Entrapment of two-spotted spider mite, *Tetranychus urticae* (Acari: Prostigmata: Tetranychidae), by type IV glandular trichomes of *Lycopersicon* species

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Abstract

Two-spotted spider mite (TSSM) is becoming resistant to many of the pesticides used in the tomato fields. A potential alternative method of control is host plant resistance, which may be mediated by glandular trichomes. In this experiment, level of entrapment and mortality of the pest by type IV glandular trichomes were studied on accessions of Lycopersicon hirsutum Humb & Bonpl, L. pennellii (Cor.) D'Arcy and L. esculentum Mill on leaflets with trichomes intact or with exudates removed. Three accessions of L. hirsutum (LA1740, LA1777 and LA2860), two accessions of L. pennellii (LA2963 and LA2580) and one susceptible variety (Sankranthi) of L. esculentum were used. Leaflets from the terminal pair of the third-last fully expanded leaves were excised and leaf disks prepared. Ten female mites of Tetranychus orticae Koch were placed on the adaxial leaflet surface of each disk and after 2 h, the number of mites trapped, untrapped and moved into water were recorded. Again after 24 and 48 h, mites were recorded either dead, morbid or moved into water. Results indicated that the highest number of entrapment was on L. hirsutum LA1777, followed by L. pennellii accessions. None of the mites was entrapped on L. esculentum. Moreover, L. hirsutum (LA1777 and LA1740) and L. pennellii accessions had greater number of dead mites than L. esculentum after 48 h. Lycopersicon esculentum did not possess type IV glandular trichomes. The highest density of type IV glandular trichomes was recorded on abaxial and adaxial leaf surfaces of L. hirsutum LA1777 (86.72 and 34.44 trichomes/mm², respectively). Removal of trichome exudates has significantly increased the mite survival in resistant accessions. Correlation between the density of type IV glandular trichomes and entrapment rate of TSSM was significantly positive.

Key words: entrapment, mortality, *Tetranychus urticae*, tomato, glandular trichomes, *Lycopersicon*, two-spotted spider mite

چکیدہ

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افزایش زندهمانی کنهی تارتن روی لاینهای مقاوم شد. همبستگی بین تراکم کرکهای غدهای نوع IV و به دام افتادن کنهی
تارتن دولکهای معنیدار و مثبت بود.
واژگان کلیدی: به دام افتادن، مرگ و میر، Tetranychus urticae، گوجهفرنگی، کرکهای غدهای، Lycopersicon کنـهی
تارتن دولکهای
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Introduction

Tomato (*Lycopersicon esculentum* Mill) is a widely grown vegetable crop in the world. Two-spotted spider mite (TSSM), *Tetranychus urticae* Koch, is one of the most important pests of tomato. The short life span, high fecundity and its ability to develop resistance to many acaricides have made chemical control of this mite particularly difficult. Therefore, a program based on integrated pest management is essential for the control of the pest (Luczynski *et al.*, 1990).

Host plant resistance to arthropods, mediated by mechanisms that reduce pest feeding on the plants, can be an important component of an integrated pest management program (Weston *et al.*, 1989). Various studies have shown that resistance of *Lycopersicon* species to insects and mites depend on chemical and physical characteristics of glandular trichomes (Williams *et al.*, 1980; Kennedy & Dimock, 1983; Good & Snyder, 1988; Eigenbrode & Trumble, 1993).

Glandular trichomes are known to secrete a variety of secondary metabolites that are able to physically entangle pests and also usually associated with a toxin to kill the invaders. Ranger & Hower (2001) reported that first-instar, and possibly second-instar of the potato leafhopper, *Empoasca fabae* (Harris) were entrapped by exudates produced by the glandular trichomes on the FGplh13 (resistant line) alfalfa. Secretion of glandular trichomes of *Solanum berthaultii* Hawks entraps and immobilizes the green peach aphid, *Myzus persicae* (Sulzer); the potato aphid, *Macrosiphum euphorbiae* (Thomas); the potato leafhopper, *E. fabae* and the two-spotted spider mite, *T. urticae* (Gibson & Turner, 1977; Tingey & Gibson, 1978). Polymerization and hardening of these exudates on the insects impede their movement, occlude their mouthparts, and ultimately entrap the small arthropods on the foliage (Gibson, 1971). The mechanism of entrapment consists of releasing polyphenol oxidase (PPO) enzyme, a peroxidase (PO) enzyme and phenolic substrates from internal storage space of glandular trichomes, upon rupture of their head by insects contact (Ave & Tingey, 1986).

In *Lycopersicon* species, especially *L. hirsutum* Humb & Bonpl and *L. pennellii* (Cor.) D'Arcy, resistance to many arthropods depends on the type, density and exudates composition

of type IV and VI glandular trichomes (Williams *et al.*, 1980; Kennedy & Dimock, 1983; Good & Snyder, 1988; Goffreda & Mutschler, 1989; Weston *et al.*, 1989; Eigenbrode & Trumble, 1993; Simmons *et al.*, 2003). Exudates of the trichomes can entrap the pest (Simmons *et al.*, 2003, 2004) or consist of toxic or repellent chemicals (Williams *et al.*, 1980; Kennedy & Dimock, 1983; Goffreda & Mutschler, 1989). Simmons *et al.* (2003, 2004) observed that the entrapment rate and mortality of the green peach aphid, *M. persicae*, and *Helicoverpa armigera* (Hübner) were high in *L. hirsutum* and *L. pennellii* accessions in comparison to cultivated tomato (*L. esculentum*) due to the presence of type IV glandular trichomes.

The objective of this experiment was to study the entrapment rate and mortality of TSSM by type IV glandular trichomes of *Lycopersicon* species in order to increase the level of host resistance in cultivated tomato, by introgression with resistant accessions.

Materials and methods

Plant materials and leaf sampling

Germplasms were composed of three accessions of *L. hirsutum* (LA1740, LA1777 and LA2860), two accessions of *L. pennellii* (LA2963 and LA2580) and one susceptible cultivar (Sankranthi) of *L. esculentum* (table 1). Plants were raised in an insectaria enclosed with sheet net under natural conditions of photoperiod, temperature and humidity. Study was carried out at GKVK campus, UAS, Bangalore from September to November 2005. The range of temperature and humidity during September were 19.2-27.6 °C and 53-93%, during October 18.8-26.8 °C and 58-94% and during November 16.1-25 °C and 56-92% respectively.

Tomato leaflets were collected from equivalent positions. Fully expanded young leaves (third leaves below the apical meristem) were collected. Leaf disks (2 cm in diameter) were prepared for the experiment by using a cork borer.

Maintenance of the mite stock culture

The strain of *T. urticae* used in this study originated from infested tomato leaves in Hebbal Campus of University Agricultural Science, Bangalore in September 2003. Mite rearing was carried out on susceptible variety 'Sankranthi' of *L. esculentum* under greenhouse conditions (temperature = $25 \pm 5^{\circ}$ C, photoperiod 12 L: 12 D and RH = $55 \pm 10^{\circ}$). The individual mites used for the bioassays were transferred to the leaves using a fine camel hair brush.

Table 1. Accessions of *Lycopersicon* for studying the entrapment rate of *T. urticae* by type IV glandular trichomes.

Species	Accession/Cultivar	Source of collection
L. esculentum	Sankranthi	Department of Genetics and Plant Breeding, UAS, GKVK, Bangalore, India
L. hirsutum	LA1740, LA1777, LA2860	Nunhems Proagro seeds, PVT. LTD. Bangalore, India
L. pennellii	LA2580, LA2963	Nunhems Proagro seeds, PVT. LTD. Bangalore, India

Entrapment rate of TSSM by type IV glandular trichomes of Lycopersicon

Entrapment rate and mortality of the pest by type IV glandular trichomes were studied on the leaflets with trichome exudates intact or trichome exudates removed. Trichome exudates were removed using 0.15 % solution of Triton X-100 as follows: leaflets from the terminal pair of the third-last fully expanded leaves were excised. They were first wiped gently with a dry cotton swab, then by cotton saturated with 0.15% solution of Triton X-100. To ensure that the exudates were completely removed, foliages rinsed in 0.15% solution of Triton X-100, then in distilled water (Kennedy & Dimock, 1983; Farrar & Kennedy, 1988).

Leaf disks (2 cm in diameter) were placed with abaxial surface facing up on a watersaturated non sterile cotton wad in a plastic petri dish (12.5 cm in diameter). Ten female mites (3-5 days in age) were placed on the adaxial leaflet surface of each disk. The number of trapped or untrapped mites as well as those that moved into the water were recorded after 2 h. The mites were examined under a stereomicroscope (16X) while being gently prodded with camel hair brush. If a mite did not move and its tarsi or other body parts were entangled by sticky exudates of type IV glandular trichomes, it was recorded as trapped. Mites that were moving around on the leaf surface, unhindered and actively feeding were recorded untrapped. After 24 and 48 h, mites were observed to find whether they are dead or morbid have moved into water. By prodding with camel hair brush, the mites that were unable to react and walk recorded as morbid.

Density and droplet size of type IV glandular trichomes

The density of trichomes (number per mm²) was determined by the average of three regions of abaxial and adaxial surfaces of leaflets (Luczynski *et al.*, 1990). Six leaflets were observed for the density of type IV glandular trichomes, under a stereomicroscope (100X). To determine droplet size, thin cross section was prepared from each leaflet and droplet size of 20 trichomes measured under a phase microscope (100X), using an ocular micrometer.

Statistical analysis

Data was analyzed using SAS software (SAS Institute, 1996) and the analysis of variance (Proc ANOVA) was performed for the identification of any significant differences among the accessions. The student t-test (Proc "t" test) was also used for comparison between pair data. Correlation (Proc Corr) was conducted to describe linear relationship between variables.

Results

Number of entrapped and unaffected mites after 2 hours

In the intact trichome exudates treatments, the number of entrapped mites after 2 h differed significantly among the accessions. The highest level of entrapment rate was observed on *L. hirsutum* LA1777 (10 mites out of 10), followed by *L. pennellii* accessions. None of the mites was entrapped on *L. esculentum* (table 2). The number of unaffected mites was very low on *L. hirsutum* (LA1777 and LA1740) and *L. pennellii* accessions. On *L. hirsutum* LA2860, 3.9 out of 10 mites remained unaffected, whereas on *L. esculentum* most of the mites were unaffected (9.86 mites out of 10). In the removed trichome exudates treatments, none of the mites was entrapped after 2 h and there was no significant difference between the number of unaffected mites on the susceptible cultivar and resistant accessions (table 2).

Number of mites dead, morbid, unaffected and moved into water after 24 and 48 hours

The number of dead mites after 24 and 48 h was significantly different among the treatments. Accessions of *L. hirsutum* (LA1777 and LA1740) and *L. pennellii* caused greater number of dead mites (> 7.28 and 8.16 dead mites out of 10, respectively), whereas on the susceptible cultivar of *L. esculentum* 'Sankranthi', mortality was very low (zero and 0.14 mites after 24 and 48 h, respectively). The number of unaffected mites was almost zero on *L. hirsutum* and *L. pennellii* accessions after 24 and 48 h, while it was 9.57 or 8.86 out of 10 mites on the susceptible cultivar 'Sankranthi' (tables 3 & 4).

The tables (3 & 4) showed that the number of entrapped mites on *L. hirsutum* LA2860 was significantly lower, but the number of mites that moved into water was significantly greater than *L. hirsutum* and *L. pennellii* accessions. There was also no significant difference among the unaffected mites on *L. hirsutum* and *L. pennellii* accessions after 24 and 48 h.

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Curatas	Assessment	No. entra		No. of mites m	oved into water	No. unaff	ected mites
samade	Accession	011 Trichome intact Trichome rei	noved	Trichome intact	Trichome intact Trichome removed	e removed Trichome intact Trichome re	Trichome removed
	LA2860	$4.20 \pm 0.72 c$		$1.80 \pm 0.55 a$	$0.70 \pm 0.29 \text{ ns}$	$3.90 \pm 0.85 \text{ b}$	9.43 ± 0.31 **
L. hirsutum	LA1777	$10 \pm 0.00 a$		0.00 ab	0.85 ± 0.26 *	0.00 c	9.15 ± 0.26 **
	LA1740	$8.62 \pm 0.34 \text{ b}$		$1.38 \pm 0.34 \text{ ab}$	$0.42 \pm 0.21 \text{ ns}$	0.00 c	9.58 ± 0.21 **
	LA2963	9.57 ± 0.30 ab		$0.14 \pm 0.10 c$	$0.28 \pm 0.19 \text{ ns}$	$0.28 \pm 0.18 \text{ c}$	9.72 ± 0.28 **
r. pennetut	LA2580	$9.60 \pm 0.18 \text{ ab}$		0.40 = 0.18 bc	$0.42 \pm 0.20 \text{ ns}$	0.00 c	9.58 ± 0.29 **
L. esculentum	Sankranthi	0.00 d		$0.14 \pm 0.11 c$	$0.15 \pm 0.11 \text{ ms}$	$9.86 \pm 0.14 \text{ a}$	$9.85 \pm 0.14 \text{ ns}$
Means with the same letter	r in each column are not si	onificantly different at $P = 0$	s Multin	· Range Test			

were werden von die keiter in each column are not significantly different at P = 0.01, using Dunran's Multiple Range Test. *** "Mean values are significantly different within accessions using "t" test at P = 0.01 and P = 0.05, respectively. In s = non-significant.

Table 3. Mean $(\pm SE)$ comparison of dead, morbid, moved into water and unaffected *T. urticae* among and within the *Lycopersicon* accessions in trichome exudates intact and trichome exudates removed treatments after 24 h.

		Q	ead	Morbid	bid	Moved i	Moved into water	Unal	Unaffected
Species	Accession	Trichome	Species Accession Trichome Trichome Trichome Trichome	Trichome	Trichome	Trichome		Trichome	Trichome
		intact	removed	intact	removed	intact		intact	removed
	LA2860	$3.90 \pm 0.87 \text{ b}$	$0.57 \pm 0.21 **$	$2.10 \pm 0.68 \text{ ab}$	$1.60 \pm 0.21 *$	$3.20 \pm 0.75 a$	$2.14 \pm 0.34 \text{ns}$	$0.80 \pm 0.36 b$	$5.72 \pm 1.00 **$
L. hirsutum	LA1777	8.50.±0.31 a	0.57 ± 0.29 **	$1.50 \pm 0.29 \text{ ab}$	0.00 **	0.00 b		0.00 b	6.86 ± 0.59 **
	LA1740	$8.13 \pm 0.14 a$	0.71 ± 0.28 **	$1.87 \pm 0.14 \text{ ab}$	0.00 **	0.00 b		0.00 b	6.72 ± 0.61 **
.11	LA2963	$7.50 \pm 0.48 \text{ a}$	0.57 ± 0.22 **	1.50 ± 0.42 ab	0.00 **	1.00 ± 0.13 ab		0.00 b	8.57 ± 0.31 **
r. penneuu	LA2580	$7.29 \pm 0.36 a$	0.58 ± 0.21 **	2.57 ± 0.36 a	0.00 **	0.14 ± 0.14 b		0.00 b	8.85 ± 0.26 **
L. esculentum	Sankranthi	0.00 c	0.00 ns	0.00 b	$0.00 \mathrm{ns}$	$0.43 \pm 0.3 b$		$9.57 \pm 0.29 \text{ a}$	$9.58 \pm 0.19 \text{ ns}$
Means with the same l	etter in each column a	re not significantly dif	ferent among the acces	sions at $P = 0.01$, usi:	ng Duncan's Multij	ple Range Test.			

ns = non-significant.

		De	ad	Moi	Morbid	Moved into water	ito water	Unafi	fected
Species	Accession	Trichome intact	Trichome removed	Trichome intact	Trichome removed	Trichome intact	Trichome removed	Trichome intact	Trichome removed
	LA2860	5.30 ± 0.92 b	$1.00 \pm 0.21 **$	0.30 ± 0.18 a	$0.14 \pm 0.12 \text{ ns}$	$3.70 \pm 0.75 a$	$3 \pm 0.43 \text{ ns}$	0.70 ± 0.48 b	$5.86 \pm 1.00 **$
L. hirsutum	LA1777	$9.38 \pm 0.29 a$	$0.71 \pm 0.28 **$	0.62 ± 0.28 a	0.00 ns	0.00 b	$2.80 \pm 0.50 **$	0.00 b	6.42 ± 0.75 **
	LA1740	$9.29 \pm 0.28 a$	0.86 ± 0.26 **	$0.71 \pm 0.29 a$	0.00 *	0.00 b	3.43 ± 0.37 **	0.00 b	6.49 ± 0.57 **
.11	LA2963	$8.17 \pm 0.30 a$	$0.71 \pm 0.18 **$	0.29 ± 0.18 a	0.00 ns	$1.54 \pm 0.15 \text{ ab}$	$1.14 \pm 0.13 *$	0.00 b	8.00 ± 0.26 **
L. penneuu	LA2580	$9.00 \pm 0.19 \text{ a}$	0.72 ± 0.18 **	$0.57 \pm 0.20 \text{ a}$	0.00 ns	$0.43\pm0.18~\mathrm{b}$	1 ± 0.15	0.00 b	8.15 ± 0.18 **
L. esculentum	Sankranthi	$0.16 \pm 0.14 \text{ c}$	$0.14 \pm 0.13 \text{ ns}$	0.00 a	0.00 ns	$1.00 \pm 0.30 \text{ ab}$	$1 \pm 0.31 \text{ ns}$	$8.86 \pm 0.39 a$	$8.86 \pm 0.42 \text{ ns}$

Table 4. Mean (\pm SE) comparison of dead, morbid, moved into water and unaffected *T. urticae* among and within the *Lycopersicon* accessions in trichome exudates intact and trichome exudates removed treatments after 48 h.

 L. esculentum
 Sankranthi
 $0.16 \pm 0.14 \pm 0.14 \pm 0.13$ ns
 0.00 a 0.00 ns 1.00 ± 0.00 ns

 Means with the same letter in each column are not significantly different among the accessions at P = 0.01, using Duncan's Multiple Range Test.
 **, *Mean values are significantly different within accessions using "t" test at P = 0.01 and P = 0.05, respectively.

 n = non-significant.
 non-significant.

Removing the trichome exudates significantly increased the mite survivals and the number of unaffected mites in resistant accessions. In the susceptible cultivar, however, there was no significant difference between mortality and the number of unaffected mites in the intact or removed trichome exudates treatments (tables 3 & 4). In resistant accessions, the number of mites that moved into water significantly increased after removing of trichome exudates.

Density and droplet size of type IV glandular trichomes

Type IV glandular trichomes were observed only on *L. hirsutum* and *L. pennellii* accessions. The highest and lowest density of the type IV glandular trichomes was recorded on *L. hirsutum* LA1777 and *L. esculentum* respectively (table 5). The density of type IV glandular trichomes was greater on abaxial than adaxial leaf surface, especially on *L. hirsutum* accessions. Droplet size of type IV glandular trichomes significantly varied among the accessions. Accessions of *L. pennellii* had greater droplet size (1.93 times) than *L. hirsutum* accessions. The density and droplet size of type IV glandular trichomes were strongly related to the TSSM entrapment on *Lycopersicon* species (table 6).

Table 5. Mean $(\pm SE)$ density and droplet size of type IV glandular trichomes on abaxial and
adaxial leaf surfaces of Lycopersicon accessions.

Encoing	Accession	Density ((No./mm ²)	Droplet size
Species	Accession	Abaxial surface	Adaxial surface	(μm)
	LA2860	$6.94 \pm 0.69 \text{ d}$	4.83 ± 0.94 c	1.02 ± 0.14 b
L. hirsutum	LA1777	86.72 ± 5.10 a	34.44 ± 6.11 a	$1.13 \pm 0.05 \text{ b}$
	LA1740	74.78 ± 4.10 b	29.94 ± 5.32 ab	1.07 ± 0.05 b
T	LA2963	24.88 ± 0.78 c	21.06 ± 2.91 b	2.08 ± 0.04 a
L. pennellii	LA2580	25.72 ± 1.60 c	20.28 ± 0.87 b	2.07 ± 0.04 a
L. esculentum	Sankranthi	0.00 d	0.00 c	

Means with the same letter in each column are not significantly different at P = 0.05 using Duncan's Multiple Range Test.

Table 6. Correlation (r^2) between density and droplet size of type IV glandular trichomes of *Lycopersicon* species and entrapment of *T. urticae*.

	Entrapment after 2 h	Mortality after 24 h	Mortality after 48 h
Density on abaxial surface	0.70 **	0.65 **	0.63 **
Density on adaxial surface	0.80 **	0.71 **	0.71 **
Droplet size	0.81 **	0.79 **	0.81 **

** Significant at P = 0.01

Discussion

It was found that the TSSM was entrapped by sticky exudates of type IV glandular trichomes on *L. hirsutum* and *L. pennellii* accessions. Exudate of the type IV glandular trichomes which sticks to different body parts of the mites (especially legs and mouthparts) kills the entrapped mites after a few hours (figs 1 & 2). Rasmy (1985) reported that sticky exudates from glandular trichomes of *Solanum* species often trap or hinder locomotion of small insects or mites, which subsequently affect their feeding, oviposition and survival.

A significant positive relationship between density and droplet size of type IV glandular trichomes and number of entrapped mites, suggests that the sticky exudates of type IV glandular trichomes in *L. hirsutum* and *L. pennellii* play a major role in the entrapment of TSSM. The mites' entrapment rate was significantly reduced in all accessions after removing of the trichome exudates (tables 2, 3 & 4). Type IV glandular trichomes are proved to be a basis of resistance in *L. pennellii* to TSSM (Weston *et al.*, 1989), *M. persicae* (Simmons *et al.*, 2003), *H. armigera* (Simmons *et al.*, 2004) and resistance of *L. hirsutum* to *Spodoptera exigua* (Hübner) (Eigenbrode & Trumble, 1993) based on the chemical composition of the type IV glandular trichomes. Simmons *et al.* (2003, 2004) reported the entrapment of *M. persicae* and *H. armigera* larvae by sticky exudates of type IV glandular trichome on *L. pennellii* accessions. Muigai *et al.* (2003) studied the mechanisms of resistance in *Lycopersicon* species to the whitefly *Bemesia argentifolii* Bellows & Perring and found that its entrapment on *L. hirsutum* and *L. pennellii* accessions by type IV glandular trichomes was a major cause of its mortality.

There was a significant relationship between mortality of the mite and density and droplet size of type IV glandular trichomes (table 6). The high mortality of the mite took place on *L. pennellii* and *L. hirsutum* (LA1777 and LA1740) accessions, which their type IV glandular trichomes density was high, underlining the role of type IV glandular trichomes in resistance to TSSM. Simmons *et al.* (2003, 2004) found that entrapment rate and mortality of *M. persicae* and *H. armigera* on *L. hirsutum* and *L. pennellii* accessions after 24 and 48 h, were significantly greater than on *L. esculentum* and reported that the removal of trichome exudates significant lowered their effeciency. An increase in the movement of TSSM towards water after the removal trichome exudates is an indication of the additional resistance factors which are present on the leaf surface of *L. hirsutum* and *L. pennellii* accessions.

Farrar & Kennedy (1988) reported that resistance factors in PI134417 (an accession of *L. hirsutum* f. *glabratum*) which operate against *Heliothis zea* (Boddie) larvae on post-first

instar, were associated primarily with the leaf lamella instead of trichomes. Eigenbrode *et al.* (1996) suggested that identification of lamellar factors of *L. hirsutum* LA1777 facilitates the use of this accession in breeding programs for resistance to *S. exigua*.



Figure 1. Trichome types and their occurrence on stems of *Lycopersicon* species (Luckwill, 1943).



Figure 2. Type IV glandular trichomes on *L. pennelli* LA2963 (A) and entrapment of *T. urticae* by type IV glandular trichomes on *L. hirsutum* LA1777 (B).

Type IV glandular trichomes were largely responsible for the resistance of *Lycopersicon* species to TSSM. It appears that the entrapment of TSSM combined with the toxic effects of the trichome exudates are the main factors for the mortality of TSSM. In this study, we have discovered five new sources of resistant to TSSM from *L. hirsutum* and *L. pennellii* accessions. Among the studied accessions, only *L. hirsutum* LA1777 has already been reported to be resistant to *S. exigua* (Eigenbrode & Trumble, 1993) and *B. argentifolii* (Muigai *et al.*, 2003). There is a possibility of enhancing the level of pest resistance in cultivated tomato by introgression with *L. pennellii* and *L. hirsutum* and selection of resistant individuals in the hybrids, based on the density of type IV glandular trichomes. Saeidi *et al.* (2007) reported that the density of type IV glandular trichomes was the main factor for the resistance to TSSM in the interspecific hybrids of *L. pennellii* LA2963 × *L. esculentum* 'Nandi'.

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