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Development of *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) in tomato genotypes

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Abstract

Tomato plants are the most widely cultivated fruit vegetables globally. The tomato leaf miner (*Tuta absoluta*) is the leading pest of this crop and can cause up to 100% loss of production. Therefore, the aim was to evaluate the development and resistance of antibiosis and non-preference types (antixenosis) for oviposition and feeding of *T. absoluta* in commercial tomato hybrids in choice and no-choice tests. For the experiments, an open-pollinated tomato cultivar was used as a control: 'Santa Clara' cultivar - susceptible - Italian type, along with eight commercial tomato hybrids were used: 'Compack' - salad type, 'Caniati' - Italian type, 'Grazianni' - Italian type, 'Sweet Heaven' - grape type, 'Cascade' - cherry type, 'Ellen' - salad type, 'Bento' - Italian type, and 'Dominador' - salad type, all having an indeterminate growth habit. According to the evaluated biological parameters (dendrogram and principal component analysis - PCA), the 'Sweet Heaven' hybrid showed a negative effect on the development of *T. absoluta*, with an increase in the duration of the larval, adult, and total phases, and low larval and total viability. The tomato hybrid 'Cascade' exhibited lower attractiveness for *T. absoluta* oviposition in no-choice tests. The tomato hybrids 'Sweet Heaven', 'Compack', and 'Cascade' showed a lower percentage of leaf area consumed. However, 'Dominador', 'Santa Clara', and 'Ellen' were the tomato genotypes that showed higher susceptibility to the development of *T. absoluta*, encompassing high larval, pupal, and total viability (larva-adult period). Concluding that the 'Sweet Heaven' hybrid negatively affected the development cycle of *T. absoluta*, while the 'Cascade' hybrid exhibited lower attractiveness for oviposition.

Keywords: antibiosis, antixenosis, plant resistance, *Solanum lycopersicum L.*, tomato leaf miner

Introduction

Tomato (*Solanum lycopersicum* L.), belonging to the Solanaceae family, is a highly consumed and cultivated fruit vegetable worldwide (Souza & Castillo, 2023). The tomato fruit has high levels of lycopene, β-carotene, and other biochemical attributes (Seabra Júnior et al., 2022; Dalbianco et al., 2023). In addition to their popularity as a culinary ingredient, tomatoes play a crucial role in the global economy due to their significant economic importance, which drives the expansion of production in various regions (Dalbianco et al., 2022; Souza & Castillo, 2023).

Tuta absoluta (Meyrick, 1917) (Lepidoptera: Gelechiidae), the tomato leaf miner, is the key pest of tomato plants, causing up to 100% losses in production and presenting alarming levels of infestation, both due to the damage caused and difficulty in control (Bacci et al., 2021).

In Brazil, *T. absoluta* is often controlled by applying multiple insecticides (Bacci et al., 2021; Silva et al., 2021). However, this approach is undesirable for either environmental or economic reasons. The repeated use of insecticides can negatively affect the natural enemies of pests, compromising the ecological balance of agroecosystems (Dominguez et al., 2016). In addition, there is a risk of selection for *T. absoluta* populations, making their control even more challenging (Silva et al., 2021).

Therefore, plant resistance to insects has emerged as an alternative for controlling this pest and can be employed in conjunction with other management strategies. This approach aims to reduce the population of undesirable insects by reducing their ability to repel or tolerate pests while minimizing the adverse effects of chemicals on the environment (Desneux et al., 2022). Therefore, understanding the potential sources

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of resistance in commercial tomato hybrids against *T. absoluta* is necessary.

Plants possess defense mechanisms that can influence insect behavior to protect themselves from attacks. These mechanisms involve synthesizing natural chemicals, also known as allelochemicals, that protect against various herbivores (Yang et al., 2020). These allelochemicals can exert toxic effects on insect metabolism (antibiosis) or act as deterrent agents (non-preference) (Silva et al., 2022). A plant exhibits non-preference resistance when it is less attractive to the insect to feed, lay eggs, or shelter than other plants under similar conditions. In contrast, antibiotic resistance occurs when plants contain substances harmful to insect development (Mani et al., 2022).

Several species of the *Solanum* genus exhibit both antibiosis and non-preference resistance, which are primarily related to the action of chemical substances present in the plant leaf trichomes (Dias et al., 2019).

Therefore, this study aimed to evaluate the development of and resistance to antibiosis, oviposition preference, and feeding preference in commercial tomato hybrids against *T. absoluta* using choice and no-choice tests.

Material and Methods

The bioassays were conducted in the laboratory of the Integrated Pest Management Research Group in Agriculture (AGRIMIP) at the Department of Plant Protection at São Paulo State University "Júlio de Mesquita Filho" (UNESP), located on the Botucatu Campus, São Paulo, Brazil (latitude 22°50'40.1'' S, longitude 48°26'02.5'' W), at an altitude of 804 m. The experiments were carried out in climate-controlled rooms at a temperature of 25 ± 2 °C, a photoperiod of 12 hours, and a relative humidity of 70 ± 10%.

For the experiments, an open-pollinated tomato cultivar was used as a control: 'Santa Clara' cultivar – susceptible - Italian type, along with eight tomato hybrids: 'Compack' – salad type, 'Caniati' - Italian type, 'Grazianni' - Italian type, 'Sweet Heaven' - grape type, 'Cascade' – cherry type, 'Ellen' – salad type, 'Bento' – Italian type, and 'Dominador' – salad type, all having an indeterminate growth habit and commonly used in commercial tomato crops, were used (supplementary material - **Table S1**). Seedlings were grown in pots (40 cm × 20 cm) in a greenhouse. Plants were used 60 days after emergence (Bottega et al., 2018).

The soil used for seedling cultivation was composed of 1 x 1 x 1 x 1 (fine sand × clay × organic fertilizer (bovine manure) x substrate (Carolina Soil)).

Table S1. Tomato genotypes used in this study (Italian, salad, cherry, and grapefruit types).

Genotypes	Type	Source	Record in MAPA[1]	Fruit size (g)	Days to harvest	Growth habit	Disease Resistance[2]
Compack	Hybrid (Salad)	Seminis Sementes LTDA	26851	220 to 250	75 to 80	Indeterminate	ToMV:0,2, TSWV, Fol:1,2, For, Va:1, Vd:1, Ma, Mi, Mj
Caniati	Hybrid (Italian)	Syngenta Seeds LTDA	40622	180	100 to 105	Indeterminate	Fol:1-2, Va, Vd, ToMV, Ss, TSWV, Ma, Mi, Mj
Grazianni	Hybrid (Italian)	Sakata Seed Sudamerica LTDA	05401	190	115	Indeterminate	Vd:1, Fol:1,2,3, ToMV, TSWV, ToSRV
Cascade	Hybrid (Cherry)	Feltrin Sementes LTDA	10079	12 to 15	90 to 100	Indeterminate	ToMV, Fol: 0,1,2
Ellen	Hybrid (Salad)	Feltrin Sementes LTDA	19530	200 to 260	100 to 115	Indeterminate	ToMV, TYLCV, V, F1, F2, N
Bento	Hybrid (Italian)	Feltrin Sementes LTDA	38745	160 to 180	90 to 100	Indeterminate	TSWV, Mi, TYLCV, ToMV, TaNV, V, Fol 1, 2
Dominador	Hybrid (Salad)	Agristar do Brasil LTDA	12142	230	120	Indeterminate	Fol:0,1, For, Ma, Mi, Mj, ToMV, TYLCV, Va, Vd
Sweet Heaven	Hybrid (Grape)	Sakata Seed Sudamerica LTDA	30818	15	120	Indeterminate	Fol:0,1, ToMV, Ss
Santa Clara	Variety (Italian)	Agristar do Brasil LTDA	03395	130 to 150	100 to 110	Indeterminate	Fol:1, Va, Vd

[1] Ministry of Agriculture, Livestock and Food Supply (MAPA) (https://sistemas.agricultura.gov.br/snpc/cultivarweb/cultivares_registradas.php).

[2] Fol (*Fusarium oxysporum f. sp. lycopersici*); N (*Meloidogyne* spp.); Ma (*Meloidogyne arenaria*); Mi (*Meloidogyne incognita*); Mj (*Meloidogyne javanica*); ToMV (Tomato mosaic virus); ToTV (Tomato torrado virus); TYLCV (Tomato yellow leaf curl virus); Ve (*Verticillium* spp.); Vd (*Verticillium dahliae*); TSWV (Tomato spotted wilt virus); For (*Fusarium oxysporum f. sp. raphani*); Va (*Verticillium albo-atrum*); Ss (*Stemphylium solani*); ToSRV (*Tomato severe rugose virus*); TYLCV (Tomato yellow leaf curl virus); TaNV (*Tomato apex necrosis virus*); V (*Verticillium dahliae, Verticillium albo-atrum*).

Chemical and physical analyses of the soil were conducted. Fertilization was performed according to the recommendations of Ribeiro (1999). The seedlings were irrigated using a drip irrigation system.

Tuta absoluta, originating from commercial tomato crops, was reared in rectangular cages (0.4 m × 0.4 m base and 0.5 m height) made of plastic with a side opening covered with nylon mesh. Plastic pots (diameter: 20 cm × height: 17 cm) containing soil with tomato plants (30 days after transplanting/6 leaves) without insecticide application were placed inside the cages. The eggplants were transferred to another cage with the exact dimensions for hatching. Healthy plants were replaced every three days as the caterpillars were fed. Upon reaching the pupal stage, they were kept inside these cages with dried plants until the emergence of adults and were then released back into the oviposition cages. Adults were fed a 10% honey solution, and caterpillars were fed tomato plants (cultivar Santa Cruz) (Bottega et al., 2018).

Preference tests for oviposition of Tuta absoluta, with choice and no-choice tests

Two experiments were conducted following a completely randomized design (CRD) for tests with and without choice. The experiment comprised nine tomato genotypes (treatments) and five replicates (with and without choice).

The choice oviposition preference test was conducted in rectangular cages (1.0 m × 1.0 m base and 0.6 m height) made of plastic with side openings covered with nylon mesh. In each repetition, the tomato plants were arranged in a circular pattern at equal distances, and two pairs of newly emerged *T. absoluta* adults were released at the center of the cage for each tomato genotype (Boiça Junior et al., 2012). The adults were fed a 10% honey solution.

The no-choice oviposition preference test was conducted in cages made of acetate (10.5 cm height x 9.0 cm diameter), closed at the bottom, and top with an acrylic Petri dish with a diameter of 9.0 cm. One plant of each tomato genotype was placed in each cage, and two pairs of newly emerged *T. absoluta* adults were released. Adults were fed a 10% honey solution (90% distilled water to 10% pure wild honey soaked in cotton).

In both assays, the number of eggs per plant was counted using a stereoscope at 24, 48, and 72 h after adult release (Boiça Junior et al., 2012).

Preference tests for feeding of Tuta absoluta, with choice and no-choice tests

A randomized block design (RBD) was used for the choice tests, and a completely randomized design (CRD) was used for the no-choice tests. The experiment consisted of nine tomato genotypes (treatments) and five replicates (with and without choice) for two trials. Feeding non-preference tests were conducted on 12-day-old caterpillars (fourth instar).

The feeding preference test was conducted in aluminum trays with a diameter of 30 cm and a height of 5 cm, lining the bottom with damp filter paper. Leaflets from each genotype, collected from the upper third of the plants with a leaf area between 14 and 17 cm^2, were arranged in a circular, equidistant pattern inside the arenas (trays). At the center, two caterpillars per genotype were released, and the arena was sealed with plastic wrap (Oliveira et al., 2009; Boiça Junior et al., 2012).

The no-choice feeding preference test was conducted in 9.0 cm diameter Petri dishes, lining the bottom with damp filter paper. One leaflet from the corresponding tomato genotype was placed in the center of each Petri dish, and two caterpillars were released onto the leaflet.

In both preference tests (choice and no-choice tests), the attractiveness of the caterpillars to the treatments was evaluated at 15, 30, 60, 120, 360, 720, and 1440 minutes after caterpillar release. Finally, to obtain the consumed leaf area (%), the initial leaf area was subtracted from the final leaf area for each leaflet of each tomato genotype using the 'Easy Leaf Area' app (Easlon & Bloom, 2014).

Antibiosis test

For the antibiosis test, the experimental design was completely randomized (CRD), consisting of nine tomato genotypes (treatments) and five repetitions, each containing five newly hatched *T. absoluta* caterpillars.

Initially, eggs were collected and placed in Petri dishes using a brush until hatching. Newly hatched caterpillars were then placed in Petri dishes containing slightly damp filter paper at the bottom and leaflets from each tomato genotype. The leaflets provided to the caterpillars were fully developed; new leaflets were supplied every two or three days, taken from the middle and apical parts of the plant (Safaeeniya et al., 2017).

Petri dishes were observed daily, recording the occurrence of pupae, and were weighed and individually placed in glass tubes (8.5 cm height x 2.5 cm diameter) 24 h after pupation and kept there until adult emergence. The emerging adults were sexed. The evaluated parameters included the duration and viability of the larval and pupal stages, the duration and viability from caterpillar hatching to adult emergence (total) (equation 1), adult longevity without food, pupal weight at 24 h, and sex ratio (equation 2) (Safaeeniya et al., 2017).

$$\text{Viability (\%)} = \frac{\text{Number of caterpillars, pupae, or adults obtained}}{\text{Initial number of insects in each stage of development}} \times 100 \quad (1)$$

$$\text{Sex ratio} = \frac{\text{Number of females}}{\text{Number of females + Number of males}} \quad (2)$$

Statistical analysis

Statistical analysis of the data was performed using analysis of variance (ANOVA) with the F-test. When significant, the means were compared using Tukey's test at a 5% probability level. The computational program SISVAR version 5.8 (Ferreira, 2011) was used for the data analysis. The numbers of eggs and *T. absoluta* insects attracted were transformed using the formula (x + 0.5)1/2, and the original data were tabulated.

Multivariate analysis using the hierarchical clustering method was performed based on the standardized mean Euclidean distance (D) and Ward's minimum variance method to classify the tomato genotypes based on *T. absoluta* development. For an integrated assessment, the data were subjected to principal component analysis (PCA) by selecting two principal components that considered all variables using a graphical analysis biplot. Multivariate analyses were conducted using OriginPro® 2021 software (Originlab Corporation, 2022).

Results and Discussion

Preference tests for oviposition of Tuta absoluta, with choice and no-choice tests

No-choice test results for oviposition preference (**Table 1**) showed significant differences only in the evaluation of eggs 24 hours after adult release, where the 'Cascade' hybrid exhibited a lower mean number of deposited eggs (7.00 eggs), differing from 'Caniati' (30.0 eggs) and 'Grazianni' (34.0 eggs). At 48 and 72 hours, the 'Cascade' hybrid also showed fewer, 27.0 and 43.8 eggs, respectively.

In the no-choice oviposition test, significant differences were observed only in the evaluation of eggs 72 hours after adult release, where the tomato hybrid 'Cascade' showed a lower mean number of eggs deposited (18.2 eggs), differing from the 'Bento' tomato hybrid (80.2 eggs) (**Table 2**). The lowest oviposition preference was observed among *T. absoluta* adults for the 'Cascade' hybrid, while a higher preference was noted for the tomato hybrids 'Caniati', 'Grazianni', and 'Bento' after 72 hours of observation.

The non-preference of oviposition by *T. absoluta* on the 'Cascade' tomato hybrid may be attributed to its chemical and morphological characteristics. It has a high degrees Brix (°Brix) content, ranging from 6 to 12 °Brix or more, depending on the conditions. The leaflets are generally irregularly shaped, oval, or lanceolate, with serrated edges. They can vary in size but are usually smaller than the leaves of larger tomato varieties. In addition, trichomes on leaves can hinder insect access to the leaf surface or impede their movement. They may also trap insects in the toxic or sticky exudates produced by the glandular trichomes (Vitta et al., 2016).

The presence of trichomes in tomatoes (BGH985) reduced the preference for oviposition, shelter, or feeding by *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae) (Fernandes et al., 2012). Moreover, trichomes can store chemical components that are deterrent or toxic to arthropods (glandular trichomes) (Biondi et al., 2018). In the susceptible tomato variety 'Santa Clara', non-glandular trichomes are more frequent, averaging 360 trichomes/cm² (Oriani & Vendramim, 2010).

Another source of resistance against *T. absoluta* is a strain rich in 2-tridecanone, acyl sugars (allelochemicals), and zingiberene (Oliveira et al., 2012). For *T. absoluta*, tomato genotypes with high zingiberene content (allelochemical) affected their behavior and development. Despite adults remaining on the leaflets of genotypes with high zingiberene levels, rejection was observed because of the reduced number of eggs deposited compared with the susceptibility standard and low allelochemical genotype (Oliveira et al., 2020). Maciel et al. (2018) found lower oviposition by *T. absoluta* in experimental tomato hybrids than in lines with low acyl sugar content and controls ('Santa Clara' and 'Bravo').

Volatile compounds, such as sesquiterpenes, negatively affect the survival (antibiosis) and preference (antixenosis) of herbivorous insects for tomato plants. These compounds influence the flight behavior and oviposition of female *T. absoluta* during mating. Notably, females showed a higher tendency to land and deposit their eggs on the tomato genotype, which was more susceptible to these volatile compounds, indicating a direct relationship between the presence of these compounds and female preference for egg laying (Silva et al., 2017).

Preference tests for feeding of Tuta absoluta, with choice and no-choice tests

In the feeding preference test concerning attractiveness, significant differences were observed in the evaluation conducted 15 min after the release of caterpillars (**Table 3**). The 'Sweet Heaven' tomato hybrid

Table 1. Number of *Tuta absoluta* eggs at 24, 48, and 72 hours after adult release in different tomato genotypes) in a choice oviposition test (mean ± standard deviation). Air temperature: 25 ± 2 °C, relative humidity: 70 ± 10%, and photophase: 12h.

Tomato genotype	Number of eggs after 24 hours	Number of eggs after 48 hours	Number of eggs after 72 hours
'Compack'	16.8 ± 5.79 ab	40.0 ± 9.95	53.6 ± 10.0
'Caniati'	30.0 ± 5.16 b	70.6 ± 20.3	81.2 ± 20.6
'Grazianni'	34.0 ± 5.04 b	60.0 ± 10.8	70.2 ± 8.10
'Cascade'	7.00 ± 1.67 a	27.0 ± 5.97	43.8 ± 7.60
'Ellen'	19.0 ± 5.68 ab	45.4 ± 13.4	63.6 ± 12.7
'Bento'	18.0 ± 4.44 ab	38.2 ± 6.11	49.4 ± 7.15
'Dominador'	25.0 ± 6.11 ab	45.2 ± 7.49	67.4 ± 10.7
'Sweet Heaven'	12.2 ± 1.62 ab	36.8 ± 8.65	52.2 ± 8.42
'Santa Clara' (control cultivar)	12.8 ± 1.71 ab	34.6 ± 9.13	46.0 ± 7.40
F	3.45*	1.45^{ns}	1.31^{ns}
C.V. (%)	27.7	27.0	20.2

*Means followed by the same letter in a column do not differ significantly according to Tukey's test at 5% probability. ^{ns} = Not significant. F = F-test: significance test. C.V. = coefficient of variation.

Table 2. Number of *Tuta absoluta* eggs at 24, 48, and 72 hours after adult release in different tomato genotypes in a no-choice oviposition test (mean ± standard deviation). Air temperature: 25 ± 2 °C, relative humidity: 70 ± 10%, and photophase: 12h.

Tomato genotype	Number of eggs after 24 hours	Number of eggs after 48 hours	Number of eggs after 72 hours
'Compack'	4.00 ± 2.02	10.6 ± 3.71	19.2 ± 6.58 ab
'Caniati'	3.60 ± 2.40	16.8 ± 7.29	28.0 ± 12.6 ab
'Grazianni'	0.20 ± 0.20	10.2 ± 5.73	23.0 ± 12.1 ab
'Cascade'	2.40 ± 2.16	6.60 ± 5.36	18.2 ± 15.2 a
'Ellen'	6.80 ± 2.27	18.4 ± 6.45	35.8 ± 9.73 ab
'Bento'	7.00 ± 3.69	34.8 ± 11.3	80.2 ± 23.2 b
'Dominador'	5.40 ± 2.62	29.2 ± 10.0	49.8 ± 13.4 ab
'Sweet Heaven'	2.60 ± 1.78	7.00 ± 3.92	23.2 ± 6.78 ab
'Santa Clara' (control cultivar)	5.00 ± 2.88	11.8 ± 6.84	36.2 ± 11.4 ab
F	1.14^{ns}	1.42^{ns}	2.24*
C.V. (%)	66.9	62.1	54.3

*Means followed by the same letter in a column do not differ significantly according to Tukey's test at 5% probability. ^{ns} = Not significant. F = F-test: significance test. C.V. = coefficient of variation

Table 3. *Tuta absoluta* caterpillars attracted to tomato genotypes at different time intervals after their release and consumed leaf area in a choice feeding test (mean ± standard deviation). Air temperature: 25 ± 2 °C, relative humidity: 70 ± 10%, and photophase: 12h.

Tomato genotype	Time after the release of caterpillars (minutes)							Consumed leaf area (%)
	15'	30'	60'	120'	360'	720'	1440'	
'Compack'	0.20 ± 0.20 ab	0.60 ± 0.40	0.60 ± 0.40	0.80 ± 0.37	0.80 ± 0.37	0.80 ± 0.37	0.80 ± 0.37	4.66 ± 2.71 a
'Caniati'	1.40 ± 0.68 ab	2.20 ± 0.80	2.20 ± 0.80	2.20 ± 0.80	2.20 ± 0.80	2.20 ± 0.80	2.40 ± 0.81	15.5 ± 6.88 ab
'Grazianni'	0.80 ± 0.20 ab	1.60 ± 0.87	1.80 ± 0.86	1.80 ± 0.86	1.60 ± 0.93	1.60 ± 0.93	1.60 ± 0.93	19.7 ± 10.3 ab
'Cascade'	0.60 ± 0.40 ab	1.80 ± 1.11	1.80 ± 1.11	2.00 ± 1.10	2.00 ± 1.10	2.00 ± 1.10	2.20 ± 1.11	6.90 ± 5.49 ab
'Ellen'	0.80 ± 0.20 ab	1.20 ± 0.49	1.20 ± 0.49	1.20 ± 0.49	1.20 ± 0.49	1.20 ± 0.49	1.00 ± 0.55	9.75 ± 4.01 ab
'Bento'	1.40 ± 0.93 ab	2.20 ± 1.07	2.20 ± 1.07	2.00 ± 1.05	2.00 ± 1.05	2.00 ± 1.05	2.20 ± 1.24	12.4 ± 3.94 ab
'Dominador'	2.00 ± 1.14 ab	3.00 ± 1.26	3.20 ± 1.39	3.00 ± 1.26	3.20 ± 1.39	3.20 ± 1.39	3.20 ± 1.20	24.9 ± 7.37 ab
'Sweet Heaven'	0.00 ± 0.00 a	0.60 ± 0.40	0.60 ± 0.40	0.60 ± 0.40	0.80 ± 0.37	0.80 ± 0.37	0.80 ± 0.37	2.99 ± 1.60 a
'Santa Clara' (control cultivar)	2.80 ± 1.36 b	3.40 ± 1.29	3.60 ± 1.29	3.60 ± 1.29	3.60 ± 1.29	3.60 ± 1.29	3.20 ± 0.86	32.2 ± 5.68 b
F	2.24*	1.23^{ns}	1.29^{ns}	1.09^{ns}	0.90^{ns}	0.90^{ns}	1.01^{ns}	2.75*
C.V. (%)	42.9	44.4	44.5	43.4	44.3	44.3	43.2	57.2

*Means followed by the same letter in a column do not differ significantly according to Tukey's test at 5% probability. ^{ns} = Not significant. F = F-test: significance test. C.V. = coefficient of variation.

was the least preferred genotype for feeding, with zero attracted caterpillars, differing from the control 'Santa Clara,' which attracted more caterpillars (2.80). At 30, 60, 120, 360, 720, and 1440 minutes after the release of the caterpillars, although tomato genotypes did not show significant differences, the 'Sweet Heaven' hybrid attracted fewer caterpillars than the 'Santa Clara' cultivar.

Significant differences were observed in the leaf areas consumed by the caterpillars in the choice test (**Table 3**). The tomato hybrids 'Sweet Heaven' (2.99%) and 'Compack' (4.66%) stood out with the lowest consumption, differing from the control 'Santa Clara' (32.2%).

Regarding attractiveness, the no-choice feeding preference test did not show significant differences, indicating equal attractiveness among the options (**Table 4**). However, the leaf area consumed by the caterpillars differed significantly in the no-choice feeding test (**Table 4**). The tomato hybrids 'Sweet Heaven' (3.83%) and

'Cascade' (5.00%) stood out with the lowest consumption, differing from the control 'Santa Clara' (16.6%).

In the choice-feeding preference test, little movement was observed among the caterpillars across genotypes during the initial minutes of evaluation. They settled into their chosen genotypes as soon as they were released. This indicates that the volatiles emitted by the leaves did not affect caterpillar behavior, as this is the first phase of host selection for feeding and/or oviposition by phytophagous insects (Boiça Junior et al., 2012). This observation was also confirmed in the no-choice feeding test, in which most caterpillars moved towards the available food source and continued to feed. This demonstrates that genotype did not influence the attractiveness of *T. absoluta* caterpillars. Several tomato genotypes are resistant to *T. absoluta* (Oliveira et al., 2009). The presence of many small mines suggests that insects are not feeding properly on the plant (Agbessenou et al., 2020). This lack of adequate insect feeding can be a sign of the natural resistance of the plant to damage caused by *T. absoluta*.

The genotype LA 1777 of *Solanum habrochaites* (wild tomato) showed a high number of small mines and a low number of large mines compared to 'Santa Clara' and IPA-5 (Ecole et al., 1999). These characteristics indicate that resistance to this genotype may be associated with compounds that inhibit or deter the feeding of *T. absoluta* (Ecole et al., 1999).

Antibiosis test

Differences in the development of *T. absoluta* among the different tomato genotypes existed (**Tables 5 and 6**). Caterpillars fed on 'Sweet Heaven' hybrid leaflets showed a longer larval period, lasting 14.4 days, differing from 'Compack' and the control 'Santa Clara', which had the shortest larval periods, lasting 9.87 and 11.0 days, respectively (**Table 5**). The 'Sweet Heaven' hybrid also exhibited the lowest larval viability at 44.0%, differing from the 'Dominador' and 'Ellen' hybrids, with the highest survival rates at 80.0% and 84.0%, respectively. No significant differences were observed in the duration or survival of the pupal stages (**Table 5**).

The increase in the larval period of *T. absoluta*, when fed on the 'Sweet Heaven' genotype, reduces the insect's generations, which is detrimental to the pest. This is because a prolonged larval period decreases the developmental rate of the insect, consequently reducing its reproductive speed and increasing its population (Agbessenou et al., 2020). As a result, the impact of *T. absoluta* on tomatoes was minimized as there were fewer pest generations over time. This effect is favorable for integrated pest management, as it lowers population pressure and can facilitate the control of this pest at acceptable levels for agricultural production.

The longevity of adults was also affected by different tomato genotypes. *T. absoluta* individuals reared on 'Sweet Heaven' hybrid leaflets provided a significantly longer biological cycle, lasting 14.2 days, whereas those fed on leaflets of 'Ellen' (7.53 days), 'Caniati' (8.05 days), 'Cascade' (8.33 days) hybrids, and the control 'Santa Clara' cultivar (8.60 days) had shorter cycles (**Table 6**).

For the evaluation of the total period, from hatching to adult emergence, the 'Sweet Heaven' hybrid had the longest duration, lasting 37.0 days, differing from the other genotypes used in this study, except for the 'Dominador' hybrid (31.7 days) (**Table 6**). Regarding the survival of the total period, from caterpillar hatching to adult emergence, the 'Sweet Heaven' hybrid showed a lower viability percentage (32.0%), significantly differing from 'Dominador' (80.0%), 'Santa Clara' (76.0%), 'Ellen' (76.0%), 'Compack' (64.0%), and 'Grazianni' (64.0%), which had the highest values. The data regarding the average pupal mass and sex ratio were not significantly different (**Table 6**).

The 'Sweet Heaven' hybrid had a negative effect on *T. absoluta* compared to other treatments, showing a prolonged duration of larval, adult, and total stages, along with low larval and overall viability. However, the 'Ellen' hybrid had more beneficial effects on the development of *T. absoluta*, exhibiting a higher larval survival rate than the control 'Santa Clara' cultivar and matching it in adult longevity, total duration, and overall viability assessments.

When there are adverse effects on the pest, indicating that antibiosis is one of the factors responsible for lower susceptibility, the causes associated with lower susceptibility should be linked to glandular and non-glandular trichomes, and those related to leaves, midribs, fruits, crystal idioblasts, or growth habits (Bottega et al., 2015).

In addition to tomato genotypes, the age of the plant and the developmental stage of the leaf can also play a significant role in pest susceptibility. This is because of variations in the concentrations of volatile compounds, such as 2-tridecanone (2-TD), which can influence the behavior of *T. absoluta* (Bottega et al., 2015).

The 'Bento' hybrid was preferred for oviposition by *T. absoluta* in the no-choice test after 72 hours (**Table 2**). Yet, it did not exhibit superior overall caterpillar-adult viability compared to the other genotypes (**Table 6**). The observed differences in the oviposition and mortality of *T. absoluta* among treatments may indicate the presence

Table 4. *Tuta absoluta* caterpillars attracted to tomato genotypes at different time intervals after their release and consumed leaf area in a no-choice feeding test (mean ± standard deviation). Air temperature: 25 ± 2 °C, relative humidity: 70 ± 10%, and photophase: 12h.

Tomato genotype	Time after the release of caterpillars (minutes)							Consumed leaf area (%)
	15'	30'	60'	120'	360'	720'	1440'	
'Compack'	1.80 ± 0.20	1.80 ± 0.20	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	1.80 ± 0.20	1.20 ± 0.20	5.81 ± 0.65 ab
'Caniati'	1.80 ± 0.20	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	5.77 ± 2.08 ab
'Grazianni'	1.60 ± 0.40	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	11.6 ± 3.71 ab
'Cascade'	1.20 ± 0.37	1.20 ± 0.37	1.20 ± 0.37	1.20 ± 0.37	1.40 ± 0.40	1.40 ± 0.40	1.40 ± 0.40	5.00 ± 2.06 a
'Ellen'	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	1.60 ± 0.24	5.20 ± 1.29 ab
'Bento'	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	1.80 ± 0.20	13.5 ± 3.59 ab
'Dominador'	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	11.2 ± 4.42 ab
'Sweet Heaven'	1.00 ± 0.32	1.60 ± 0.24	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	1.40 ± 0.24	3.83 ± 0.97 a
'Santa Clara' (control cultivar)	1.60 ± 0.40	1.60 ± 0.40	1.60 ± 0.40	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	1.80 ± 0.20	16.6 ± 2.50 b
F	0.94^{ns}	1.04^{ns}	1.24^{ns}	1.97^{ns}	1.12^{ns}	0.94^{ns}	1.53^{ns}	3.28*
C.V. (%)	20.5	14.6	13.8	10.6	10.9	11.5	13.0	32.9

*Means followed by the same letter in a column do not differ significantly according to Tukey's test at 5% probability. ^{ns} = Not significant. F = F-test: significance test. C.V. = coefficient of variation

Table 5. Duration and survival of larval and pupal stages of *Tuta absoluta* reared on leaves of different tomato genotypes (mean ± standard deviation). Air temperature: 25 ± 2 °C, relative humidity: 70 ± 10%, and photophase: 12h.

Tomato genotype	Larval stage		Pupal stage	
	Duration (days)	Survival (%)	Duration (days)	Survival (%)
'Compack'	9.87 ± 0.58 b	68.0 ± 8.00 abc	8.36 ± 0.20	96.0 ± 4.00
'Caniati'	11.8 ± 0.66 ab	48.0 ± 8.00 ab	8.07 ± 0.27	96.0 ± 4.00
'Grazianni'	11.9 ± 0.74 ab	68.0 ± 10.2 abc	8.29 ± 0.31	96.0 ± 4.00
'Cascade'	12.4 ± 1.24 ab	56.0 ± 7.48 abc	8.35 ± 0.32	88.0 ± 4.90
'Ellen'	12.8 ± 0.71 ab	84.0 ± 7.48 c	7.44 ± 0.23	92.0 ± 4.90
'Bento'	12.5 ± 0.56 ab	64.0 ± 7.48 abc	8.30 ± 0.16	88.0 ± 4.90
'Dominador'	12.3 ± 0.68 ab	80.0 ± 8.94 bc	7.93 ± 0.19	100 ± 0.00
'Sweet Heaven'	14.4 ± 0.49 a	44.0 ± 4.00 a	8.45 ± 0.07	88.0 ± 4.90
'Santa Clara' (control cultivar)	11.0 ± 0.28 b	76.0 ± 4.00 abc	8.28 ± 0.28	100 ± 0.00
F	3.06*	3.46*	1.81^{ns}	1.53^{ns}
C.V. (%)	6.61	13.4	3.26	4.88

*Means followed by the same letter in a column do not differ significantly according to Tukey's test at 5% probability. Ns = Not significant. F = F-test: significance test. C.V. = coefficient of variation

Table 6. Longevity of adults, duration, and survival from caterpillar to adult, average pupal mass, and sex ratio of *Tuta absoluta* reared on leaves of different tomato genotypes (mean ± standard deviation). Air temperature: 25 ± 2 °C, relative humidity: 70 ± 10%, and photophase: 12h.

Tomato genotype	Adult longevity (days)	Caterpillar-adult duration (days)	Caterpillar-adult survival (%)	Average pupal mass (mg)	Sex ratio
'Compack'	9.50 ± 1.20 ab	27.7 ± 1.60 b	64.0 ± 4.00 bc	4.61 ± 0.17	0.52 ± 0.08
'Caniati'	8.05 ± 1.78 b	27.9 ± 2.06 b	44.0 ± 7.48 ab	4.54 ± 0.36	0.72 ± 0.13
'Grazianni'	9.21 ± 0.56 ab	29.4 ± 0.86 b	64.0 ± 9.80 bc	3.95 ± 0.22	0.51 ± 0.10
'Cascade'	8.33 ± 0.53 b	29.0 ± 1.51 b	44.0 ± 7.48 ab	4.57 ± 0.26	0.72 ± 0.13
'Ellen'	7.53 ± 0.69 b	27.8 ± 1.21 b	76.0 ± 7.48 bc	4.59 ± 0.07	0.60 ± 0.08
'Bento'	8.73 ± 0.96 b	29.6 ± 1.33 b	52.0 ± 4.90 abc	4.63 ± 0.28	0.47 ± 0.15
'Dominador'	11.4 ± 1.37 ab	31.7 ± 1.98 ab	80.0 ± 8.94 c	4.73 ± 0.29	0.50 ± 0.06
'Sweet Heaven'	14.2 ± 1.28 a	37.0 ± 0.94 a	32.0 ± 8.00 a	4.50 ± 0.21	0.63 ± 0.13
'Santa Clara' (control cultivar)	8.60 ± 1.03 b	27.9 ± 1.26 b	76.0 ± 4.00 bc	4.62 ± 0.18	0.62 ± 0.14
F	2.62*	3.75*	5.73*	0.94^{ns}	0.66^{ns}
C.V. (%)	15.0	5.66	14.6	5.92	26.7

*Means followed by the same letter in a column do not differ significantly according to Tukey's test at 5% probability. ^{ns} = Not significant. F = F-test: significance test. C.V. = coefficient of variation.

of different categories of resistance. The chemical compounds can influence oviposition preference in tomato genotypes, which affect the neuroreceptors or neurotransmitters of insects and interfere with neural signal transduction. These compounds also inhibit enzymatic activity or affect protein functionality (Wink, 2018).

Chemical compounds that affect the nervous and enzymatic systems of insects can cause behavioral changes, reduce reproductive and behavioral performance, and ultimately lead to mortality (Wink, 2018).

Multivariate analysis: hierarchical clustering and principal component analysis (PCA)

Through hierarchical cluster analysis, different tomato genotypes could be distinguished and grouped based on their degrees of similarity. This technique allowed the formation of clusters with similar characteristics within each group while showing significant differences from the other groups (**Figure 1**). Based on the linkage distance graph, a Euclidean distance of 14 was set, suggesting the division of genotypes into four distinct groups: the first group consists of 'Compack' and 'Grazianni' genotypes; the second group includes 'Caniati', 'Cascade', and 'Bento' genotypes; the third group comprises 'Ellen', 'Dominador', and 'Santa Clara' genotypes; and 'Sweet Heaven' forms the fourth group, standing apart from the others due to its more negative effect on *T. absoluta* (**Figure 1**).

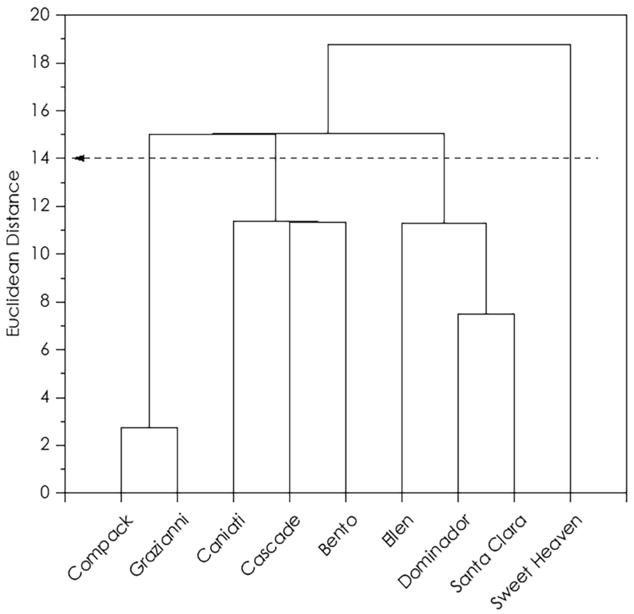

Figure 1. Dendrogram based on the biological parameters of *Tuta absoluta* fed on nine tomato genotypes. The clustering method used was Ward's minimum variance with Euclidean distance as the dissimilarity measure. The arrow indicates the Euclidean distance used for group separation.

Principal Component Analysis (PCA) was applied to establish a descriptive model for clustering the analyzed variables based on the development of *T. absoluta* in different tomato genotypes according to PC1 and PC2 (**Figure 2**).

PC1 and PC2 explained 62.37% of the variance in the data (**Figure 2**). The first principal component (PC1) accounted for the largest percentage of data variability (40.44%), with the parameters that most influenced this principal component being adult longevity (AL), total caterpillar-adult duration (TD), and larval duration (LD).

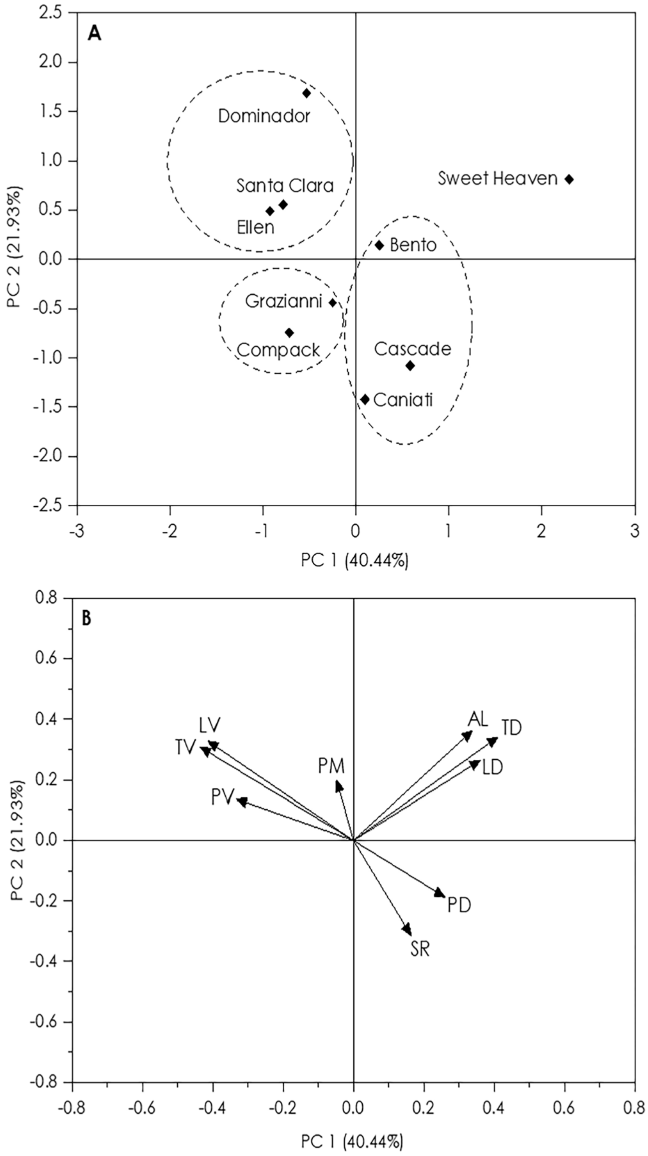

Figure 2. Distribution of tomato genotypes (A) and biological parameters (B) according to the principal component analysis obtained from *Tuta absoluta* reared on tomato genotypes. LD: Larval duration; LV: Larval viability; PD: Pupal duration; PV: Pupal viability; AL: Adult longevity; TD: Total caterpillar-adult duration; TV: Total viability; PM: Pupal mass; and SR: Sex ratio.

The second principal component (PC2) captured 21.93% of the variability in the original variables, with larval viability (LV) and total viability (TV) being the parameters that most influenced PC2. pupal mass (PM), pupal duration (PD), pupal viability (PV), and sex ratio (SR) had the least influence on the differentiation and classification of tomato genotypes based on their levels of resistance to *T. absoluta*.

The results obtained through PCA were consistent with the hierarchical cluster analysis results regarding the number of groups formed by the tomato genotypes. This indicates that the two analytical techniques provided similar information regarding the structures of similarity and dissimilarity among the genotypes.

The 'Sweet Heaven' genotype was distinct from the other genotypes when analyzed concerning the first principal component (PC1+) (**Figure 2a**). This genotype had a negative effect on the development of *T. absoluta*, with the most influential biological parameters being prolonged larval duration (LD), total duration of caterpillar-adult (TD) phases, and adult longevity (AL) (**Figure 2b**).

However, the genotypes 'Dominador', 'Santa Clara', and 'Ellen' formed a distinct group, with high larval viability (LV) and total viability (TV) parameters exerting more significant influence. These genotypes demonstrate a higher capacity for pest development.

No changes in the genotypes of each group formed by the principal component analysis were observed compared with the hierarchical cluster analysis. This indicates consistency in the results between the two analytical approaches, reinforcing the reliability of the identified groups.

The 'Sweet Heaven' genotype was isolated from the other genotypes in both multivariate analyses. This isolation occurred because of the influence of the longer larval period, total duration, and adult longevity of this genotype (**Figures 1 and 2**).

The tomato hybrid 'Sweet Heaven' exhibited higher resistance to *T. absoluta* than the other hybrids. It is characterized by a high resistance level to *Fusarium oxysporum* f. sp. *lycopersici* race 1, tomato mosaic virus (ToMV) strain Tm-1, and *Stemphylium solani*. It has been genetically improved to have a sweeter taste, with high levels of acyl sugars (higher degrees of Brix) (Eisele et al., 2022). Another genetically improved characteristic is the lycopene content (Eisele et al., 2022), which is effective in obtaining plants resistant to *T. absoluta* (Pereira et al., 2008; Maciel et al., 2011).

Tomato plants with high levels of acyl sugars have greater resistance, with fewer lesions on the leaflets and a lower percentage of leaflets attacked by pests. These results suggest that acyl sugars play an important role in protecting tomato plants from phytophagous insects (Gonçalves Neto et al., 2010).

Conclusions

The tomato hybrid 'Cascade' exhibited lower attractiveness for *T. absoluta* oviposition preference in the no-choice test.

The lack of feeding preference by *T. absoluta* in the choice and no-choice tests regarding attractiveness did not show significant differences, indicating equal attraction to the evaluated genotypes. 'Sweet Heaven', 'Compack', and 'Cascade' tomato hybrids exhibited a lower percentage of consumed leaf area.

The 'Sweet Heaven' tomato hybrid had a more negative effect on the development of *T. absoluta*, exhibiting prolonged durations of the larval, adult, and total stages as well as low larval and total viability, demonstrating high resistance.

'Dominador', 'Santa Clara', and 'Ellen' were the tomato genotypes that showed higher susceptibility to the development of *T. absoluta*, encompassing high larval, pupal, and total viability (caterpillar-adult period).

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