RESEARCH ARTICLE OPEN ACCESS

NEW VALLEY JOURNAL OF AGRICULTURAL SCIENCE

Published by Faculty of Agriculture, New Valley University, Egypt

Print ISSN 2805-2420 **Online ISSN** 2805-2439

10.21608/NVJAS.2023.205111.1197

The Role of Trichomes Type and Density in The Resistance Mechanism of Some Tomato Varieties to Tomato Leafminer Tuta Absoluta (Meyrick) (Lepidoptera: Gelechiidae)

Marwa F. K. Aly*

Department of Plant Protection, Faculty of Agriculture, Minia University, El-Minya, Egypt.

*** Corresponding author**

Marwa F. K. Aly

Received: 09/04/2023

Revised: 05/08/2023

Accepted: 13/08/2023

Published: 13/08/2023

Abstract

Tomato leafminer *Tuta absoluta* is one of the most devastating pests of tomato (*Solanum lycopersicum*) worldwide. This study compared the distribution of the *Tuta absoluta* infesting three commercial *Lycopersicon lycopersicum* tomato varieties (Early girl, Roma and Rutgers) and two closely related *Lycopersicon spp.* presumed to be resistant (LA 716 and PI 134417) in response to leaflets trichomes. The number of *Tuta absoluta* mines blotches, larvae and damaged leaf area% were determined for individual leaflets on every half branch of five plants per variety. ÷In addition, the density of non-glandular and glandular trichomes were assessed in the same leaflet samples. *T. absoluta* infestations were only found on Early girl< Roma and Rutgers. *Tuta absoluta* mines, larvae, and damaged leaf area% were absent from the younger branches except Roma variety, appeared in the middle and increased toward the oldest branches indicating a positive relationship with leaflet and branch age. Obviously, the densities of both non-glandular and glandular trichomes were greatly higher in younger branches and gradually decreased in the mature or fully developed branches and oldest branches or senescing leaflets. No non-glandular trichomes were found on LA 716, but it had the greatest number of glandular trichomes than other tomato varieties. High negative correlation was found between number of mines, larvae and damaged leaf area and number of non-glandular and glandular trichomes. These results showed that commercial varieties have potential vulnerabilities to *T. absoluta* not present in closely related species suggesting plant attributes that could be exploited in breeding programs.

Keywords: Non-glandular and glandular trichomes, Resistance, *Tomato leafminer*, Wild tomato

Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most economically important vegetable crops worldwide (**FAO 2015and El Balla et al., 2013**). Egyptian tomatoes are considered the fifth largest producer of tomatoes worldwide. At the national level, tomato is ranked as the first crop among vegetables in terms of total production capacity and cultivated area. In 2015, the area cultivated with tomato was estimated at 469 000 feddans, representing 32% of the total area cultivated with vegetables in Egypt (**FAO 2019**). Tomato plants are infested with numerous insect pest. One of the most invasive pests that attack it; is the tomato leafminer *Tuta absoluta* (Meyrick**)** (Lepidoptera: Gelechiidae) (**Biondi et al., 2018 and Mansour el al., 2018**). *Tuta absoluta* is native to Peru in South America and since the early 2000s, it has spread through the rest of America, Africa, Europe, and Asia. (**Yule et al., 2021**). *Tuta absoluta* larvae feed on the mesophyll of aerial parts of host plants, producing large galleries (blotch mines) in leaves, stems, apics, flowers and fruits (**Miranda et al., 1998 and Cherif et al., 2019**), leading to heavy losses causing up to 100% yield losses (**Apablaza, 1992; Mohamed et al., 2012**). Insecticides are widely used to suppress the high *T. absoluta* population in Egypt because of their suitable climate temperatures (**Mohammed, 2015**). Consequently, increasing the risk of insecticide resistance and harm to the environment and non-target organisms. Another approach management strategy is to improve the genetic resistance of the crop to *Tuta absoluta* is planting pest-resistant genotypes (**Silva et al., 2011**). Wild species of tomato are often adopted as a source of resistance to pests and diseases in the improvement of commercial cultivars of tomato (**Lima et al., 2016; Lucini et al., 2015**), such as the species *Solanum pennellii*, accession 'LA-716', which shows resistance to pests such as *Tuta absoluta* (**Moreira et al., 2013; Dias et al., 2019**). The mechanisms related to natural resistance are classified into three main groups: antixenosis (or non-preference), antibiosis and tolerance (**Fancelli et al. 2005**). Where antixenosis and antibiosis are considered the major mechanisms responsible for tomato genotypes' natural resistance to arthropod pests (**Shapiro et al. 1994; Oliveira et al. 2009**).

Trichomes are considered the most necessary factor conferring pest resistance. Glandular trichomes produce allelochemicals that provide a resistance mechanism to tomato leaflets (**Gianfagna et al. 1992; Ecole et al. 1999; Maluf et al. 2007**). The genus *Solanum* possesses seven types of trichomes: types II, III and V are non-glandular, and types I, IV, VI and VII are glandular (**Gurr and McGrath 2001**; **Simmons and Gurr 2005**). Additionally, glandular trichomes secrete secondary metabolites including acylsugars, methylketones and sesquiterpenes that probably be toxic, repellent, trap insects or act as a physical barrier, and interfere with insect feeding, oviposition (**Dimock and Kennedy 1983; Snyder and Carter 1984; Sharma et al. 2009**) and has harmful impacts on their development (**Simmons et al. 2003; Resende et al. 2006**). Therefore, this study aimed to evaluate the resistance mechanism of tested tomato varieties to *Tuta absoluta*, to determine if some tomato leaflet morphological characteristics, such as trichomes, could confer the plant resistance to this pest. Characterization of the resistance mechanism would facilitate the use of these tomato genotypes in breeding programs.

Materials and Methods

1. *Tuta absoluta* rearing colony

The insect colony was initiated from collected samples of infested tomato leaflets with *T. absoluta* larvae from growing tomatoes in the field. The laboratory colony was maintained following the methodology of **(Silva et al., 2011)**, and kept under controlled conditions (25±2 °C, 70± 5 R. H.% and 16 h L: 8 h D photoperiod). The insects were reared in wooden cages (40×40×40 cm) covered with fine mesh netting. One cage was used for oviposition; one for maintaining the leaflets with eggs and first instar larvae; one containing second, third and fourth instar larvae and one cage for pupae and adult emergence. The larvae were fed on tomato leaflets, cultivated in a greenhouse without the application of insecticides.

2. Tomato cultivation and sampling

Five tomato varieties were selected to evaluate their susceptibility and resistance to *T. absoluta*. Three presumed susceptible and two assumed resistant varieties as notable in **(Table 1)**.

Table (1): Tested tomatoes varieties and their pest resistance status according to the seed source.

Tomato variety	Scientific name	Variety type	Defense against pests
Early Girl Hybrid	*Lycopersicon lycopersicum*	Commercial	Susceptible
Italian Roma	*Lycopersicon lycopersicum*	Commercial	Susceptible
Rutgers	*Lycopersicon lycopersicum*	Commercial	Susceptible
LA 716	*Lycopersicon pennellii*	Wild	Resistant
PI 134417	*Lycopersicon hirsutum f. glabratum*	Wild	Resistant

Individual tomato plants were grown from seed in 4-inch pots without pesticide treatments. Each variety was sown to provide five replicate plants. Plants were watered as needed to keep the soil moist once the seed was planted. Fertilizer (3.5g) was mixed with the soil at planting. Plants were transferred to a cage covered with off-white Dacron chiffon netting to confine T. absoluta. Each variety was kept inside a separate cage in the greenhouse where temperature and light can be maintained under summertime conditions. Ten mated females were released inside each cage and kept for 10 days to allow females for oviposition when the plants were 45 days old. Leaflet samples were collected from infested plants systematically from each plant replicate for the half of each branch (one side) to determine T. absoluta parameters (number of mine blotches, larvae, and damaged leaf area %) and leaflet trichomes densities (non-glandular and glandular trichomes per mm2). All leaflets on half of each opposing branch, including the apical leaflet were collected from five infested plants/varieties. Leaflet samples were tracked with respect to leaf branch and leaflet position **(Figure 1)** and kept in Ziplock bags and transferred to the laboratory to quantify *T. absoluta* and leaflet traits parameters.

3. Quantification of non-glandular and glandular trichomes

Three predetermined locations were selected on each sampled leaflet to quantify trichomes. Digital images of the leaflet sample locations were acquired using a dissecting microscope (Leica MI25, Wetzlar, Germany) attached to a Leica EC3 ICC50 camera (Leica, Wetzlar, Germany) with a magnification of 2.0X=1.00. Counts were made of the number of glandular and non-glandular trichomes for each sample. The microscope and software operated on a Dell Optiplex GX 280 computer. Each image was calibrated at 1 Pixel= 0.0032 mm using Leica Application Suite Software. The number of glandular and non-glandular trichomes for each leaflet sample were counted and measured by creating a 1mm^2 **(Figure 2).**

4. Damaged leaf area (mines) measurement

The individual leaflet was scanned digitally using a Hewlett-Packard ScanJet 4850 desktop scanner. The leaflet was placed on the scanner; the lid was closed, and the scan was displayed. The images were saved as TIFF file. Digital images were analyzed using Adobe Photoshop CS2 to measure the damaged leaf area (cm).

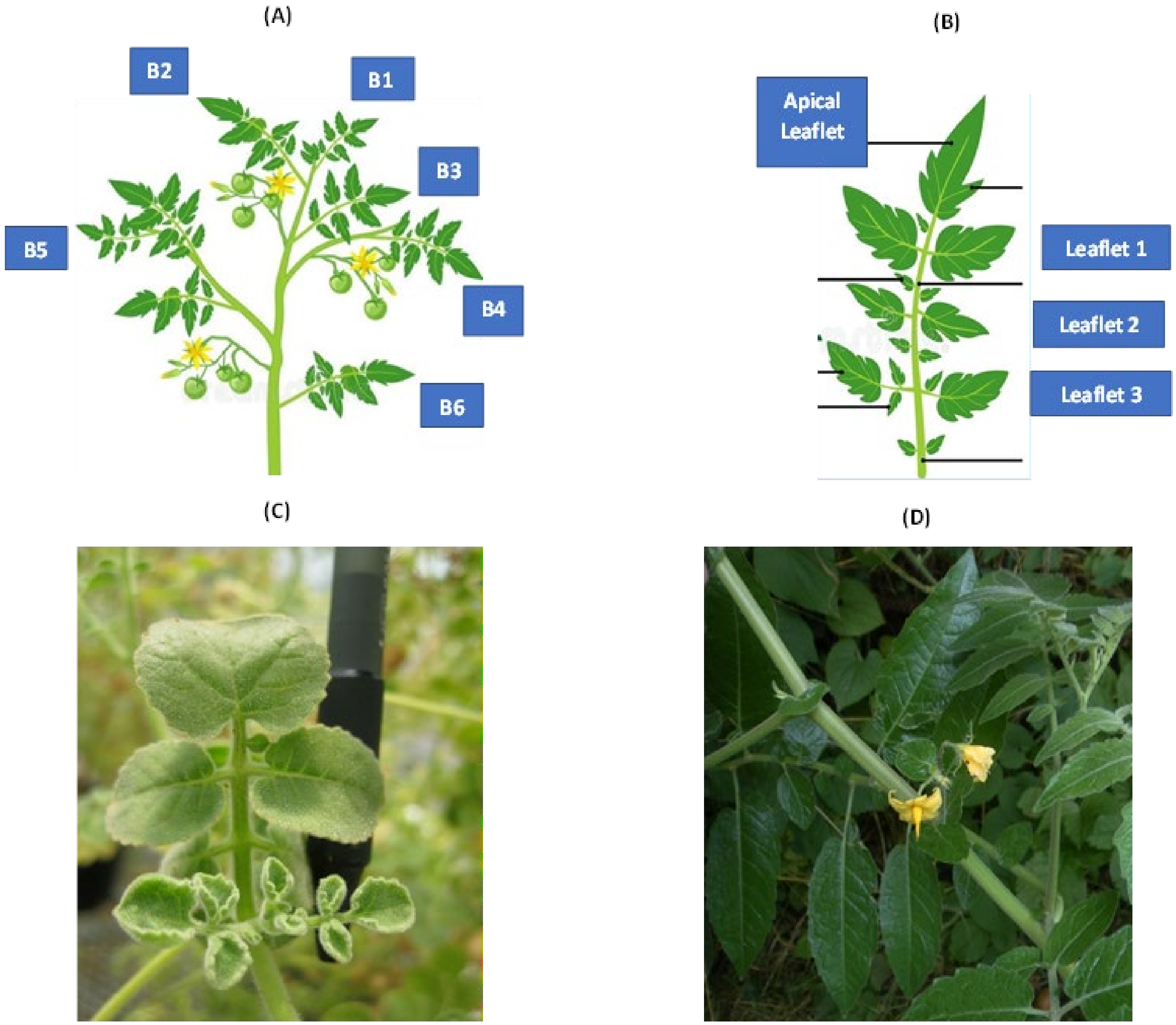

Figure (1): Tomato plant morphology and the way of leaflet sampling. A: Tomato plants represented leaflets in branches, B: Tomato leaflets in separate branch and their consequence into the branch, C: LA 716 Lycopersicon pennellii and D: PI 133417 Lycopersicon hirsutum f. glabratum Wild resistant tomato varieties

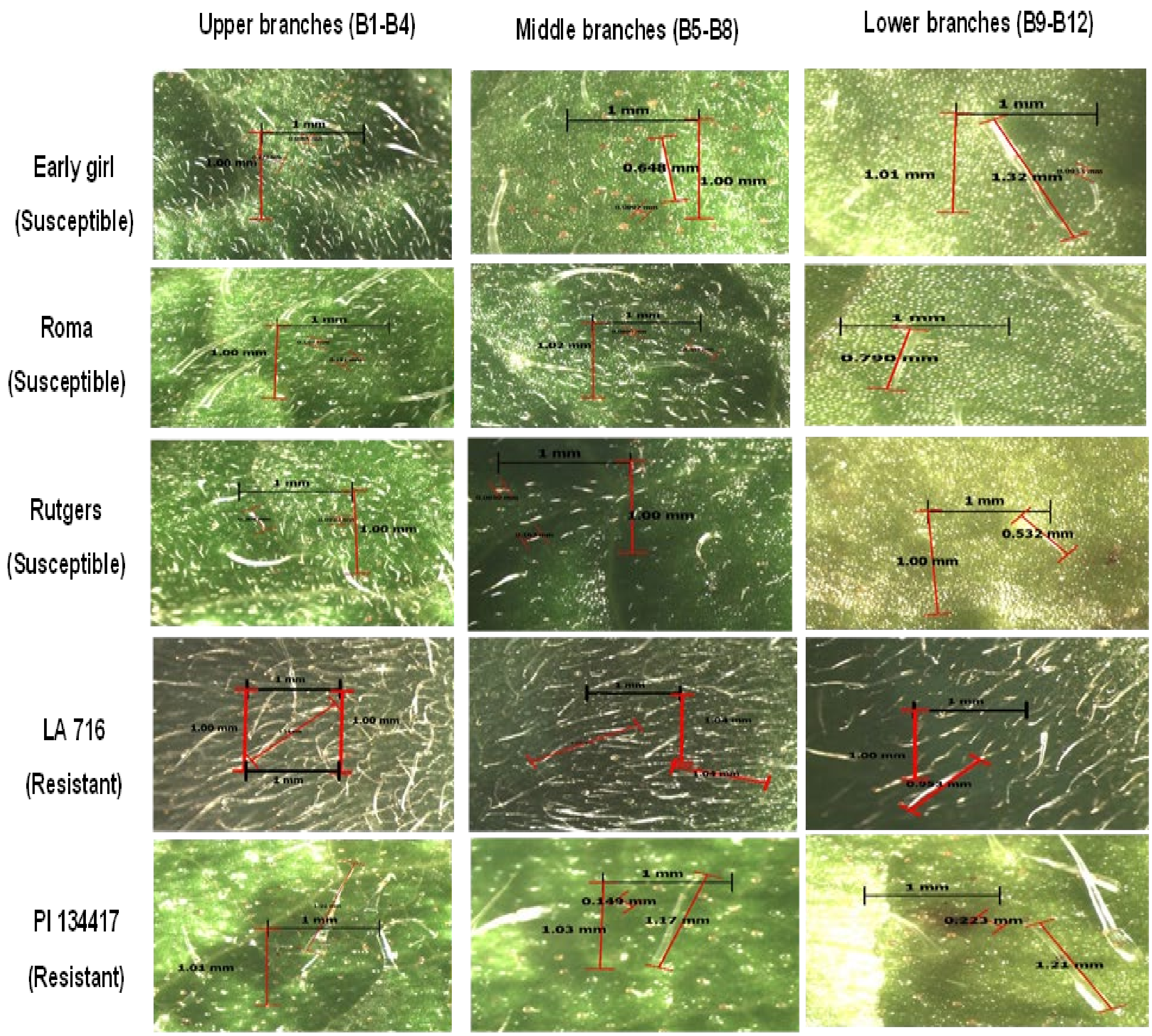

Figure (2): Non-glandular and glandular trichomes measured per mm² in upper (B1-B4), middle(B5-B8) and lower branches (B9-B12) of different evaluated tomato varieties. B is an abbreviation for branch.

5. Data analysis

The data were statistically analyzed by analysis of variance (one-way and two-way ANOVA) and the group means were compared by Tukey-Kramer HSD multiple range test at 0.01 and 0.05 Probability level using JMP Pro 16 (SAS 2013, Cary, NC). In addition, pairwise Correlation was carried out to investigate the relationship between *T. absoluta* parameters (number of mines, number of larvae and damaged leaf area%) and tomato leaflets traits (densities of non-glandular and glandular trichomes).

Results

1. Trichomes density and type

The density of non-glandular and glandular trichomes (per mm^2) was counted on half branch starting from first branch to the last branch for each evaluated tomato **variety (Table 2).** Non-glandular and glandular trichomes were found on all tomato varieties at comparatively low levels except LA716, which did not have non-glandular trichomes but had the greatest number of glandular trichomes. Apparently, the densities of both trichomes types were greatly higher in younger branches

Table (2): Mean± SE of non-glandular and glandular trichomes density (per mm^2) on half branch (4 leaflets) from the first branch to the last branch of the plant for different tomato varieties

Tomato cultivars	Trichomes density (per mm^2)														
	Non-glandular trichomes/ half branch														
	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15
Early girl	21.9±0.9	19.5±0.9	20.9±0.7	14.8±1.0	10.2±2.2	6.2±1.0	1.7±0.4	0.9±0.1	0.9±0.1	-	-	-	-	-	-
Roma	23.6±2.3	21.0±0.7	20.1±1.0	14.8±0.7	9.7±0.9	7.3±0.7	3.4±0.6	2.3±0.3	2.5±1.2	0.9±0.1	1.2±0.2	0.6±0.1	0.8±0.5	-	-
Rutgers	28.3±0.1	21.3±2.0	21.1±1.0	18.0±1.1	12.8±1.2	7.3±1.4	4.1±0.9	2.9±0.8	1.2±0.3	0.8±0.1	0.6±0.1	0.9±0.3	-	-	-
LA 716	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	
PI134417	1.5±0.1	1.4±0.1	1.4±0.1	1.5±0.02	1.3±0.1	1.1±0.1	1.0±0.1	1.0±0.1	1.0±0.04	1.1±0.1	0.9±0.09	1.0±0.06	0.7±0.07	0.4±0.1	0.0±0.0
	Glandular trichomes/ half branch														
Early girl	14.7±0.7	15.5±1.6	10.6±2.1	4.6±1.3	3.6±0.8	1.4±0.6	0.1±0.1	0.0±0.0	0.0±0.0	-	-	-	-	-	-
Roma	16.8±0.8	14.0±0.5	13.4±0.6	9.4±1.1	6.0±1.2	3.7±0.4	2.1±0.3	1.6±0.4	1.5±1.1	0.1±0.06	0.1±0.1	0.06±0.06	0.0±0.0	-	-
Rutgers	21.9±0.1	19.4±0.8	15.2±1.9	13.3±1.0	6.6±1.2	3.9±0.9	1.9±0.5	0.2±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	-	-	-
LA 716	19.7±0.2	19.7±0.4	20.7±0.4	19.8±1.1	19.2±0.7	17.1±0.5	16.7±0.9	15.0±1.4	14.0±0.7	12.6±0.9	11.3±0.3	12.8±0.3	10.9±0.5	11.3±0.7	-
PI134417	15.4±0.2	14.2±2.5	12.0±0.4	11.8±0.2	10.4±0.3	9.5±0.7	7.9±0.6	6.6±0.2	5.5±0.6	4.5±0.4	3.4±0.3	2.9±0.3	2.2±0.3	1.8±0.3	1.5±0.1

(from the 1st branch to the 4th branch) and gradually decreased in the mature or fully developed branches (the 5th branch to the 8th branch) and oldest branches or senescing leaflets (the 9th branch to the 12th branch). Significant differences were found between branches in non-glandular trichomes (DF=8, F=73.9, P< 0.0001) and variety*branch (DF=44, F=11.6, P< 0.0001). Results for non-glandular trichomes showed that Early Girl, Roma and Rutgers had a significantly high number of non-glandular trichomes than LA 716 and PI134417. The number of non-glandular trichomes of the 1st branch to the 4th branch for Early Girl, Roma and Rutgers ranged between 14.8-28.3 trichomes. Branches for the same varieties from the 5th branch to the 8th branch had < 13 trichomes, while from the 9th branch to the 13th branch possessed < 3 trichomes. PI 134417 had an almost stable number of non-glandular trichomes from the 1st branch to the 13th branch < 2 trichomes, then started to decrease where no non-glandular trichomes were found in the 15th branch. No non-glandular trichomes were observed on LA 716 for the whole branches. Glandular trichomes were also differed between branches (DF=8, F=95.6, P< 0.0001) and variety*branch (DF=44, F=4.5, P< 0.0001). LA 716 showed the highest number of glandular trichomes from the 1st branch until the 14th branch, ranging between 10.9-20.7. PI 134417 recorded a range of 11.8-15.4 trichomes from the 1st branch to the 4th branch, 6.6-10.4 trichomes from the 5th branch to the 8th branch and 1.5-5.5 trichomes from the 9th branch to the 15th branch. Mostly of younger branches (branch 1- branch 4) for Early girls, Roma and Rutgers possessed a high number of glandular trichomes < 22. However, mature branches (branch 5- branch 8) had < 7 trichomes, while the oldest branches showed <2 trichomes decreased to zero in Early girl and Rutgers.

The overall mean number of non-glandular and glandular trichomes was estimated for each third of the plant, presenting the upper third (branch 1 to 4), middle third (branch 5 to branch 8), and lower third (branch 9 to branch 12). Tomato varieties significantly differed in non-glandular and glandular trichomes (DF=4, F=36, and 29, P <0.0001). Rutgers and Early girl showed significantly higher overall mean numbers for non-glandular trichomes (11.0 trichomes) followed by Roma (9.0 trichomes) than LA 716 and PI 134417 (zero and one trichomes, respectively). For the overall mean number of glandular trichomes, LA 716 (16.0 trichomes) had the significantly greatest number of glandular trichomes compared to other tested varieties, ranging between 5.8-7.6 trichomes (**Figure 3**).

Additionally, the number of non-glandular and glandular trichomes significantly differed among leaflet positions per variety (Figure 3). Roma and Rutgers had significantly more non-glandular trichomes and glandular trichomes (non-glandular: DF=2, F=51.8, P <0.0001, glandular: DF=2, F=48.2, P <0.0003 for Roma) (non-glandular: DF=2, F=37.3, P <0.0001, glandular: DF=2, F=45.1, P <0.0001 for Rutgers) on upper branches than middle and lower branches. The number of non-glandular trichomes on upper branches for Roma and Rutgers was 19.9 and 22.2 trichomes, respectively. While middle and bottom branches had fewer non-glandular trichomes ranging between 0.9-6.8 trichomes. The upper branches for those varieties had more glandular trichomes 13.4 and 17.4 trichomes than the middle and bottom branches, which exceeded 3.5 trichomes. In contrast, no glandular trichomes were found on lower branches for Rutgers. The number of non-glandular and glandular trichomes significantly differed among leaflet positions for Early girl (non-glandular: DF=2, F=42.4, P <0.0003, glandular: DF=2, F=47.4, P <0.0002). Upper branches had the most significant number of non-glandular trichomes (20.8 trichomes) than middle and lower branches (10.4 and 1.2 trichomes, respectively). Upper branches showed the most significant number of glandular trichomes (13.6 trichomes) than the middle (3.2 trichomes) and lower branches (0.03 trichomes), which did not

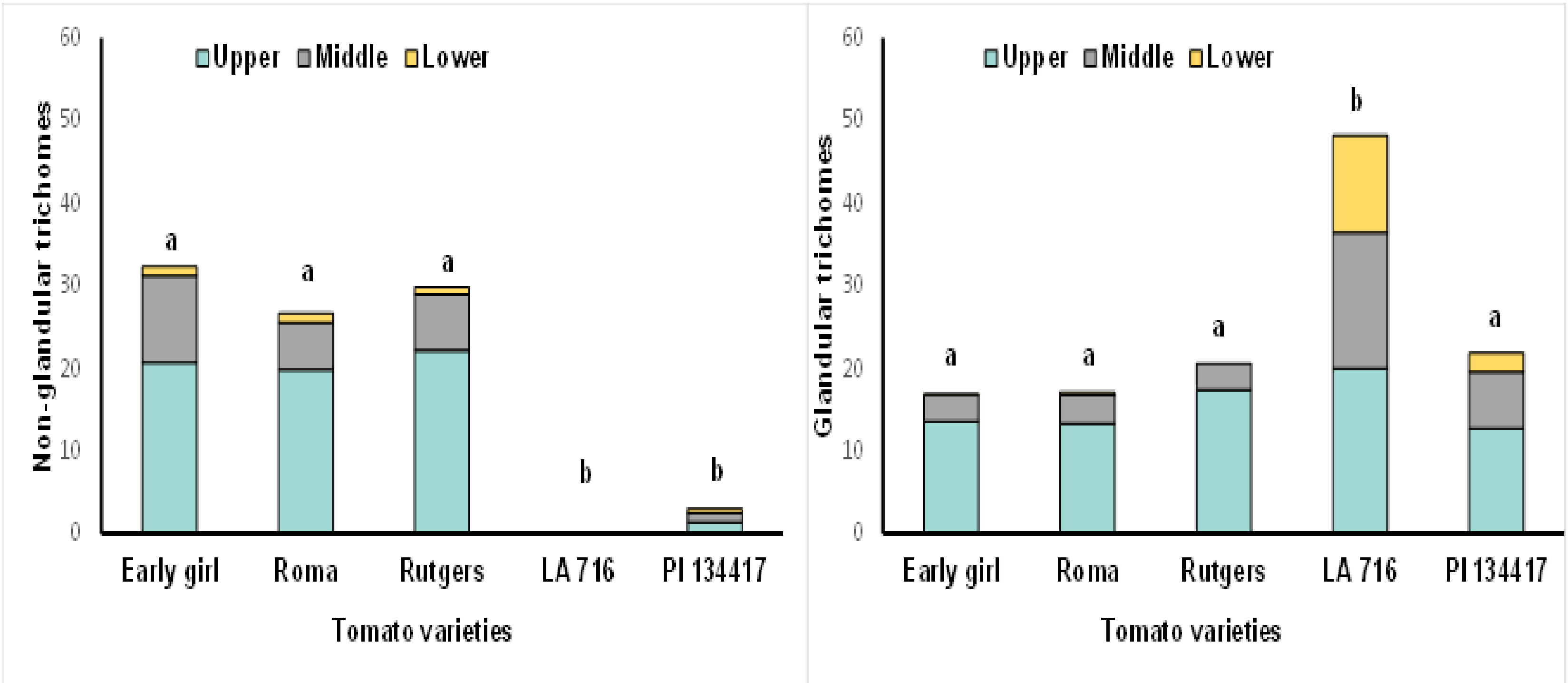

Figure (3): Overall mean number of non-glandular and glandular trichomes on upper third (branch 1-branch 4), middle third (branch 5-branch 8) and lower third (branch 9-branch 12) of the plant counted in half branch for tomato varieties. Columns followed by the same letter are not significantly different (P < 0.05) Tukey-Kramer HSD (P <0.01)

significantly differ from each other. No non-glandular trichomes were observed on LA 716. But the number of glandular trichomes was significantly higher in the upper branches (20 trichomes) compared to the middle (16.4 trichomes) and lower branches (11.8 trichomes) (DF=2, F=42.3, P <0.0001). The number of non-glandular and glandular trichomes differed among upper, middle, and lower branches (non-glandular: DF=2, F=16.0, P <0.0004, glandular: DF=2, F=49.0, P <0.0001) in PI 134417. Upper and middle branches had almost the same number of non-glandular trichomes (1.4 and 1.0 trichomes, respectively), but greatly higher than lower branches (0.6 trichomes) **(Figure 4).**

The overall average number of non-glandular and glandular trichomes was estimated and compared for each branch position among varieties presenting upper branches (branch 1 to branch 4), middle (branch 5 to branch 8), and lower (branch 9 to branch 12**) (Table 3).** No non-glandular trichomes were recorded on LA 716 for all upper, middle, and lower branches. Upper branches significantly differed among varieties in both non-glandular and glandular trichomes (non-glandular: DF=4, F=74.4, P < 0.0001, glandular trichomes: DF=4, F=5.8, P < 0.005). Early girl, Roma and Rutgers showed a significantly higher number of non-glandular trichomes, ranging between 19.9-22.2 trichomes, than PI 134417 (1.4 trichomes). LA 716 had the greatest number of glandular trichomes (20 trichomes) of all tomato varieties except Rutgers. Moreover, Middle branches significantly differed in non-glandular and glandular trichomes (non-glandular: DF=4, F=8.8, P=0.0006, glandular: DF=4, F=33.5, P=0.0001). High number of non-glandular trichomes were found on Early girl (10.4 trichomes) followed by Rutgers (6.8 trichomes) and Roma (5.7 trichomes), while one trichome was observed on PI 134417. A similar number of glandular trichomes were noticed on Early girl, Roma and Rutgers ranging between 3.2-3.4 trichomes and more glandular trichomes were detected on PI 134417 (6.8 trichomes). In comparison, the greatest number was found on LA 716 (16.4 trichomes). Furthermore, lower branches significantly differed in both non-glandular and glandular trichomes among varieties (non-glandular: DF=4, F=5.5, P=0.005, glandular: DF=4, F=286.4, P < 0.0001). A similar number of non-glandular trichomes was recorded on Early girl and Roma (1.2 trichomes). PI 134417 and Rutgers showed less numbers of non-glandular trichomes (0.6 and 0.9 trichomes, respectively), but not significantly different from Early girl and Roma. Otherwise, the highest number of glandular trichomes was recorded on LA 716 (11.8 trichomes), while no glandular trichomes were found on Rutgers. The number of glandular trichomes ranged between 0.03-2.4 for other tomato varieties.

Table (3): Comparison of overall mean number (±SE) for non-glandular and glandular trichomes among leaflet position on different tomato plants presenting upper third, middle third and lower third of the plant counted in half branch of each plant for tomato varieties*.

Tomato varieties		Leaflet position: Upper (Branch 1-branch 4)		Middle (Branch 5-branch 8)		Lower (Branch 9-branch 12)	
		Non-glandular	Glandular	Non-glandular	Glandular	Non-glandular	Glandular
Early girl		20.8 ± 0.7a	13.6± 1.5 b	10.4± 2.5a	3.2± 0.9b	1.2± 0.3a	0.03± 0.03c
Roma		19.9± 1.9a	13.4± 1.5b	5.7± 1.7abc	3.4± 1.0b	1.2± 0.3a	0.4± 0.3c
Rutgers		22.2± 2.2a	17.4± 2.0ab	6.8± 2.2ab	3.2± 1.4b	0.9± 0.1ab	0.0± 0.0c
LA 716		0.0± 0.0b	20.0± 0.2a	0.0± 0.0c	16.4± 0.9a	0.0± 0.0b	11.8± 0.4a
PI 134417		1.4± 0.03b	12.8± 0.9b	1.0± 0.03bc	6.8± 0.9b	0.6± 0.2ab	2.4± 0.4b
Statistical analysis	**F**	74.4	5.8	8.8	33.5	5.5	286.4
	P	< 0.0001	< 0.005	0.0006	0.0001	0.005	0.0001

***Columns followed by the same letter do not differ from each other by the Tukey-Kramer HSD (P <0.01)**

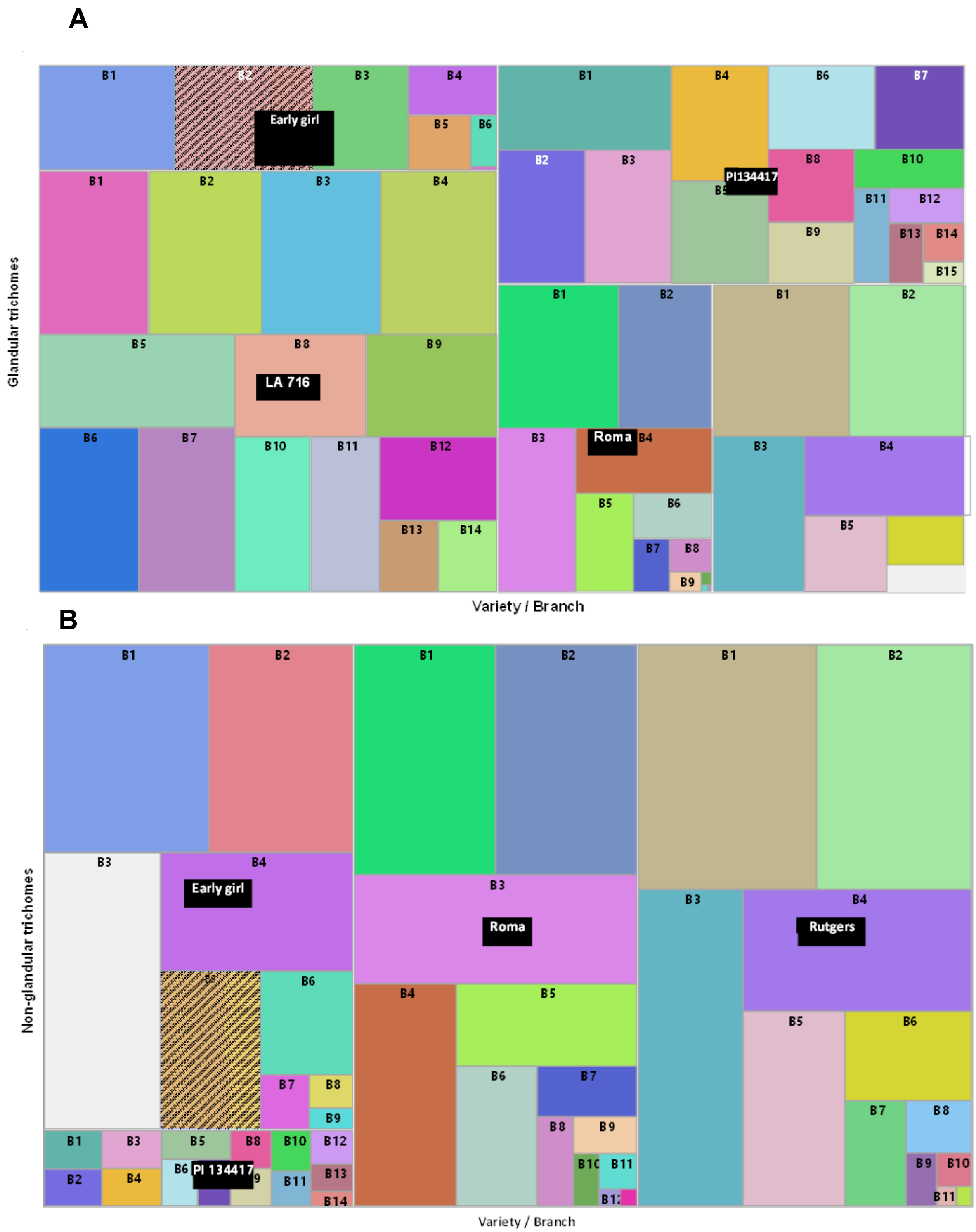

Figure (4): Map distribution of (A) non-glandular and (B) glandular trichomes measured on half of each branch from the first branch to the last branch of the plant for different tomato varieties. The size of each section indicates the density of the trichomes.

2.Tuta absoluta leaflet parameters

The number of *T. absoluta* mine blotches, larvae and percentage of damaged leaf area were determined in each leaflet on the half of each branch for the whole plant/variety and illustrated in **(Table 4)**. Obviously, no mines, larvae and damaged area were observed on the in younger branches (from the1st branch to the 4th branch) for all varieties except Roma and gradually increased in the mature branches (the 5th branch to the 8th branch) and oldest branches (the 9th branch to the 12th branch). Significant differences were found between branches in number of mines, larvae, and damaged leaf area (DF= 8, F=17.2 for mines, F=12.8 for larvae and F=22.1 for damaged leaf area, P <0.0001) and variety*branch (DF=44, F=8.0 for mines, F=8.2 for larvae and F=8.9 for damaged leaf area, P< 0.0001). LA716 and PI134417 varieties appeared to be the most resistant varieties to *T. absoluta* infestations, where no mines, larvae and damaged leaf area as well were found on all plant branches of those two varieties. For the number of mines, no mines were observed on the 1st branch to the 4th branch for Early girl and Rutgers, however Roma had 0.4 mines on the 4th branch. For Early girl, Roma and Rutgers, the number of mines in the 6th, 7th and 8th branches ranged between 1.3 and 4.0. The number of mines increased in oldest branches, especially on Roma, and reached 9.7 mines in the 12th branch. Similar results were recorded for the number of larvae, where only Roma showed 0.3 larvae on the 4th branch. The number of larvae did exceed 3.0 larvae on Early girl, Roma and Rutgers for the 6th, 7th, and 8th, then elevated on the oldest branches and recorded the highest number of 8.7 larvae in the 12th branch for Roma. The damaged leaf area % started to appear on the 4th branch for Roma with 7.6% then gradually enlarged from the 6th branch to the oldest branches for Early girl, Roma and Rutgers ranged between 13.0-33.2% for the 6th, 7th and 8th branches. Rutgers showed the highest damaged leaf area of 40.7% and 53.6% for the 10th and 11th branches, respectively.

The overall mean number of mines, larvae and damaged leaf area was estimated for upper branches (from branch 1 to branch 4), middle branches (from branch 5 to branch 8) and lower branches (branch 9 to branch 12) **(Figure 5)**. Results showed that the number of mines (Early girl: DF=2, F=20.3, P=0.002, Roma: F=8.1, P=0.008 and Rutgers: F=14.1, P=0.002), larvae (ANOVA one-way, Early girl: F=39.9, P=0.0003, Roma: F=9.3, P=0.005 and Rutgers: F=18.5, P=0.0006) and damaged leaf area (Early girl: F=23.8, P=0.0014, Roma: F=16.5, P=0.0007and Rutgers: F=24.2, P=0.0002). However, it significantly differed among leaflet positions. The number of mines was significantly higher in the middle (0.4 mines) and lower (3.5 mines) branches than upper ones in Early girl (zero mines). While Roma and Rutgers had more mines in the middle (1.9 mines and 2.1 mines, respectively) and lower (5.8 mines and 4.3 mines, respectively) branches than upper branches (0.09 mines and zero mines, respectively), but not significantly differ from each other. The number of larvae was significantly higher on the middle and lower branches than upper branches for Early girl (0.3 larvae, 2.6 larvae and zero larvae, respectively), Roma (1.5 larvae, 5.5 larvae and 0.06 larvae, respectively) and Rutgers (1.3 larvae, 3.6 larvae and zero larvae, respectively). Similar results were observed for damaged leaf area%, where Early girl, Roma and Rutgers significantly showed larger damaged leaf area% for the middle (4.7%, 14.0% and 16.5%, respectively) and lower (30.5%, 39.4% and 42.3%, respectively) branches compared to upper ones (zero %, 1.9 % and zero%, respectively).

The overall average number of *T. absoluta* mines, larvae, and damaged leaf area% were estimated and compared for each branch position among varieties presenting upper branches (branch 1 to branch 4), middle (branch 5 to branch 8) and lower (branch 9 to branch 12) **(Table 5).**

Table (4) Mean number (± SE) of *Tuta absoluta* mine blotches, larvae and damaged leaf area % found on leaflets of the half branch of each plant recorded for evaluated tomato varieties

Tomato cultivars	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15
Number of mine blotches															
Early girl	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	1.3±0.8	2.3±0.5	4.0±0.8	4.3±0.9	-	-	-	-	-	-
Roma	0.0±0.0	0.0±0.0	0.0±0.0	0.4±0.4	0.0±0.0	1.5±0.9	2.1±1.2	3.9±0.8	4.4±2.0	7.8±1.4	1.3±0.7	9.7±1.9	6.0±2.0	-	-
Rutgers	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	1.3±0.8	3.8±1.3	3.5±1.3	3.6±1.8	4.6±1.0	5.3±2.0	3.7±0.7	-	-	-
LA 716	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	-
PI 134417	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Number of larvae															
Early girl	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.8±0.5	2.0±0.4	3.0±0.3	2.8±0.6	-	-	-	-	-	-
Roma	0.0±0.0	0.0±0.0	0.0±0.0	0.3±0.3	0.0±0.0	1.2±0.7	2.0±1.2	3.0±0.4	4.2±1.9	7.6±1.5	1.3±0.7	8.7±1.9	5.5±1.5	-	-
Rutgers	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.5±0.3	2.8±1.0	2.0±1.1	2.8±1.3	3.5±1.2	4.5±1.9	3.7±0.7	-	-	-
LA 716	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	-
PI 134417	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Damaged leaf area %															
Early girl	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	14.2±8.6	23.8±1.8	33.2±1.1	34.5±0.8	-	-	-	-	-	-
Roma	0.0±0.0	0.0±0.0	0.0±0.0	7.6±7.0	0.0±0.0	16.4±9.6	13.0±7.5	26.8±5.3	26.7±9.2	40.5±2.4	27.0±14.0	51.0±2.6	51.7±0.8	-	-
Rutgers	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	18.9±11.0	29.6±10.1	17.4±9.6	32.4±11.0	42.6±1.9	40.7±11.7	53.6±0.3	-	-	-
LA 716	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	-
PI 134417	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0

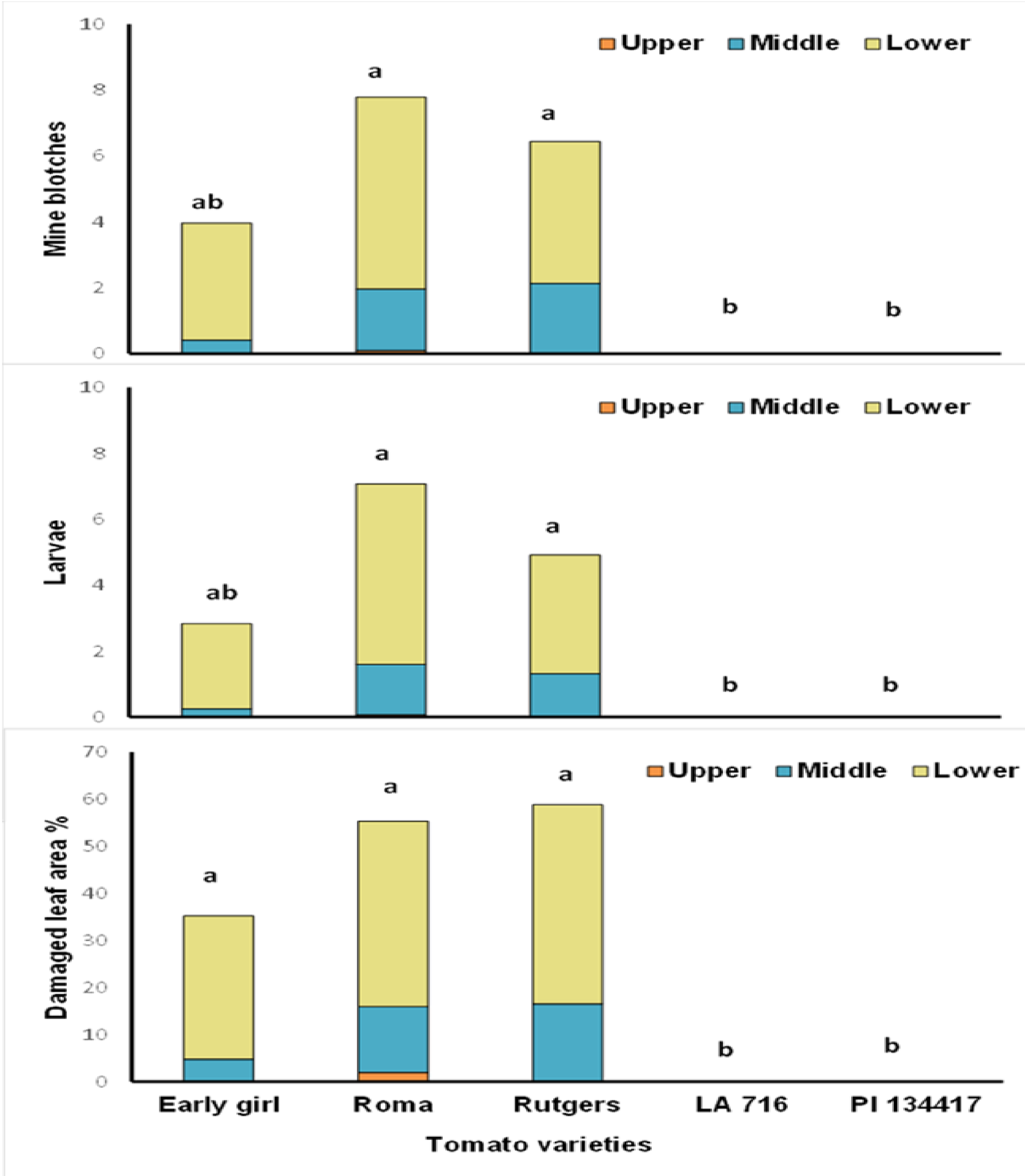

Figure (5): Overall mean number of mines blotches, larvae and damaged leaf area (%) on upper third (branch 1-branch 4), middle third (branch 5-branch 8) and lower third (branch 9-branch 12) of the plant counted in half branch for tomato varieties. Columns followed by the same letter are not significantly different ($P < 0.05$) Tukey-Kramer HSD ($P < 0.01$)

Table (5): Comparison of overall mean number (±SE) for Tuta absoluta mine blotches, larvae and damaged leaf area (%) among leaflet position on different tomato plants presenting upper third, middle third and lower third of the plant counted in half branch of each plant for tomato varieties*.

Tomato varieties		Upper (Branch 1-branch 4)			Middle (Branch 5-branch 8)			Lower (Branch 9-branch 12)		
		No. of mine blotches	No. of larvae	Damaged Leaf area %	No. of mine blotches	No. of larvae	Damaged Leaf area %	No. of mine blotches	No. of larvae	Damaged Leaf area %
Early girl		0.0±0.0a	0.0±0.0a	0.0±0.0a	0.4±0.4b	0.3±0.3b	4.7±4.7ab	3.5±0.6ab	2.6±0.3ab	30.5±3.4a
Roma		0.1±0.1a	0.1±0.1a	1.9±1.9b	1.9±0.8a	1.5±0.6a	14.0±5.5ab	5.8±1.4a	5.5±1.3a	39.4±5.5a
Rutgers		0.0±0.0a	0.0±0.0a	0.0±0.0a	2.1±0.9a	1.3±0.6a	16.5±6.1a	4.3±0.4a	3.6±0.4a	42.3±4.4a
LA 716		0.0±0.0a	0.0±0.0a	0.0±0.0a	0.0±0.0a	0.0±0.0b	0.0±0.0b	0.0±0.0b	0.0±0.0b	0.0±0.0b
PI 134417		0.0±0.0a	0.0±0.0a	0.0±0.0a	0.0±0.0a	0.0±0.0b	0.0±0.0b	0.0±0.0b	0.0±0.0b	0.0±0.0b
Statistical	**F**	1.0	1.0	24.2	4.0	3.7	4.4	12.6	13.1	38.8
analysis	**P**	0.4	0.438	0.0002	0.02	0.02	0.01	<0.0001	<0.0001	<0.0001

***Columns followed by the same letter do not differ from each other by the Tukey-Kramer HSD (P <0.05)**

No mines, larvae and damaged leaf area% were found on the upper, middle, and lower branches of LA 716 and PI134417 varieties. Upper branches were not significantly differed among varieties in the number of mines and larvae but were significantly different in damaged leaf area%. No mines, larvae and damaged leaf area were observed on upper branches for Early girl and Rutgers, while a few numbers of mines (0.1 mines), larvae (0.1 larvae) and small damaged area% (1.9%) were recorded on Roma. On the middle branches, the number of mines and larvae were significantly higher on Roma and Rutgers (1.9 and 2.1 mines, respectively and 1.5 and 1.3 larvae, respectively) than Early girl (0.4 mines and 0.3 larvae). On the other hand, small, damaged area% was observed on Early girl (4.7%), while larger ones were found on Roma and Rutgers (14.0% and 16.5%). Lower branches received the most *T. absoluta* infestation and had the highest number of mines, larvae, and damaged leaf area%. Early girl, Roma and Rutgers did not significantly differ from each other in measured parameters, where the number of mines, larvae and damaged leaf area% ranged between 3.5-5.8 mines, 2.6-5.5 larvae and 30.5-42.3%, respectively.

3. Correlation among tomato leaflet characteristics and *T. absoluta* parameters

The correlation between *T. absoluta* measured parameters (such as the number of mines, the number of larvae, and damaged leaf area) and tomato leaflet morphology (non-glandular trichomes, glandular trichomes) was estimated and presented in **(Figure 6).** The number of mines was significantly positively correlated with the number of larvae and damaged leaf area (r=0.975 and r=0.875, respectively, P< 0.0001). In contrast, negative correlations were found between number of mines and non-glandular trichomes and glandular trichomes (r=-0.268, P=0.0006 and r=-0.592, P< 0.0001, respectively). Similar results were observed for the number of larvae and damaged leaf area with non-glandular and glandular trichomes. Furthermore, the correlations between the number of larvae were significantly negative with the number of non-glandular trichomes and glandular trichomes (r=-0.257, P=0.001 and r=-0.563, P< 0.0001, respectively). Additionally, significant negative correlations were found between damaged leaf area and the number of non-glandular and glandular trichomes (r=-0.282, P=0.0004 and r=-0.652, P< 0.0001, respectively).

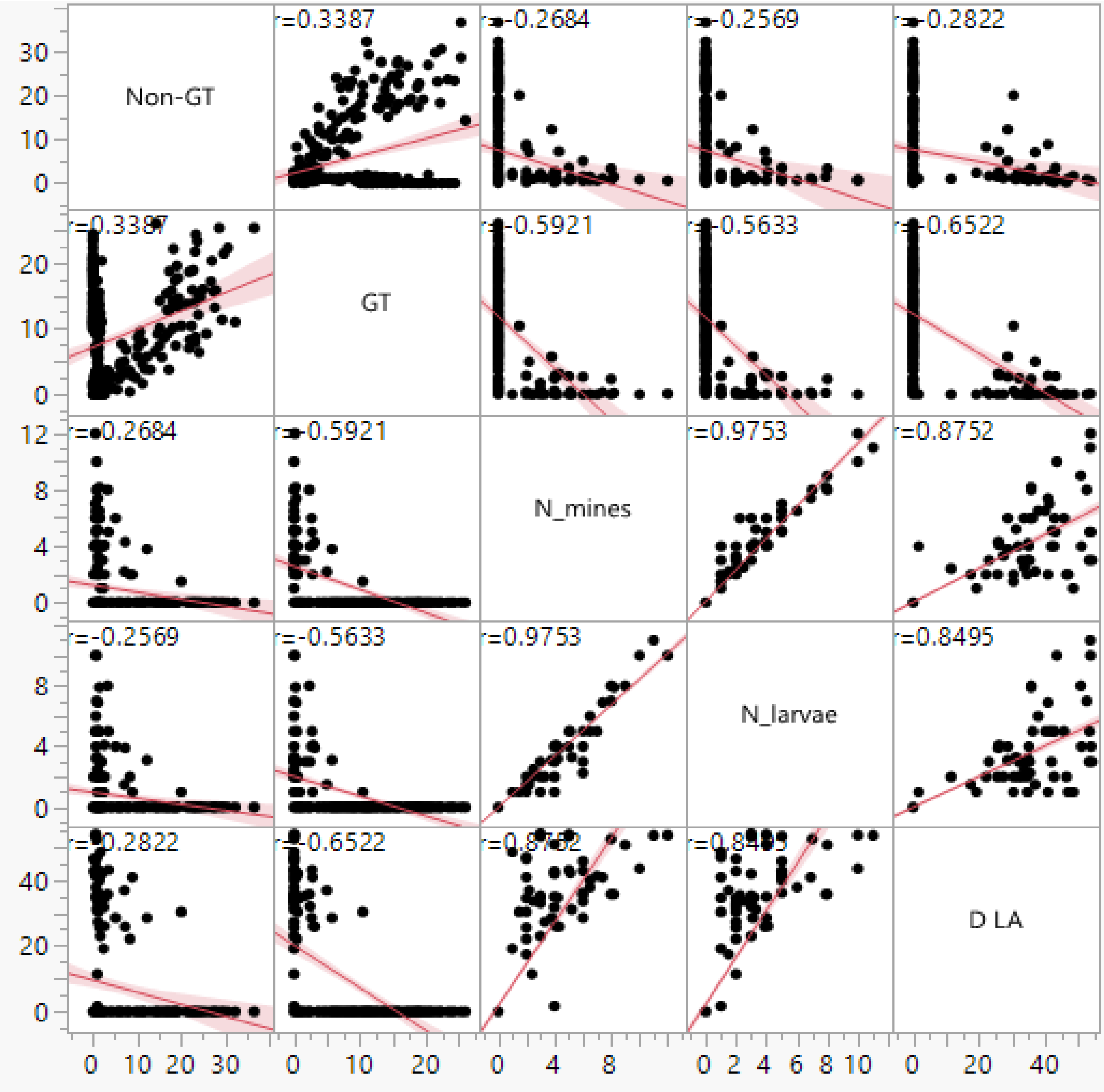

Figure (6): Estimates of Pairwise correlations among the evaluated characteristics in tomato varieties submitted to infestation of *Tuta absoluta.* Non-GT: is non-glandular trichomes, GT: glandular trichomes, N_mines: number of mines, N_larvae: number of larvae and DLA: damaged leaf area.

Discussion

Resistant varieties are considered one of the modern integrated pest management methods (IPM) to reduce using insecticides, reduce production costs, and finally environment without pollution. Wild tomatoes can produce specific metabolic compounds that improve resistance to a variety of insects (**Bleeker et al., 2012; Lucatti et al., 2013; Mirnezhad et al., 2010; Vosman et al., 2018 and Wang et al., 2020**). Leaf morphology surfaces play an essential role in plant preference (**Hanna et al., 1981 and Skorupska 2004**). Physical barriers often provide the first line of defense against herbivores and pathogens, such as trichome density and quality, cuticle thickness, and cell wall strength (**War et al., 2012**). Our research investigated the resistance mechanism of three presumed susceptible and two resistant varieties against *T. absoluta*. Results indicated that Early girl, Roma and Rutgers are susceptible to *T. absoluta* infestation. While LA716 and PI1334417 greatly resisted this pest, there were no mines, larvae and damaged leaf area on both varieties. LA716 showed the highest number of glandular trichomes compared to other varieties, and this suggests that glandular trichomes hindered *T. absoluta* performance in this variety. Although PI134417 had a few numbers of non-glandular, it had a high number of glandular trichomes, which also gives the variety resistance to *T. absoluta*. This result agrees with Gonçalves et al., (1998) who mentioned that PI134417 is resistant to several arthropods, including spider mites. These resistances have been related to high contents of 2-tridecanone (2-TD) and other methyl ketones in the leaves. Other studies revealed that a higher density of glandular trichomes (type VI and type IV), as well as non-glandular trichomes (type II and V), confer resistance to herbivory (**Kennedy, 2003 and Kivimäki et al., 2007**). Glandular trichomes secrete flavonoids, poisonous terpenoids and alkaloids (**War et al., 2012** and **Glas et al., 2012**) that act as deterrent for oviposition and feeding of arthropod pests (**Handley et a., 2005**) and serve as mechanoreceptors of herbivores (**Peifer et al., 2009**). Type VI trichomes accumulate JA, an important sensor for detecting insect movement on the leaf surface (**Peifer et al., 2009**). In addition, glandular and non-glandular trichomes play an important role in host plant resistance by affecting the performance of herbivores **(Bitew, 2018).** Higher Zingiberene (**Azevedo et al., 2003**), 2-tridecanone (**Maluf et al., 1997**) were identified as major factors responsible for *T. absoluta* resistance in tomatoes. Furthermore, glandular trichomes secrete mucous, resins, volatile oils, and other substances, which can interfere with damage from herbivores and pathogens (**McDowell et al., 2011; Ambrósio et al., 2008 and Tian et al., 2012**). Studies have shown that the glands on the surface of trichomes can secrete toxic chemicals, such as resins and nicotine, to ward off external hazards (**Ishida et al., 2008 and Yan et al., 2012**). The glandular trichomes of alfalfa can secrete chemicals to kill pests that attack its leaves and stems (**Elad and Shtienberg 1995**). In addition, the trichomes of the plants themselves block the free movement of insects and can also secrete volatile or nonvolatile toxic substances, making it difficult for pests to feed on the plant surface and thereby affecting the feeding position of insects. Several annual or perennial plants of the genus alfalfa also exhibit this characteristic. Anemones with long glandular trichomes also secrete flavonoids and terpenes to prevent leafhoppers from feeding on the plants. The cowpea's hairy body also plays a similar role in biological control (**Williamson et al., 2007**). Recent studies prove that trichomes may be sensors for detecting insect movement on the leaf surface (**Peiffer et al., 2009**). The literature indicates that the trichome density of plants is significantly correlated with their insect resistance. In addition, the high density of trichomes in *Solanum habrochaites* prevents insects from moving freely among the trichomes, reducing the destructive power of the insect (**Zhang et al., 2020**). In current study, we found that the overall mean number of mines, larvae and damaged leaf area % are higher on Roma (2.6 mines, 2.4 larvae and 18.4% damaged leaf area) and Rutgers (2.1 mines, 1.6 larvae and 19.6% damaged leaf area) than Early girl (1.3 mines, 0.9 larvae and 11.7% damaged leaf area) which suggested that they are more susceptible to *T. absoluta* infestation than Early girl. However, LA716 and PI134417 had the highest resistance to *T. absoluta,* where no mines, larvae and damaged leaf area were recorded on both varieties. These results suggest that PI134417 and LA716 was not a suitable host for developing immature stages and performing *T. absoluta* in response to their trichomes. Our findings are consistent with According to **Burke et al. (1987**) who mentioned that *Solanum pennellii* accessions have a high density of type IV trichomes on their leaves, stems and fruits and that these trichomes release a sticky substance that consists of 90 % Acylsugar. Moreover, wild tomato accessions such as *S. habrochaites*, *S. pennellii*, *S. galapagense* are resistant to silverleaf whitefly because of a high density of trichome type IV (**Maluf et al., 2010; Firdaus et al., 2012; Firdaus et al., 2013, Lucatti et al., 2013**). Glandular trichomes are the major sites of different phytochemical production that prevent herbivore attack than non-glandular trichomes (**Schilmiller et al., 2010**). **Mulusew (2018) and Sridhar et al., (2019)** mentioned that commercial varieties of tomato such as LA1777 (*S. habrochaites*) and LA716 (*S. pennellii*) could be a source of resistance to *T. absolute* according to storge of acyl sugars in trichomes type IV and stated that those varieties would be successfully recommended in the future breeding program. On the other hand, our results revealed that the oldest (lower) branches and mature (middle) branches are preferred to *T. absoluta* larvae development than younger (upper) branches; this may be due to the absence or presence of a few numbers of trichomes on those leaflets. Our findings agree with (**Yule et al., 2021**), who stated that the number of *T. absoluta* larvae was significantly higher in the lower stratum of the plant, followed by the middle stratum and upper stratum, respectively. However, PI134417 and LA716 varieties were resistant to *T. absoluta* infestations. **Yule et al., (2021)** declared that *T. absoluta* larvae did not choose LA 716 for its preference in the two-choice assay when compared to the cultivar Moneymaker. LA716 (*S. pennellii*). In addition, LA1718 and LA1777 (*S. habrochaites*) have the lowest number of surviving larvae (0.28 ± 0.39, 0.42 ± 0.39 and 0.14 ± 0.32, respectively). The lowest oviposition rate was found in accessions LA1718 (0.06 ± 0.13). **Torres et al., (2001) and Cely et al., (2010**) suggested that *T. absoluta* females laid their eggs on the upper and middle strata of the plants, and as the plants grow, the larvae is then found in the lower and middle strata of the plant, as the infested tissues were part of the upper and middle parts of the plant. A negative correlation was found among the number of T. absoluta mines, larvae and damaged leaf area, and non-glandular and glandular trichomes. These results suggest that trichomes may negatively influence both larval feeding and oviposition by insects (Handley et al 2005), resulting in the lowest number of larvae and, consequently lower damage to leaflets. **Muigai et al. (2003)** reported a negative correlation between type IV trichomes and the number of eggs and nymphs of whitefly. Similarly, **Oriani and Vendramim (2010)** found that the density of glandular trichomes in LA-716 was negatively correlated with the attractiveness and oviposition of whitefly and positively correlated with the number of trapped insects by trichomes. **Eigenbrode and Trumble (1993)** verified that the percentage of survival of the larval stage of *Spodoptera exigua* Hubner was negatively correlated with the density of type IV trichomes in different accessions of Solanum. Previous studies have related *T. absoluta* resistance of tomato to the presence of principal compounds, as cuticular lipids such as tricosane presented a negative correlation with the number of mines unlike tacosane and hexacosane presented a positive correlation (**Oliveira et al., 2009**). **Mulusew (2018) and Sridhar et al., (2019)** mentioned that oviposition rate and larvae survival was negatively correlated with trichomes type IV and I, respectively, indicating a role of those trichome types in resistance.

Conclusion

Resistance has been successfully found on wild tomato varieties LA716 and PI134417. This study demonstrated behavioral differences of *Tuta absoluta* associated with the presence or absence of leaf trichome densities. Trichomes confer tomato varieties resistance against pests because they independently produce toxic or repellent chemicals and can defend themselves against certain arthropods and insects, reducing or eliminating extensive synthetic pesticide utilization and cost.

References

Ambrósio, S. R., Oki, Y., Heleno, V. C. G., Chaves, J. S., Nascimento, P. G. B. D., Lichston, J. E., Constantino, M. G., Varanda, E. M., & Da Costa, F. B. (2008). Constituents of glandular trichomes of Tithonia diversifolia: Relationships to herbivory and antifeedant activity. *Phytochemistry* 69: 2052–2060.

Apablaza, J. (1992). The tomato moth and its management. *Tattersal* 79: 12– 13.

Azevedo, S. M., Faria, M. V., Maluf, W. R., Oliveira, A. C. B., & Freitas, J. A. (2003). Zingiberene-mediated resistance to the South American tomato pinworm derived from *Lycopersicon hirsutum* var. *hirsutum*. Euphytica 134: 347–351.

Biondi, A., Guedes, R. N. C., Wan, F. H., & Desneux, N. (2018). Ecology, worldwide spread, and management of the invasive South American tomato pinworm, *Tuta absoluta*: past, present, and future (review). *Annu. Rev. Entomol* 63 (1): 239– 258.

Bitew, M. K. (2018). Significant role of wild genotypes of tomato trichomes for *Tuta absoluta* resistance. *Journal of Plant Genetics and Breeding* 2: 104.

Bleeker, P. M., Mirabella, R., Diergaarde, P. J., VanDoorn, A., Tissier, A., & Kant, M. R., et al. (2012). Improved herbivore resistance in cultivated tomato with the sesquiterpene biosynthetic pathway from a wild relative. *Proc Natl Acad Sci* 109(49): 20124–9. https://doi.org/10.1073/pnas.1208756109.

Burke, B. A., Goldsby, G., & Mudd, J. B. (1987). Polar epicuticular lipids of *Lycopersicon pennellii*. *Phytochemistry* 26:2567–2571.

Cely, L., Cantor, F., & Rodríguez, D. (2010). Determination of levels of damage caused by different densities of *Tuta absoluta* populations (Lepidoptera: Gelechiidae) under greenhouse conditions. *Agron. Colomb.* 28:392–402.

Cherif, A., & Verheggen, F. (2019). A review of *Tuta absoluta* (Lepidoptera: Gelechiidae) host plants and their impact on management strategies. *Biotechnol. Agron. Soc. Environ*. 23:270–278. doi: 10.25518/1780-4507.18211.

Dias, D. M., de Resende, J. T. V., Zeist, A. R., Gabriel, A., Santos, M. H. & Vilela, N. C. (2019). Resistance of processing tomato genotypes to leafminer (*Tuta absoluta*). *Hortic. bras., Brasília*, 37(1): 40-46.

Dimock, M. B. & Kennedy G. G. (1983). The role of glandular trichomes in the resistance of *Lycopersicon hirsutum* f. *glabratum* to *Heliothis zea. Ent. exp. & appl*. 33: 263-268.

Ecole, C. C., Picanco, M., Jhan, G. M. & Guedes, R. N. C. (1999). Variability of *Lycopersicum hirsutum* f. *typicum* and possible compounds involved in its resistance to *Tuta absoluta*. *Agric For Entomol* 1:249–254.

Eigenbrode, S. D., & Trumble, J. T. (1993). Antibiosis to beet armyworm (*Spodoptera exigua*) in Lycopersicon accessions. *HortScience* 28:932–934.

Elad, Y., & Shtienberg, D. (1995). Botrytis cinerea in greenhouse vegetables: Chemical, cultural, physiological and biological controls and their integration. *Integr. Pest Mgt. Rev*. 1, 15–29.

Elballa, M. M. A., Hamid, A. A., & Abdelmageed, A. H. A. (2013). Effects of time of water stress on flowering, seed yield and seed quality of common onion (*Allium cepa* L.) under the arid tropical conditions of Sudan. *Agricultural Water Management* 121: 49-157.

Fancelli, M., Vendramim, J. D., Frighetto, R. T. S., & Lourenc¸a˜o A. L. (2005). Glandular exudate of tomato genotypes and development of *Bemisia tabaci* (Genn.) (Sternorryncha: Aleyrodidae) biotype B. *Neotrop Entomol* 34:659–665.

FAO (2015). FAOSTAT Database on Production, FAO Statistics Division, Food and Agriculture Organization of the United Nations, Rome. Available online at http://faostat.fao.org/ site/339/default.aspx. Accessed 28 Aug 2015.

FAO (2019). FAOSTAT Database on Production, FAO Statistics Division, Food and Agriculture Organization of the United Nations, Rome. Available online at https://www.fao.org/3/ca5885en/CA5885EN.pdf.

Firdaus, S., van Heusden, A. W., Hidayati, N., Supena, E. D. J., Mumm, R., de Vos, R. C. H., & Vosman, B. (2013). Identification and QTL mapping of whitefly resistance components in Solanum galapagense. *Theoretical and Applied Genetics* 126(6): 1487-1501.

Firdaus, S., van Heusden, A. W., Hidayati, N., Supena, E. D. J., Visser, R. G. F., & Vosman, B. (2012). Resistance to *Bemisia tabaci* in tomato wild relatives. *Euphytica* 187(1): 31-45.

Gianfagna, T. J., Carter, C. D., & Sacalis, J. N. (1992). Temperature and photophase influence on trichome density and sesquiterpeno content of *Lycopersicum hirsutum* f. *hirsutum. Plant Physiol* 100:1403–1405.

Glas, J. J., Schimmel, B. C. J., Alba, J. M., Escobar-Bravo, R., Schuurink, R. C., & Kant, M. R. (2012). Plant glandular trichomes as targets for breeding or engineering of resistance to herbivores. *Int J Mol Sci*. 13(12):17077–103.

Gonçalves, M. I. F., Maluf, W. R., Gomes, L. A. A. & Barbosa, L.V. (1998). Variation of 2-Tridecanone level in tomato plant leaflets and resistance to two mite species (*Tetranychus sp*.). *Euphytica* 104: 33–38. https://doi.org/10.1023/A:1018611514287.

Gurr, G. M., & McGrath, D. (2001). Effect of plant variety, plant age and photoperiod on glandular pubescence and host-plant resistance to potato moth (*Phthorimaea operculella*) in *Lycopersicon spp*. *Ann. appl. Biol*. 138:221-230.

Handley, R., Ekbom, B., & Ågren, J. (2005). Variation in trichome density and resistance against a specialist insect herbivore in natural populations of Arabidopsis thaliana. *Ecol Entomol*. 30(3):284–92.

Hanna, M. A., Zaher, M. A., & Sawires, Z. R. (1981). Influence of host resistance on the biology of *Tetranychus urticae* Koch in soybean (Acarina: Tetranychidae). *Zagazig J. Agric. Res*. 379: 1-5.

Ishida, T., Kurata, T., Okada, K., & Wada, T. (2008). A genetic regulatory network in the development of trichomes and root hairs. *Annu. Rev. Plant Biol*. 59: 365–386.

Kennedy, G. G. (2003). Tomato, Pests, Parasitoids, and Predators: Tritrophic Interactions Involving the Genus Lycopersicon. *Annu Rev Entomol*. 48:51–72. 34.

Kivimäki, M., Kärkkäinen, K., Gaudeul, M., Løe, G., & Ågren, J. (2007). Gene, phenotype and function: GLABROUS1 and resistance to herbivory in natural populations of Arabidopsis *lyrata. Mol Ecol*. 16(2):453–62.

Lima, I. P., Resende, J. T. V., Oliveira, J. R. F., Faria, M. V., Dias, D. M., & Resende, N. C. V. (2016). Selection of tomato genotypes for processing with high zingiberene content, resistant to pests. *Horticultura Brasileira* 34: 387-391.

Lucatti, A. F., van Heusden, A. W., de Vos, R. C., Visser, R. G., & Vosman, B. (2013). Differences in insect resistance between tomato species endemic to the Galapagos Islands. *BMC Evol Biol*. 13(1):175. https://doi.org/10.1186/1471-214 8-13-175.

Lucatti, F. A., Adriaan, W. van Heusden, W. A., de Vos, H. C. R., & Visser, F. G. R. (2013). Differences in insect resistance between tomato species endemic to the Galapagos Islands. *Netherlands Metabolomics Centre*, 1 - 31.

Lucini, T., Faria, M. V., Rohde, C., Resende, J. T. V., & Oliveira, J. R. F. (2015). Acylsugar and the role of trichomes in tomato genotypes resistance to *Tetranychus urticae*. *Arthropod Plant Interactions* 9: 45-53.

Maluf, W. R., Barbosa, L. V., & Santa, C. L. C. S. (1997). 2-Tridecanonemediated mechanisms of resistance to the South American tomato pinworm *Scrobipalpuloides absoluta* (Meyrick, 1917) (Lepidoptera-Gelechiidae) in *Lycopersicon spp*. *Euphytica* 93: 189–194.

Maluf, W. R., Inoue, I. F., Ferreira, R. P.D., Gomes, L. A. A., Castro, E. M., & Cardoso, M. G. (2007). Higher glandular trichome density in tomato leaflets and repellence to spider mites. *Pesqui Agropecu Bras* 42:1227–1235.

Maluf, W., Fátima Silva, V., Graças Cardoso, M., Gomes, L., Neto, Á., Maciel, G., & Nízio, D. (2010). Resistance to the South American tomato pinworm *Tuta absoluta* in high acyl sugar and/or high zingiberene tomato genotypes. *Euphytica* 176(1): 113 - 123.

Mansour, R., Schuster, D. J., Cordero, R., & Toapanta, M., (2018). Occurrence, biology, natural enemies and management of *Tuta absoluta* in Africa. *Entomol. Generalis* 38: 83–112.

McDowell, E.T., Kapteyn, J., Schmidt, A., Li, C., Kang, J. H., Descour, A., Shi, F., Larson, M., Schilmiller, A., & An, L., et al. (2011). Comparative functional genomic analysis of Solanum glandular trichome types. *Plant Physiol*. 155: 524–539.

Miranda, M. M. M., Picanço, M., Zanuncio, J. C., & Guedes, R. N. C. (1998). Ecological life table of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Biocontrol Sci. Technol*. 8 (4): 597–606.

Mirnezhad, M., Romero-González, R. R., Leiss, K. A., Choi, Y. H., Verpoorte, R., & Klinkhamer, P. G. (2010). Metabolomic analysis of host plant resistance to thrips in wild and cultivated tomatoes. *Phytochem Anal*. 21(1):110–7. https:// doi.org/10.1002/pca.1182.

Mohamed, E. S. I., Mohamed, M. E. & Gamiel, S.A. (2012). First record of the tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in Sudan. *Bulletin OEPP/EPPO Bulletin* 42: 325–327.

Mohammed, E. S. I., (2015). Host plants record for tomato leaf miner, *Tuta absoluta* (Meyrick) in Sudan. *EPPO Bull*. 45: 108–111.

Moreira, G. R., da Silva, D. J. H., Carneiro, P.C.S., Picanço, M. C., Vasconcelos, Al. de A., & Pinto, C. M. F. (2013). Inheritance of *Solanum pennellii* antixenosis resistance characters to tomato leafminer in cross with 'Santa Clara'. *Hortic. bras*., 31(4): 574-581.

Muigai, S. G., Bassett, M. J., Schuster, D. J., & Scott, J. W. (2003). Greenhouse and field screening of wild Lycopersicon germplasm for resistance to the whitefly *Bemisia argentifolii*. *Phytoparasitica* 31:27–38.

Mulusew, B. K. (2018). Significant role of wild Genotypes of tomato trichomes for *Tuta absoluta* resistance. *Plant Genet Breed* 2(1): 104.

Oliveira, F. A., Silva, D. J. H., Leite, G. L. D., Jham, G. N., & Picanco, M. (2009). Resistance of 57 greenhouse-grown accessions of Lycopersicon esculentum and three cultivars to *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Sci Hortic* 119:182–187.

Oliveira, A. F., de Silva, H. J. D., Leite, D. L. G., Jham, N. G., & Picanco, M. (2009). Resistance of 57 greenhouses-grown accessions of Lycopersicon esculentum and three captives to *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Scientia Horticulturae*, 119: 182 - 187.

Oriani, M. A. G., & Vendramim, J. D. (2010). Influence of trichomes on attractiveness and ovipositional preference of *Bemisia tabaci* (Genn) B biotype (Hemiptera: Aleyrodidae) on tomato genotypes. *Neotrop Entomol* 39:1002–1007.

Peiffer, M., Tooker, J. F., Luthe, D. S., & Felton, G. W. (2009). Plants on early alert: glandular trichomes as sensors for insect herbivores. *New Phytol*. 184, 644–656.

Resende, J. T. V., Maluf, W. R., Faria, M. V., Pfann, A. Z., & Nascimento, I. R. (2006). Acylsugars in tomato leaflets confer resistance to the South American tomato pinworm, *Tuta absoluta* Meyr. *Sci Agric* 63:20–25.

Schilmiller, A., Shi, F., Kim, J., Charbonnaeu, L. A., Holmes, D., Jones, D. A., & Last, L. R. (2010). Mass spectrometry screening reveals widespread diversity in trichome specialized metabolites of tomato chromosomal substitution lines. *The Plant Journal* 62: 391 - 403.

Shapiro, J. A., Steffens, J. C., & Mutschler, M. A. (1994). Acylsugars of the wild tomato *Lycopersicon pennellii* in relation to geographic distribution of the species. *Biochem Syst Ecol* 22:545–561.

Sharma, H. C., Sujana, G., & Rao, D. M. (2009). Morphological and chemical components of resistance to pod borer, *Helicoverpa armigera* in wild relatives of pigeonpea. *Arthropod-Plant Interact* 3:151–161.

Silva, G. A., Picanço, M. C., Bacci, L., Crespo, A. L. B., Rosado, J. F., & Guedes, R. N. C. (2011). Control failure likelihood and spatial dependence of insecticide resistance in the tomato pinworm, *Tuta absoluta*. *Pest Manage. Sci*. 67: 913–920.

Simmons, A. T. & Gurr, G. M. (2005). Trichomes of Lycopersicon species and their hybrids: effects on pests and natural enemies. *Agricultural and Forest Entomology*7: 265–276.

Simmons, A. T., Gurr, G. M., McGrath, D., Nicol, H. I., & Martin, P. M. (2003). Trichomes of *Lycopersicon spp*. and their effect on *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). *Aust J Entomol* 42:373–378.

Skorupska, A., (2004). Resistance of apple variety to two-spotted spider mite, *Tetranychus urticae* Koch (Acarina, Tetranychidae): Part II. Influence of leaf pubescence of selected apple variety on fecundity of two-spotted spider mite. J. *Plant Prot. Res*. 44: 69-74.

Snyder, J. C. & Carter, C. D. (1984). Leaf trichomes and resistance of *Lycopersicon hirsutum* and *L. esculentum* to spider mites. *J. Amer. Soc. Hort. Sci*. 109(6):837-843.

Sridhar, V., Sadashiva, A. T., Rao, V. K., Swathi, P., & Gadad, H. S. (2019). Trichome and biochemical basis of resistance against *Tuta absoluta* in tomato genotypes. *Plant Genetic Resources: Characterization and Utilization* 17(3): 301–305. doi:10.1017/S147926211800062X.

Tian, D., Tooker, J., Peiffer, M., Chung, S.H., & Felton, G.W. (2012). Role of trichomes in defense against herbivores: Comparison of herbivore response to woolly and hairless trichome mutants in tomato (*Solanum lycopersicum*). *Planta* 236: 1053–1066.

Torres, J. B., Faria, C. A., Evangelista, W.S., & Pratissol D. (2001). Within-plant distribution of the leaf miner *Tuta absoluta* (Meyrick) inmatures in processing tomatoes, with notes on plant phenology. *Int. J. Pest. Manag.* 47:173–178. doi: 10.1080/02670870010011091.

Vosman, B., van't Westende, W. P., Henken, B., van Eekelen, H. D., de Vos, R. C., & Voorrips, R. E. (2018). Broad spectrum insect resistance and metabolites in close relatives of the cultivated tomato. *Euphytica*. 214(3):46. https://doi. org/10.1007/s10681-018-2124-4.

Wang, F., Park, Y., & Gutensohn, M. (2020). Glandular trichome-derived sesquiterpenes of wild tomato accessions (*Solanum habrochaites*) affect aphid performance and feeding behavior. *Phytochemistry*. 180:112532. https://doi.org/10.1016/j.phytochem.2020.112532.

War, A. R., Paulraj, M. G., Ahmad, T., Buhroo, A. A., Hussain, B., & Ignacimuthu, S., et al. (2012). Mechanisms of Plant Defense against Insect Herbivores. *Plant Signal Behav*. 7(10):1306–20.

Williamson, B., Tudzynski, B., Tudzynski, P., & Van Kan, J. A. L. (2007). Botrytis cinerea: The cause of grey mold disease. *Mol. Plant Pathol*. 8: 561–580.

Yan, A., Pan, J., An, L., Gan, Y., & Feng, H. (2012). The responses of trichome mutants to enhanced ultraviolet-B radiation in Arabidopsis thaliana. *J. Photochem. Photobiol. B Biol*. 113: 29–35.

Yule, S., Htain, N. N., Oo, A. K., Sotelo-Cardona, P., & Srinivasan R. (2021). Occurrence of the South American Tomato Leaf Miner, *Tuta absoluta* (Meyrick) in Southern Shan, Myanmar. *Insects* 12(11):962. doi: 10.3390/insects12110962. PMID: 34821763; PMCID: PMC8618818.

Zhang, Y., Song, H., Wang, X., Zhou, X., Zhang, K., Chen, X., Liu, J., Han, J., & Wang, A. (2020). The Roles of Different Types of Trichomes in Tomato Resistance to Cold, Drought, Whiteflies, and Botrytis. *Agronomy* 10(411): 2-16.

https://doi.org/10.3390/agronomy10030411.