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Original Article

Morphological and Biochemical Basis of Resistance in Certain Tomato Cultivars Against *Tuta absoluta* (Lepidoptera: Gelechiidae)

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Abstract

Background

The tomato leafminer, *Tuta absoluta*, causes severe yield losses worldwide, highlighting the need for sustainable host plant resistance. This study evaluated the susceptibility of eight commercial tomato cultivars to *T. absoluta* over two seasons in Egypt, investigating associated structural [Scanning Electron Microscopy (SEM) leaf trichomes] and biochemical defense traits.

Materials

Cultivars were arranged in a Randomized Complete Block Design. Weekly larval mines were recorded. Leaf samples were analyzed colorimetrically for major nutrients (N, P, K), primary metabolites (total carbohydrates, proteins, and free amino acids), total phenols, and defense-related antioxidant enzymes (peroxidase, alpha, and beta-esterase). SEM was used to quantify glandular and non-glandular trichomes on both leaf surfaces.

Results

Cultivars showed highly significant variations ($P < 0.001$). "Red sun" was the most susceptible (9.2 ± 1.7 and 9.3 ± 3.2 mines/10 leaflets), while "Hybrid bito 86" was the most resistant (5.0 ± 0 and 4.1 ± 0.6 mines/10 leaflets). Infestation levels were highly consistent across seasons ($r = 0.894$, $P = 0.003$; $t = 1.213$, $P = 0.265$). Infestation correlated negatively with total phenols ($r = -0.77$*), which peaked in "Hybrid Bito 86", but positively with phosphorus ($r = 0.74$*), potassium ($r = 0.81$*), and adaxial non-glandular trichome density ($r = 0.85$**). A Varimax-rotated Principal Component Analysis (PCA) integrated all evaluated traits, with the first two principal components explaining 55.60% of the total variance (PC1: 31.81% and PC2: 23.78%). The PCA score plot clearly segregated the cultivars based on their resistance levels: the susceptible "Red Sun" loaded strongly in the positive PC1 quadrant (driven by high non-glandular trichomes and nutrient levels), whereas the resistant "Hybrid Bito 86" occupied an isolated sector associated with elevated phenolic defense.

Conclusion

Host resistance against *T. absoluta* is primarily associated with a synergistic combination of biochemical antibiosis (elevated phenolic content) and morphological antixenosis (reduced upper non-glandular trichome density). "Hybrid Bito 86" possesses promising phenotypic and biochemical resistance indicators, making it a viable candidate for breeding programs targeting long-term host plant resistance.

Categories: Disease & pests of crops, Field & Horticultural crops sustainable production, Trait genetics & breeding of crops

Keywords: solanum lycopersicum, tuta absoluta, antibiosis, antixenosis, phenolic compounds, trichome density, glandular hairs, secondary metabolites

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Introduction

Tomato (*Solanum lycopersicum* L.) is a major vegetable crop in Egypt, playing a vital role in the agricultural economy. However, its production faces severe threats from the invasive tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), which is capable of causing up to 100% yield loss if left unmanaged [1-3]. The larval stage of this pest causes intensive damage by mining into leaves, stems, and fruits, which severely inhibits the plant's photosynthetic capacity and reduces marketability. Chemical control has long been the primary strategy against *T. absoluta*. However, the reliance on synthetic insecticides has led to rapid resistance development, environmental degradation, and the destruction of natural enemies. With the growing emphasis on sustainable agriculture, there is an urgent need to reduce overreliance on insecticides and adopt complementary pest management strategies, such as developing insect-resistant tomato cultivars [4]. Host Plant Resistance serves as a foundational component of modern integrated pest management (IPM), offering an eco-friendly and cost-effective alternative to suppress pest populations below economic injury levels [5].

The defense mechanisms governing host plant resistance against insect herbivores are broadly classified into antixenosis (non-preference for colonization or oviposition) and antibiosis (adverse physiological effects on pest survival and development) [6]. Screening local and commercial cultivars for these defense traits is essential to identify promising genotypes for future breeding programs. As highlighted by the researchers [6], resistance expression is highly complex and depends heavily on the specific target insect stage, where certain genotypes may exhibit high antixenosis against adult oviposition but support larval performance, or vice versa.

These defensive expressions are deeply rooted in a coordinated interplay between structural and chemical traits. Structurally, leaf trichomes constitute the primary physical barrier against insect pests [5]. Glandular and non-glandular trichomes drastically influence insect-plant interactions. While high densities of glandular trichomes typically function as a mechanical and chemical deterrent that reduces larval establishment, non-glandular trichomes can occasionally present an opposing mechanism. For instance, the study [7] demonstrated that dense non-glandular trichomes effectively deter piercing-sucking pests like *Aphis gossypii*. However, for chewing or mining insects like *T. absoluta*, these same structural features may paradoxically provide physical anchorage and a protective microenvironment that facilitates adult egg-laying, altering host plant suitability.

Chemically, plants invest substantial energy into producing defensive compounds. As comprehensively reviewed by the study [8], insect-plant interactions are significantly mediated by plant secondary metabolites (PSMs), particularly phenolic compounds. These substances act constitutively in vulnerable tissues to restrict insect growth, act as feeding deterrents, disrupt nutrient absorption, and decrease the overall nutritive value of the foliage. Conversely, primary metabolites and macro-elements (such as nitrogen, amino acids, and minerals) render the host foliage more nutritionally favorable, optimizing herbivore fitness and enhancing larval development [8]. Variations in these phytochemical balances among genotypes significantly affect the life-table parameters of *T. absoluta*, disrupting the insect's reproductive rate [9]. Furthermore, the seasonal dynamics of *T. absoluta* and its interaction with host plants are strictly tied to environmental conditions. Variations in ambient temperatures and relative humidity can shift cultivar susceptibility between successive cropping seasons by altering the insect's developmental thresholds and generation times [10]. In Egypt, screening local cultivars under open-field conditions has confirmed that distinct variations in resistance exist among commercial varieties, with specific lines demonstrating high tolerance while others completely lack defensive biochemical traits [7,11]. While exogenous elicitors and plant growth regulators have been demonstrated to successfully prime phenotypic defense pathways against *T. absoluta* in specific commercial cultivars [3], the ultimate success of such induced resistance is strictly governed by the host's baseline genetic, structural, and constitutive biochemical landscape.

Given this complex background, the present study was initiated to evaluate the natural susceptibility of eight commercial tomato cultivars to *T. absoluta* infestation under open-field conditions in Egypt across two successive seasons. This study aims to decipher the underlying morphological [trichome profiling via Scanning Electron Microscopy (SEM)] and biochemical (primary/secondary metabolites and antioxidant enzymes) traits dictating resistance, while correlating these parameters with climatic factors to provide comprehensive insights for sustainable tomato breeding.

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Materials And Methods

Plant material and experimental design

The study was conducted at the Faculty of Agriculture Farm, Ain Shams University, Shoubra El-Kheima, Egypt, during two successive seasons (2012 and 2013). Eight commercial tomato cultivars (Red Sun, Hybrid Super Strain B, Castle Rock, Riogrande, Baladi, Nemaguard, Super Set, and Hybrid Bito 86) were selected for evaluation. These cultivars were chosen based on their high commercial popularity in Egypt and to investigate their varying genetic potential for resistance.

Seedlings (6 weeks old) were transplanted into large black polyethylene bags (20 cm diameter, 30 cm length) filled with uniform clay loam soil, with three seedlings per bag. The experiment was arranged in a Randomized Complete Block Design with five replicates under natural open-field conditions. Each replicate comprised 10 bags per cultivar, totaling 50 bags (150 plants) per cultivar. Standard agronomic practices were uniformly applied across all experimental units, and no chemical pesticides were used throughout the study.

Entomological assessments

Infestation monitoring commenced for one-week post-transplanting. To avoid repeated sampling of the same tissues, new random leaflets were selected weekly for 10 weeks. A weekly sample of 250 leaflets per cultivar was collected (50 leaflets/replicates). Samples were examined under a stereomicroscope to record the number of *T. absoluta* larval mines. Infestation levels were expressed as the mean number of mines per 10 leaflets.

Phytochemical and enzymatic analyses

Leaf sampling was systematically performed during the peak vegetative stage, which coincided with the peak infestation period of *T. absoluta*. Fully expanded, healthy leaves were freshly harvested from the upper-third canopy of randomly selected plants across replicates to ensure physiological uniformity. All biochemical evaluations including primary metabolites (total carbohydrates, proteins, and free amino acids), major macro-nutrients (N, P, K), total phenolics, and defensive antioxidant enzymes (peroxidase, α-esterase, and β-esterase) were determined using fresh leaf tissues. The collected samples were placed in refrigerated iceboxes, transported immediately, and analyzed directly upon arrival at the Central Laboratory, Faculty of Agriculture, Ain Shams University, avoiding any oven-drying or freezing delays to maintain optimal cellular integrity and enzymatic activity. The following parameters were quantified:

Nutrients: Total nitrogen (N) (mg/g DW) was determined by the micro-Kjeldahl method [12]. Inorganic phosphorus (P) (mg/g DW) was measured photometrically at 650 nm [13], and Potassium (K+) (µEq/g DW) was determined via flame photometry [14].

Metabolites: Total free amino acids (µg alanine/g DW) were assayed using ninhydrin reagent [15]. Total soluble proteins (mg/g DW) were estimated using the Bradford dye-binding method [16]. Total carbohydrates (mg/g DW) were determined by the phenol-sulfuric acid method [17]. Total phenolic content (µg GAE/g DW) was determined by the Folin-Ciocalteu method as modified by the study [18], following the extraction procedure reported by Kähkönen et al. [19].

Antioxidant Enzymes: Alpha and beta-esterase activities (µg α or β-naphthol/min/g DW) were determined according to Van Asperen [20]. Peroxidase activity (ΔO.D.405/min/g DW) was measured according to Vetter et al. [21].

Analysis of leaf samples were conducted in the central laboratory of Faculty of Agriculture, Ain Shams University (Shoubra El-Kheima, Egypt).

SEM examination

To investigate the morphological basis of resistance, leaf surface features - specifically trichome density and dimensions - were examined on both the adaxial (upper) and abaxial (lower) surfaces. Leaf samples were fixed in 2.5% glutaraldehyde for 24 hours at 4°C, washed with phosphate buffer (pH 6.8), and post-fixed in 1% osmium tetraoxide for 1 hour. Samples were then dehydrated through an ascending acetone series, dried to the critical point, and sputter-coated with gold.

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Examination was performed using a Jeol Scanning Electron Microscope (T.33A) at 30 kV linked with Semafore Software at the Regional Center of Mycology and Biotechnology, Al-Azhar University, Cairo. Trichome density was quantified by counting the number of hairs within a standardized area of 1 cm^2 at 250× magnification, while dimensions (length and width) were measured in micrometers to evaluate their physical impact on *T. absoluta* oviposition and larval establishment.

Ecological and weather factor analysis

The influence of environmental conditions on *T. absoluta* population dynamics was evaluated during the 2012 and 2013 seasons. Weekly meteorological data, including minimum and maximum temperatures and mean relative humidity (RH%), were obtained from the Central Laboratory for Agricultural Climate, Agricultural Research Center, Giza. These factors were correlated with weekly infestation rates to clarify the role of climatic fluctuations in accelerating the pest's developmental cycles and altering seasonal infestation patterns across the two years.

Statistical analysis

Data were subjected to analysis of variance (ANOVA) using IBM® SPSS® Statistics software version 19.0. Mean separation was performed using the Least Significant Difference (LSD) test at $p \leq 0.05$ to evaluate significant differences among the eight tomato cultivars. To determine whether overall infestation levels differed significantly between the two studied seasons (2012 vs. 2013), a paired-samples t-test was conducted across the tested cultivars.

Furthermore, two types of statistical tests were employed to understand the plant-insect relationship:

Simple Pearson correlation coefficients (r): Used to determine the strength and direction of the relationship between constitutive phytochemical constituents, leaf morphological traits (trichome density and length), and *T. absoluta* infestation levels.

Linear regression coefficients (b): Calculated to estimate the predictive impact and the rate of change in infestation levels as influenced by these specific biochemical and morphological parameters.

Results And Discussion

Susceptibility of tomato cultivars to *T. absoluta* infestation

Data presented in Table *1* revealed highly significant variations ($p < 0.001$) among the eight evaluated tomato cultivars regarding their susceptibility to *T. absoluta* leaf infestation during the 2012 and 2013 consecutive seasons.

In both seasons, the cultivar "Red sun" exhibited the highest susceptibility, recording the maximum mean number of leaf mines (9.2 ± 1.7 and 9.3 ± 3.2 mines/10 leaflets in 2012 and 2013, respectively). Conversely, the "Hybrid bito 86" cultivar demonstrated the highest level of natural resistance, sustaining the lowest infestation rates (5.0 ± 0 and 4.1 ± 0.6 mines/10 leaflets), closely followed by "Super set" and "Nemaguard".

Furthermore, a paired-samples t-test indicated no statistically significant difference in overall mean infestation levels between the 2012 and 2013 seasons ($t = 1.213$, $df = 7$, $p = 0.265$). Bivariate correlation analysis further confirmed a strong and significant positive correlation between the two seasons ($r = 0.894$, $p = 0.003$), demonstrating that the natural resistance and susceptibility patterns of the evaluated cultivars remained highly consistent and stable across years.

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Tomato cultivars	Mean no. of *Tuta absoluta* mines/10 leaflets (mean ± SE)	
	2012	2013
Red sun	9.2±1.7[a]	9.3±3.2[a]
Hybrid super strain	8.2±1.8[a]	7.4±1.9[b]
Castle rock	5.8±1.7[b]	7.0±1.7[b]
Riogrande	6.4±1.9[b]	5.1±0.5[c]
Baladi	5.3±0.9[c]	5.4±1.4[c]
Nemaguard	5.3±0.9[c]	4.9±0.9[c]
Super set	5.4±1.1[c]	4.7±0.5[cd]
Hybrid bito 86	5.0±0[d]	4.1±0.6[d]
F value[1]	10.5***	39.9***
LSD[2]	1.0	0.8

TABLE 1: Tomato cultivar infestation by Tuta absoluta during the 2012 and 2013 seasons at Shoubra Elkheima, Qaliubya Governorate

1 = Values determined after ANOVA using IBM SPSS Statistics software, *** signifies $p < 0.001$.

2 LSD = Least Significant Difference test for mean separation, $p \leq 0.05$. Means followed by different letters within a column are significantly different.

3 Inter-annual comparison (Paired t-test): A paired t-test revealed no statistically significant overall difference in mean infestation between the 2012 and 2013 seasons (t = 1.213, df = 7, $p = 0.265$), with a strong positive correlation between seasons (r = 0.894, $p = 0.003$).

The role of climatic variations

A noticeable variation between the two seasons was observed in cultivars like "Hybrid super strain". This variation is suggested to be influenced by climatic fluctuations". The higher mean temperature (24.1°C) and lower relative humidity (49.5%) recorded in 2013 (Figure *1*) accelerated the insect's life cycle and enhanced its reproductive potential, leading to intensified larval mining compared to the milder 2012 season (20.5°C, 62.98% RH).

These fluctuating infestation levels are highly consistent with the thermal requirements established by Rashwan et al. [10] in Egypt, who determined that the developmental thresholds for *T. absoluta* larvae and pupae are 10°C and 11.2°C, respectively. Shifting the temperature from 20°C to 24°C significantly alters life table parameters and accelerates generation time, explaining why the warmer 2013 season accumulated more day-degrees (DD's) required for rapid pest development. This environmental acceleration under open-field conditions is further supported by general ecological models of invasive pests in the Mediterranean basin [1].

Alignment with local screening studies

The distinct variation in host susceptibility observed in our study is strongly corroborated by Mahmoud et al. [11], who investigated tomato variety susceptibility under Egyptian field conditions and explicitly concluded that "Beto 86" was among the least susceptible varieties, demonstrating notable tolerance. Additionally, their documentation of high susceptibility in "Castle rock" and "Strain B" variants reinforces our recorded data, confirming that these cultivars lack the necessary natural defensive traits to mitigate larval mining effectively.

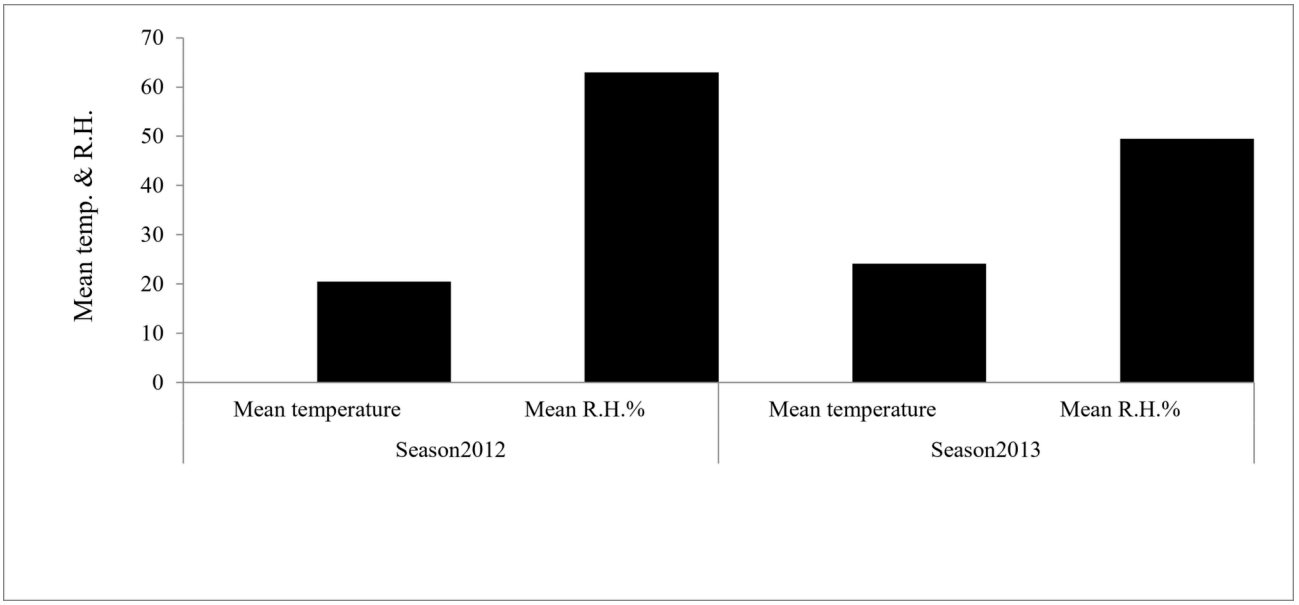


FIGURE 1: Mean temperature and relative humidity during 2012 and 2013 seasons

Biochemical factors associated with resistance

Biochemical analysis of the phytochemical components and antioxidant enzymes (Table *2*) elucidated the potential mechanisms underlying cultivar resistance.

Primary Metabolites and Macro-elements

On the other hand, positive significant correlations were detected between infestation levels and both phosphorus (r = 0.74*) and potassium (r = 0.81*) contents. Cultivars with elevated macro-elements, such as "Red sun", experienced heavier infestations, indicating that these nutrients might render the foliage more nutritionally favorable for *T. absoluta* development.

Regarding the remaining primary metabolites, nitrogen and free amino acids contents showed positive but non-significant correlations with infestation levels (r = 0.57ns and r = 0.57ns, respectively). Despite the lack of statistical significance, higher concentrations of nitrogen (10.9 mg/g DW) and free amino acids (16.6 µg alanine/g DW) were observed in the highly susceptible cultivar "Red sun", which may partially enhance its nutritional quality for larval growth. This nutritional allocation is closely linked to herbivore fitness, as reviewed by Afroz et al. [8], who highlighted that while primary nutrients like nitrogen optimize insect development, plants counter this suitability by constitutively investing energy in defensive PSMs that interfere with developmental phases, reduce nutritional value, and affect protein digestion

Secondary Metabolites and Antibiosis

A strong, highly significant negative correlation (r = -0.77*) was observed between the total phenolic content and infestation levels. The resistant "Hybrid bito 86" harbored the highest concentration of total phenols (6228.0 ± 160.9 µg GAE/g DW), whereas the susceptible "Red sun" contained the lowest level (4626.3 ± 160.9 µg GAE/g DW). This strongly suggests that phenols act as a primary chemical defense barrier against larval feeding.

Our findings regarding the defensive role of secondary metabolites are in full agreement with Vaddi et al. [22], whose screening of diverse tomato genotypes demonstrated that host resistance against *T. absoluta* is heavily governed by a combination of high total phenolic content and chemical toxicity.

The variation in infestation rates can be further explained by the biological parameters of the pest on different hosts. According to Ghaderi et al. [9], tomato cultivars significantly influence the life-table parameters of *T. absoluta*, where resistant genotypes restrict the net reproductive rate (R0) and prolong developmental time. This supports our findings, suggesting that cultivars with lower infestation rates, such as 'Hybrid bito 86', possess antibiosis factors (like high phenols) that disrupt larval development, contrary to highly susceptible cultivars like 'Red sun' which present a highly favorable nutritional profile for the pest [6]. According to Vitta et al. [6], the expression of antibiosis in wild and resistant Solanum genotypes drastically reduces larval survival and alters life-table parameters, confirming that chemical barriers play a decisive role in suppressing *T. absoluta* development.

Enzymatic Activity Responses

Peroxidase activity showed a positive trend (r = +0.68) with infestation, peaking in "Red sun" (61.5). This increase may reflect a potential physiological stress correlation associated with intensive larval mining, rather than a definitive constitutive defense mechanism. Regarding detoxification enzymes, both alpha-esterase and beta-esterase activities exhibited positive but non-significant correlations (r = 0.2ns and r = 0.24ns, respectively) with *T. absoluta* leaf mines. Cultivars like "Castle rock" and "Baladi" expressed elevated levels of these esterases, which suggests that these specific enzymatic pathways might be involved in general metabolic responses or oxidative stress management rather than direct biochemical resistance against this specific insect pest [23].

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Tomato cultivars	Mean no. of *T. absoluta* leaf mines	Phytochemical components							Antioxidant enzymes		
		Nitrogen (mg/g DW)	Phosphorus (mg/g DW)	Potassium (µEq/g DW)	Free amino acid (µg alanine /g DW)	Total protein (mg/g DW	Total carbohydrate (mg/g DW)	Total phenol (µg GAE/g DW)	Alpha esterase (µg α-naphthol/min/g DW)	Beta esterase (µg β-naphthol/min/g DW)	Peroxidase (ΔO.D. 405/min/g DW)
Red sun	9.3^{a}	10.9±0.5^{ab}	1956.7±38.5^{a}	550±28.8^{a}	16.6±0.9^{a}	67.9±2.8^{a}	125.3±5.9^{c}	4626.3±130.6^{g}	260.7±11.9^{c}	241.3±8.6^{c}	61.5±3.7^{a}
Hybrid super strain B	7.4^{b}	7.0±0.5^{d}	781.0±28.8^{e}	433.0±13.2^{bc}	4.6±0.4^{e}	45.4±3.1^{de}	107.0±4.0^{ef}	5613.0±115.4^{c}	227.0±15.5^{d}	192.0±6.9^{d}	18.3±1.3^{e}
Castle rock	7.0^{b}	11.5±0.8^{a}	1317.0±57.7^{b}	436±20.7^{b}	5.8±0.2^{d}	69.8±3.3^{a}	124.0±4.0^{c}	4833.7±173.3^{f}	423.7±13.2^{a}	323.3±7.6^{a}	32.4±1.4^{c}
Riograndе	5.1^{c}	7.3±0.2^{d}	746±13.3^{ef}	382.3±9.8^{d}	5.0±0.3^{de}	46.9±2.2^{d}	136.0±8.6b	5136.0±78.5^{e}	209.7±5.7^{d}	195.7±9.1^{d}	22.7±2.1^{d}
Baladi	5.4^{c}	10.1±0.2^{bc}	1144.3±65.8^{d}	389.3±11.5^{d}	13.4±0.8^{b}	61.8±2.8^{b}	113.0±6.3ed	5650.0±86.6^{c}	405.7±8.5^{a}	283.0±13.3^{b}	54.5±2.6^{b}
Nemaguard	4.9^{cd}	9.2±0.2^{c}	1254.7±31.5^{c}	394.7±11.5^{d}	7.7±0.4^{c}	57.2±2.8^{c}	149±4.0a	5330.3±57.7^{c}	322.3±12.8^{b}	289±5.2^{b}	17.9±1.1^{e}
Super set	4.7^{cd}	6.3±0.2^{d}	668±10.3^{g}	448.7±6.7^{b}	4.9±0.1^{de}	39.2±1.8^{f}	120.3±2.9cd	5845.3±26.1^{b}	316±9.2^{b}	194.7±8.5^{d}	16.2±0.7^{ef}
Hybrid bito86	4.1^{d}	6.8±0.5^{d}	696.0±11.5^{gf}	403.3±10.4^{cd}	4.2±0.1^{e}	41.6±1.7^{ef}	101.3±3.6^{f}	6228±73.9^{a}	214.3±8.8^{d}	182±6.9^{d}	13.9±1.1^{f}
F value	39.9***	43.1***	532.7***	29.2***	149.3***	72.9***	30.6***	98.4***	109.7***	25.3***	277.2***
LSD	0.8	0.93	57.6	30.2	1.1	4.2	8.4	160.9	24.1	32.5	3.3
r		0.57ns+	0.74*+	0.81*+	+0.57 ns	+0.61 ns	-0.02 ns	-0.77*	+0.2 ns	0.24 ns+	+0.68 ns
b			0.002+	+0.026				-0.002			

TABLE 2: Relationships between the content of phytochemical components and antioxidant enzymes in leaves of eight tomato cultivars and the mean number of Tuta absoluta mines per 10 leaflets during the 2013 season

Values represent mean ± SE. Means within a column followed by the same letter are not significantly different ($p < 0.05$) according to LSD test. r refers to Pearson's correlation coefficient between infestation levels and biochemical parameters. b: Regression coefficient Significance levels: * Significant at $p < 0.05$; ** Significant at $p < 0.01$*** Significant at $p < 0.001$; ns = non-significant; DW = Dry weight; LSD = Least Significant Difference

Leaf morphological features (Trichomes) and their role in resistance

The physical and structural characteristics of leaf surfaces play a pivotal role in mediating host plant selection by *T. absoluta*. SEM (Figure *2*) and data presented in Table *3* illustrated clear variations in the types, densities, and dimensions of both glandular and non-glandular trichomes across the studied tomato cultivars.

Glandular Trichomes as Barriers

Regarding glandular trichomes (characterized by their specialized secretory heads as shown in Figure *2* Right, Type II), an interesting negative trend (r = -0.65ns) was observed with infestation levels on the upper leaf surface. The resistant "Hybrid bito 86" cultivar contained the highest upper density of glandular trichomes (5 per cm^2), while the susceptible "Red sun" harbored only 1 per cm^2.

Although this relationship did not reach statistical significance, it underscores a potential mechanical and chemical barrier, where the exudates (such as acylsugars, terpenoids, and methylketones) from secretory heads could impede larval movement, entrap neonate larvae, or act as an oviposition deterrent. This is heavily supported by Darbain et al. [24], who reported that *T. absoluta* infestation in Egypt is strongly influenced by leaflet trichomes, where increased glandular trichome density significantly reduces infestation rates. Furthermore, Sohrabi et al. [5] evaluated various tomato cultivars and demonstrated that significant differences in leaf damage were directly linked to host morphological features, highlighting that leaf trichome density serves as a fundamental component of plant resistance against *T. absoluta*. Our results indicate that trichome density, rather than physical dimensions (length and width yielded non-significant correlations; Table *3*), is the primary morphological determinant influencing *T. absoluta* resistance. This strongly justifies the approach of integrating both chemical profiling (phenols) and structural traits (glandular trichomes) into cultivar selection for sustainable IPM programs against this devastating pest.

The Paradox of Non-Glandular Trichomes

Statistical analysis revealed a highly significant and strong positive correlation (r = 0.85**) between the density of non-glandular trichomes on the upper (adaxial) leaf surface and the mean number of *T. absoluta* leaf mines. The highly susceptible cultivar "Red sun" possessed the highest upper density of non-glandular trichomes (29 per cm^2), which are morphologically characterized by their elongated, tapering structures (Figure *2* Left, Type I). In contrast, the most resistant "Hybrid bito 86" exhibited the lowest density (15 per cm^2).

This critical finding suggests that a high density of non-glandular trichomes on the upper surface may potentially provide a supportive microenvironment or physical anchorage, hypothetically assisting adult females in oviposition (egg-laying) and shielding the eggs from adverse environmental factors or predators, thereby leading to a higher probability of intensified larval infestation. On the lower (abaxial) surface, non-glandular density showed a positive but non-significant correlation (r = 0.33ns).

Interestingly, this physical defense role presents a contrasting mechanism compared to piercing-sucking pests on the same hosts. Helmi and Mohamed [7] demonstrated that a high density of non-glandular trichomes on tomato cultivars in Qalyubiyah acted as a deterrent barrier that reduced the population density of *A. gossypii*. Conversely, our findings show a completely opposite trend for *T. absoluta.* This dual and opposing function indicates that while dense non-glandular trichomes effectively impede aphids' mechanical stylet insertion, they are hypothesized to concurrently offer an optimal

microenvironment that could facilitate oviposition for *T. absoluta* females, as suggested by previous literature. This complexity in resistance expression perfectly aligns with Vitta et al. [6], who demonstrated that resistance-level characterization heavily depends on the specific insect response evaluated; for instance, certain genotypes were highly non-preferred for oviposition (antixenosis) yet exhibited high larval survival in no-choice bioassays, reinforcing the fact that adult host selection and larval performance are mediated by distinct structural and biochemical traits.

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Tomato cultivars	Mean no. of *T. absoluta* leaf mines	Tricomes (250×)									
		Glandular						Non-glandular			
		Upper			Down			Upper		Down	
		Density No./cm2	Length µm	Width µm	Density No./cm2	Length µm	Width µm	Density No./cm2	Length µm	Density No./cm2	Length µm
Red sun	9.3[a]	1	86	51	0	0	0	29	170.5	67	183.2
Hybrid super strain B	7.4[b]	0	0	0	2	65	45	20	109.2	65	145.5
Castle rock	7.0[b]	2	56.2	46.2	1	95	68	20	111.9	50	180
Riogrande	5.1[c]	2	94	47	2	91.5	72	20	95.5	42	210.7
Baladi	5.4[c]	0	0	0	0	0	0	20	110.4	45	158.5
Nemaguard	4.9[cd]	4	85	60	0	0	0	20	91.9	77	135.6
Superset	4.7[cd]	4	105	68	2	106	78	19	98.7	67	129.8
Hybrid bito86	4.1[d]	5	91	65	0	0	0	15	144.5	38	168.9
F value	39.9***										
LSD	0.8 mine										
r		0.65ns-	0.27ns-	0.30ns-	0.04ns-	0.05ns-	-0.07ns	0.85**+	0.55ns+	0.33ns+	0.24ns+
b								0.4 +			

TABLE 3: Effect of different physical features of glandular and non-glandular trichomes on the leaflet surfaces of eight tomato cultivars and their relationship with Tuta absoluta infestation (250×)

r refers to Pearson's correlation coefficient between infestation levels and biochemical parameters.

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b = Regression coefficient Significance levels: *** Significant at $p < 0.001$. LSD = Least Significant Difference

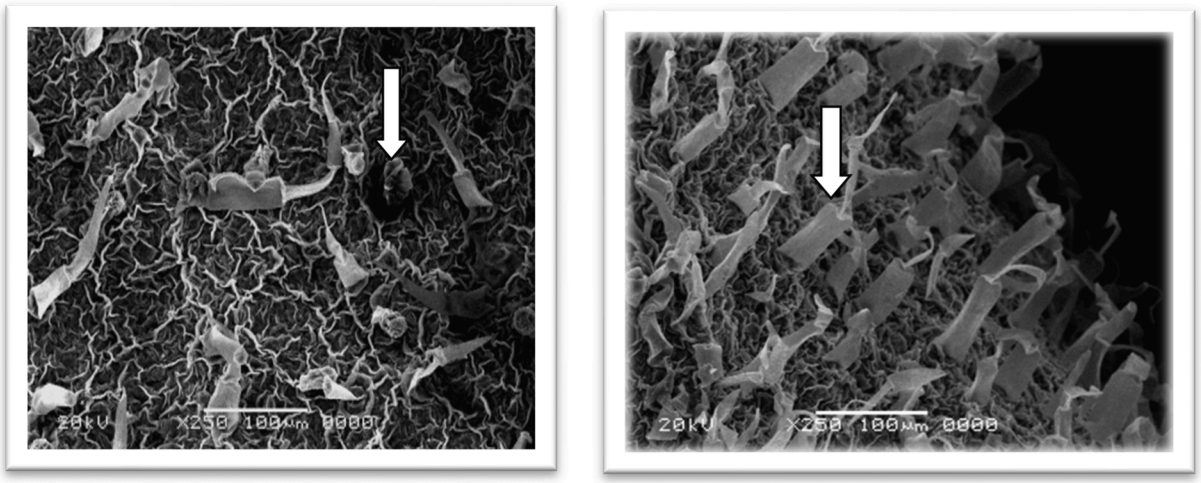


FIGURE 2: Scanning electron micrographs (SEM) of tomato leaf surface showing different trichome types

(Left) Type I = Representative image of non-glandular trichomes characterized by their elongated, tapering structure.
(Right) Type II = Representative image of glandular trichomes (indicated by the arrow) showing the specialized secretory heads.
Note: These micrographs illustrate the morphological variations observed across the studied cultivars (Scale bar = 100 µm)

Principal Component Analysis

A Principal Component Analysis (PCA) with Varimax rotation was conducted to evaluate the spatial distribution and multivariate ordination of the eight tomato cultivars based on all quantified morpho-anatomical and biochemical traits (Figure *3*). The rotated principal components (PC1 and PC2) accounted for a cumulative variance of 55.60%, where PC1 explained 31.81% and PC2 contributed 23.78% of the total variance.

The PCA scatter plot clearly resolved the tested cultivars according to their distinct field performance and resistance levels. Cultivar "Red Sun" separated distinctly in the positive region of PC1, correlating with increased non-glandular trichome densities and nutrient contents. Conversely, the highly resistant cultivar "Hybrid Bito 86" was located in the opposite sector, associated with elevated total phenolics and reduced infestation traits. The remaining cultivars clustered in intermediate spatial positions reflecting their moderate response profiles.

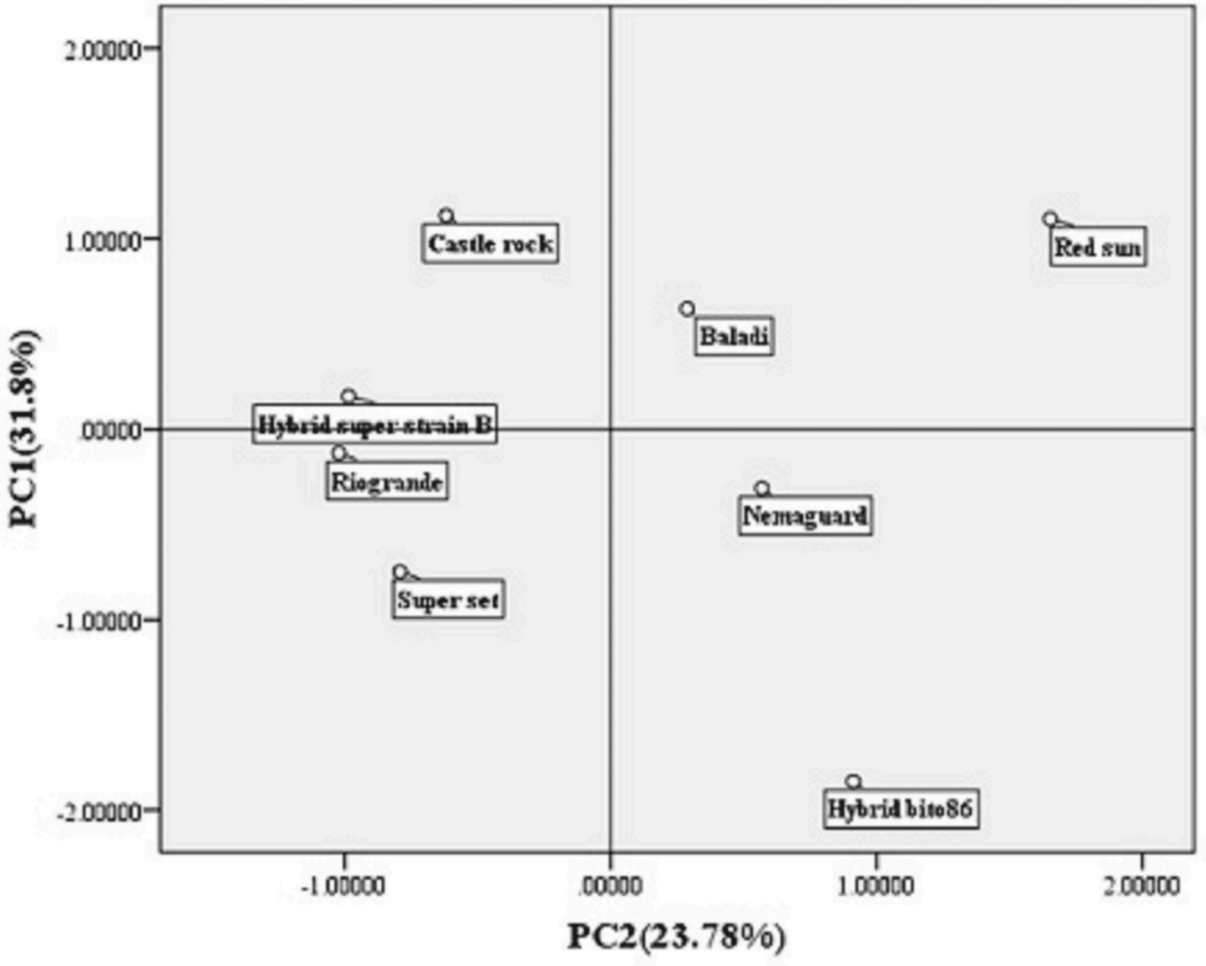


FIGURE 3: Principal Component Analysis (PCA) score plot illustrating the multivariate clustering and spatial distribution of the tested tomato cultivars according to their resistance profiles to T. absoluta

Conclusions

This study demonstrates that host plant resistance in tomato cultivars against *T. absoluta* is strongly associated with a synergistic combination of biochemical antibiosis and physical antixenosis. High total phenolic content serves as a primary chemical defense mechanism that reduces larval mining efficiency, as exhibited by the resistant cultivar "Hybrid Bito 86". Conversely, elevated leaf phosphorus and potassium levels enhance host nutritional favorability, contributing to the high susceptibility observed in "Red Sun". Morphologically, a higher density of non-glandular trichomes on the adaxial leaf surface facilitates infestation by offering oviposition cues and physical anchorage for adult females. Integrating multivariate PCA confirmed that cultivars combining elevated phenolic toxicity with reduced adaxial non-glandular trichome densities - specifically "Hybrid Bito 86" - provide strong natural resistance. Consequently, "Hybrid Bito 86" represents potential genetic candidate for resistance breeding and can serve as a useful baseline component within IPM programs, effectively reducing chemical insecticide dependence in Egypt.

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Additional Information

Author Contributions

All authors have reviewed the final version to be published and agreed to be accountable for all aspects of the work.

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Disclosures

Plant subjects: All authors have confirmed that this study did not involve any herbarium specimen.

Human subjects: All authors have confirmed that this study did not involve human participants or tissue.

Animal subjects: All authors have confirmed that this study did not involve animal subjects or tissue.

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- **Payment/services info:** All authors have declared that no financial support was received from any organization for the submitted work.
- **Financial relationships:** All authors have declared that they have no financial relationships at present or within the previous three years with any organizations that might have an interest in the submitted work.
- **Other relationships:** All authors have declared that there are no other relationships or activities that could appear to have influenced the submitted work.

Data Availability Statements

The datasets (and/or code) supporting this study are available from the corresponding author upon reasonable request.

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