) programs (6). For areas at risk of being invaded by TLM, this advanced knowledge is a valuable element in an impact mitigation program. In the study, three tomato cultivars were included, two from Brazil (susceptible *Solanum lycopersicum* cv. Santa Clara) (18, 17), TOM 687 (an improved line obtained from the original cross *S. lycopersicum*, with low AS content and *S. pennellii* LA-716, a feral accession with high AS content, and resistant to TLM) (19) and the Cuban cultivar “Vyta” (obtained from the cross between *S. lycopersicum* and *S. chilense*) (20). In Cuba, Vyta is known for its resistance to TYLCV (Tomato yellow leaf curl virus) (21). This genotype is used as a carrier of the Ty-1 gene to new commercial lines and is included within the official list of Cuban cultivars (22, 23). Also, biological parameters of TLM on Vyta, such as survival of larvae and adults, viability of pupae, total fecundity of females and sex ratio, were affected under laboratory conditions (17). Taking into account these arguments, the aim of this study was to assess i) the non-preference effect measured by oviposition pattern of TLM females and ii) the antibiosis effect measured by larval survival on three tomato cultivars under semi-controlled conditions.

MATERIALS AND METHODS

The study was carried out at the Laboratory of Biological Control, Department of Entomology, and in a greenhouse, Department of Agriculture, Universidade Federal de Lavras (UFLA), Lavras, Minas Gerais, Brazil.

Plants obtaining

Plants of three tomato cultivars (Vyta, Santa Clara and TOM 687) were used in TLM resistance trials. Seedlings and plants were obtained according to the methodology described by Duarte *et al.* (17). The plants were subjected to 23±7,6°C of temperature, 64±15,4 % of RH and a natural photoperiod in a greenhouse with semi-controlled conditions. The temperature and RH values were recorded with a digital thermo-hygrograph Easylog USB®.

Insect rearing

Tomato plants infested with eggs, larvae, and pupae of TLM were collected in areas of the campus of the Federal University of Lavras (Minas Gerais, Brazil), located at 21°14'S 45°00'W and 918 m a.s.l. Once in the laboratory, the emerged adults were released on tomato plants inside cages (90 cm x 70 cm x 70 cm) using the cultivar Santa Clara for rearing establishment of TLM at 25±2°C, 60±10 % RH., and a 12h photoperiod. New healthy tomato plants were regularly introduced into the cages to maintain a stock colony and feed the TLM larvae. For the experiments, individuals from the second generation reared on Vyta and TOM 687 cultivars were also used.

Experimental design

Adult females (72h old) were transferred from the on-plant rearing to glass tubes (5ml) with the help of a compressor-vacuum machine (FANEM®), used for sucking small insects. The tubes were sealed with PVC® paper to avoid escape of insects. In parallel, 30-day-old tomato plants were placed in mesh cages with wooden frames (70 x 70 x 110 cm). TLM individuals were released inside the cages and, after 96h (i.e., four days), all adult females were removed with a manual vacuum cleaner. The number of eggs laid by females of TLM on leaves, stems, flowers and fruits was counted per plant. Similarly, after ten days, the number of living larvae on plants was assessed. Assessments were made separately on 10-15 cm of three plant strata, namely upper, middle and lower. The methodology described by Pratissoli *et al.* (24) was used as a reference. These authors assessed oviposition of different densities of TLM adults on *S. lycopersicum* var. Santa Cruz. However, we assessed oviposition and larval survival of a single adult density of TLM per treatment on different tomato cultivars.

The following experimental treatments were set up: (1) two tomato plants (Santa Clara cultivar) + 40 female individuals TLM, (2) two tomato plants (TOM 687 cultivar) + 40 female individuals TLM, (3) two tomato plants (Vyta cultivar) + 40 female individuals TLM and (4) three tomato plants (1 Santa Clara, 1 TOM 687 and 1 Vyta) + 60 individuals TLM. Fifteen replications per treatment were considered.

The Shapiro-Wilk test was used to explore the distribution data in all the experiments. Generalized Lineal Models (GLMs) with negative binomial distribution and log link function were used to analyse the effect of the fixed plant strata, tomato cultivar factors and their interactions with the number of eggs laid by TLM and number of active larvae for each experiment separately (i. e., with choice and without choice). To know the effect of tomato cultivars on the number of eggs and active larvae per plant strata, the variable 'cultivar' was stratified using GLMs with negative binomial distribution and log link function, followed by Tukey post-hoc tests adjusted for a family of 3 estimates. All statistical analyses were performed in R version 4.0.2 (25).

RESULTS AND DISCUSSION

For treatments without choice, the average number of eggs laid by TLM was significantly different among plant strata (X^2=27,60, df=2, p<0,0001) and cultivars (X^2=8,40, df=2, p=0,02). TLM female preferred to lay the higher quantity of eggs on the upper part of the plants, followed by the middle part and a lesser quantity of females on the lower part in Santa Clara cultivar (X^2=32,47, df=2, p<0,0001). However, oviposition pattern of TLM did not show preference for plant strata in the other two cultivars (for TOM 687: X^2=3,52, df=2, p<0,17; for Vyta: X^2=3,90, df=2, p<0,14) (Fig. 1). The pattern of eggs in treatments with choice differed significantly only for plant strata (X^2=20,25, df=2, p<0,0001). TLM females preferred the middle and upper strata of the plants to lay the higher number of eggs for all cultivars without significant differences (for Vyta: X^2= 27,87, df=2, p=0,06; for TOM 687: X^2= 20,15, df=2, p=0,11 and for Santa Clara: X^2= 19,02, df=2, p=0,60). The quantity of TLM eggs in the lower plant strata was significantly less than the quantity laid in the middle and upper plants strata , respectively (for Vyta: X^2= 27,87, df=2, p=0,0026, p<0,0001; for TOM 687: X^2= 20,15, df=2, p=0,014, p<0,0001 and for Santa Clara: X^2= 19,02, df=2, p=0,0004, p<0,0001) (Fig. 1).

The results of oviposition pattern of TLM females showed that the insect had a similar behaviour on Vyta and TOM 687 cultivars regarding the preference for the plant stratum to lay eggs. However, combining or not tomato cultivars influenced TLM preference. Females on non-combined cultivars (i. e., without choice) did not showed preference for any plant stratum, while on combined cultivars (i. e., with choice), they preferred the middle and upper part of the plants. However, the behaviour of TLM females on Santa Clara cultivar showed a different pattern and the cultivar combination also influenced the preference for oviposition. With non-combined cultivars (i. e., without choice), they showed clear preference for the upper plant stratum while with combined cultivars (i.e. with choice), no distinction was shown between the upper and middle strata.

Our findings agreed with Pratissoli *et al.* (24), who evaluated the oviposition preference for different densities of TLM on *S. lycopersicum* var. Santa Cruz and concluded that the pest prefered to lay the higher quantity of eggs in the upper plant stratum. However, this preference was evidenced only on Santa Clara cultivar offered individually. When the three cultivars were combined, the females preferred the upper plant stratum followed by the middle one .

TLM on Vyta and TOM 687 responded with less preference for oviposition when these cultivars were offered singly (Fig. 1 and Tab. 1). This suggests that antixenosis is the main mechanism of resistance involved. Such mechanism reduces the host properties of the plant and limits its use by insects for egg laying, feeding or shelter (26). Thomazini *et al.* (15) also attributes these mechanisms as being responsible for the egg-laying rate of TLM being lower on the feral accessions *S. peruvianum*

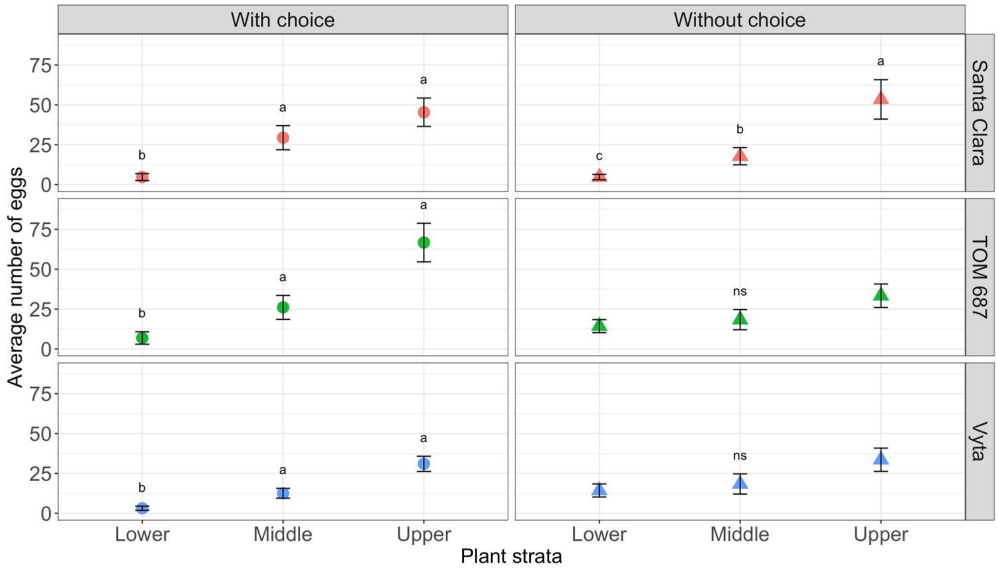

Figure 1. Oviposition pattern of TLM females on different tomato cultivars per plant strata in treatment with and without choice. *Different letters on bars indicate significant differences and bars followed by ns are not statistically significant (GLM binomial distribution and function log, followed by Tukey HSD post-hoc test: $P < 0{,}05$). /*Patrón de oviposición de las hembras de TLM en diferentes cultivares de tomate por estrato de la planta en tratamiento, con y sin elección. *Las letras distintas en las barras indican diferencias significativas y las barras seguidas de ns no son estadísticamente significativas (Distribución binomial GLM y función log, seguida de la prueba post-hoc HSD de Tukey: P < 0,05).*

Table 1. Total number of eggs and live larvae of TLM per tomato cultivar in experiments with and without choice./ Número total de huevos y larvas vivas de TLM por cultivar de tomate en experimentos con y sin elección.

Cultivars	Eggs				Larvae			
	With choice		Without choice		With choice		Without choice	
	Total	Sd	Total	Sd	Total	Sd	Total	Sd
Vyta	700	4,5	927	6,3	375	2,3	279	2,2
TOM 687	1495	10,6	924	5,3	320	2,1	249	1,4
Santa Clara	1188	8,0	1140	9,4	160	1,2	403	4,9

(PI 134417) and *S. hirsutum* f. *glabratum* (LA 444-1) than on the commercial tomato cultivars . Additionally, this low preference of the insect on Vyta was observed in laboratory conditions (17), and it could be associated with the repellent activity of the highly toxic volatile compounds, which could have inhibited oviposition by TLM females (27, 2). High concentrations of 2-tridecanona, zingiberene and amino-acids (allelochemicals) produced by glandular trichomes in tomato plants may play an important role in resistance to TLM (18, 26).

Moreover, TLM oviposition on hybrids from the pre-commercial cultivar TOM 687 with higher AS contents was lower than on lines such as TOM-650, TOM-694, TOM-699 and TOM-700 and the commercial varieties (Bravo, Bônus y Santa Clara), with lower AS (19), confirming resistance of TOM-687 and susceptibility of Santa Clara to TLM. However, both TOM-687 and Santa Clara were shown more preferred by TLM to lay eggs than Vyta, (except TOM-687 as a non-combined treatment) (Tab. 1).

The high number of TLM live larvae agreed with the oviposition pattern of the pest. For treatments without choice, the average number of active larvae was significantly different among plant strata (X^2=57.29, df=2, p<0.0001), cultivar (X^2=27.19, df=2, p<0.0001) and their interaction (X^2=29.52, df=2, p<0.0001). For TOM 687 cultivar, significant differences were between plant strata (X^2=95.53, df=2, p<0.0001). The highest quantity of live TLM larvae was found in the upper plant stratum (p=0.0001) followed by the middle one, (p<0.0001); the lowest amount of live larvae was in the lower plant stratum (p<0.0001). However, significant differences related to number of active larvae were not observed between plant strata in Vyta and Santa Clara cultivars after paired data analysis despite the slight or high statistical significance for them, in the global analysis (For Vyta: X^2=5.86, df=2, p=0.05; for Santa Clara: X^2=24.98, df=2. p<0.0001) (Fig. 2).

For treatment with choice, the average number of active larvae was significantly different among plant strata (X^2=13.69, df=2, p=0.001). For Vyta and TOM 687 cultivars, the highest numbers of active larvae were found in the upper and middle plant strata, significantly diffrering from the number of larvae present in the lower plant stratum, respectively (For Vyta: X^2=14.20, df=2, p=0.0004, p=0.0062; for TOM 687: X^2=20.63, df=2, p<0.0001, p=0.0026). For Santa Clara cultivar, significant differences were only observed between the number of active larvae in the upper and lower strata of the plants (X^2=10.15, df=2, p=0.0033) (Fig. 2).

Moreover, the similar response of TLM larvae survival in Vyta and in TOM 687 cultivar (Tab. 1) could be explained by the negative effect of AS compounds present on the leaves of the genotypes evaluated on increasing their resistance. Higher contents of AS act against *T. absoluta* through resistance mechanisms as antibiosis and antixenosis (10). However, despite the important determination of these mechanisms on the results, other elements could be involved. According to Vuceti *et al.* (28) and Isah (12), induction of volatile compounds or the immune response of the plants may modify insect behaviour. These authors' results confirmed that the chemical compounds released by healthy, damaged or insect-attacked plants can affect neighbouring plants and allow interactions that influence herbivores and natural enemies. The term "Allelobiosis" describes the links between allelopathy and insect behaviour (29).

Such arguments mentioned above may explain why Santa Clara in combination with other cultivars was less affected by TLM larvae and TOM 687 combined was more attractive for TLM females to lay eggs (Tab. 1). Also, Junior *et al.* (2012) found the influence of this factor in larval attraction when they assessed non-preference of TLM larvae for feeding on different substrates.

Different classes of volatile compounds suggest having a unique role in plant defence against herbivorous insects. However, each compound includes and establishes specific roles. Due to the low molecular weight, lipophilic nature and high vapour pressures at ordinary temperatures of monoterpenes and sesquiterpenes, they can transmit long-distance signals in the culture environment (30). However, not only secondary metabolite accumulation plays a role in plant defence, but also phytohormone signalling as salicylic acid (SA), jasmonic acid (JA), abscisic acid (ABA), and ethylene (ET) strongly contribute to the attraction or repellence of pests or natural enemies (13).

In our study, combination of tomato genotypes evokes contrary effects on TOM 687 and Santa Clara against TLM, because this combination modified their response, as it is observed in Tab. 1. However, these are the first results of a Cuban tomato cultivar against TLM and other studies are needed to characterize Vyta according to its AS contents or volatile compounds, which could explain the response of this cultivar against the pest. In this sense, practical implications should be evaluated since *S. lycopersicum* releases a diverse mixture of volatile compounds from its stem, leaves, flowers and fruits throughout its vegetative cycle (31). Other combinations of Cuban tomato varieties could be tested, including Vyta, to define the volatile profile of different parts of the plants in field conditions and that induced by the action of TLM since this mixture of volatiles could exert an impact on the insect (attraction or repellence), an effect that could be used as an alternative in this invasive pest management.

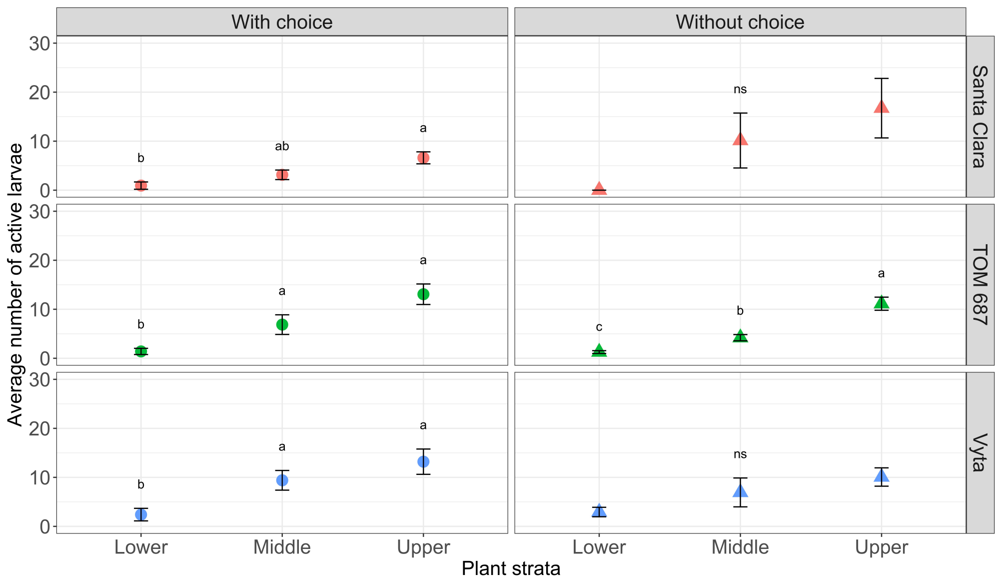

Figure 2. Larval survival of TLM on different tomato cultivars per plant stratum in treatment with and without choice. *Different letters on bars indicate significant differences and bars followed by ns are not statistically significant (GLM binomial distribution and function log, followed by Tukey HSD post-hoc test: *P* < 0,05)./ *Supervivencia de larvas de TLM en diferentes cultivares de tomate por estrato de la planta, en tratamientos con y sin elección. *Las letras distintas en las barras indican diferencias significativas y las barras seguidas de ns no son estadísticamente significativas (Distribución binomial GLM y función log, seguidas de la prueba post-hoc HSD de Tukey: P < 0,05).*

Based on our results, it can be concluded that the tomato leaf miner 'TLM' prefers to place the highest number of eggs on the upper and middle plant strata in the tomato cultivars assessed, mainly when they are combined. Also, the highest number of active larvae use these strata for feeding. This insect behaviour is an indicator to be considered in the sampling method for TLM. On the other hand, Vyta had a similar response to TOM 687 cultivar regarding the parameters evaluated. However, it was less preferred by TLM females for oviposition in combination with Santa Clara and TOM 687 cultivars. Combination of cultivars only influenced TOM 687 and Santa Clara, which suggests that Vyta has characteristics that confer it some level of resistance to this important pest. Our findings are very relevant for Cuban agriculture, as Vyta could be used as a first barrier to mitigate the impact of TLM damages, once the pest had invaded the country.

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