



Glandular trichomes that mediate resistance to green peach aphid in tomato genotypes from the cross between *S. galapagense* and *S. lycopersicum*

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ABSTRACT. The aim of this study was to verify the resistance of tomato genotypes (crossed with *Solanum galapagense*) to the green peach aphid, *Myzus persicae*, and the association of this resistance with glandular trichomes. Leaf trichomes were quantified for seven F₂ genotypes of the BPX-486 population derived from crossing *S. lycopersicum* ‘TOM-684’ and *S. galapagense* accession ‘LA-1401’, for the commercial controls ‘TOM-584’ and ‘Santa Clara’, and for the accession ‘LA-1401’. After this evaluation, the genotypes were subjected to two nonpreference resistance tests of the green peach aphid in the laboratory, one with choice and the other without choice. Five genotypes (BPX-486-17, BPX-486-62, BPX-486-10, BPX-486-46, and BPX-486-08) and the accession LA-1401 exhibited a high density of type IV glandular trichomes and a lower mean number of nymphs and adults of *M. persicae* than two genotypes (BPX-486-313 and BPX-486-383) and the controls with a low density of glandular trichomes, in all the evaluations of both tests. Significant negative correlations between the density of type IV glandular trichomes of the tomato genotypes and the preference of *M. persicae* were found, which confirms the association between this type of glandular trichome and resistance to *M. persicae* in tomato genotypes.

Keywords: plant breeding; insect pests; leaf trichomes; indirect selection.

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Introduction

One of the main pests that attack the tomato crop in its initial phase is the green peach aphid *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). This insect causes direct damage to the crop by sucking sap from leaves and new branches, which impedes plant development. In addition to direct damage, *M. persicae* causes indirect damage since it is a vector of known disease viruses, such as tomato mosaic, tomato streak, tomato yellow top, and tomato bottom yellow leaf viruses. These viruses limit crop production because for plants normally do not produce fruit and when they do the fruit does not meet the demands of the consumer market (Fornazier, Pratisoli, & Martins, 2010).

Hemiptera pests in tomato crops are still mainly controlled by chemical methods through the systematic application of insecticides. However, frequent use of these products negatively affects natural enemies, increases the possibility of developing populations of resistant pests, and may damage the environment and the health of rural workers and consumers (Baldin, Vendramim, & Lourenção, 2005; Silva et al., 2009).

Tomato genotypes with levels of resistance to insect pests constitute a more feasible alternative for integrated pest management (IPM) for the purpose of minimizing the undesirable effects of the excessive use of chemicals (Gallo et al., 2002; Rodríguez-López et al., 2011).

Some wild species of tomato have physical and chemical factors associated with pest resistance; those most studied include glandular trichomes and allelochemicals, which that are natural chemical compounds produced and exudated by the trichomes themselves. These factors have been associated with obstruction to feeding, development, and reproduction of arthropod pests (Dias, Resende, Faria, Camargo, & Lima, 2013; Silva et al., 2016).

These resistance factors can be transferred to *S. lycopersicum* through crosses with wild species to increase resistance (Gonçalves et al., 2006). The mechanisms or types of resistance found in tomato are

nonpreference (antixenosis) and antibiosis (Lucini, Faria, Rohde, Resende, & De Oliveira, 2015). Nonpreference is more desirable because it impedes initial colonization of the crop by the pests and reduces the possibility of breaking resistance (Selvanarayanan & Narayanasamy, 2004).

The wild species *Solanum galapagense* is phylogenetically nearest to the cultivated tomato *S. lycopersicum* (Peralta, Spooner, & Knapp, 2008), and some of its accessions, such as LA-1401, have high levels of pest resistance. This resistance is associated with high density of glandular trichomes and with high leaf content of the acyl sugar allelochemical (Firdaus et al., 2013; Lucatti, Van Heusden, Vos, Visser, & Vosman, 2013; Andrade et al., 2017). Therefore, *S. galapagense* constitutes an important source of genes for tomato pest resistance that can be used in crop breeding programs, providing excellent expectations for success in subsequent generations.

Thus, the aim of this study was to evaluate the resistance of interspecific crosses between *S. galapagense* and *S. lycopersicum* to green peach aphid (*M. persicae*) mediated by glandular trichomes.

Material and methods

The experiments were conducted in a greenhouse of the Hortiagro Sementes S. A. company, in the municipality of Ijaci, Minas Gerais, Brazil, and in the Plant Anatomy Laboratory of the Department of Biology and the Biological Pest Control Laboratory of the Department of Entomology, both at the Universidade Federal de Lavras, Lavras, Minas Gerais State, Brazil.

The interspecific cross (*S. lycopersicum* x *S. galapagense*) provided the F₁ and F₂ segregating populations. Plants of the F₂ population were selected for contrasting densities of leaf trichomes and were denoted BPX-486 (Andrade et al., 2017). The female parent of the cross, 'TOM-684' is a precommercial elite line of *S. lycopersicum*, with low glandular trichome density and low acyl sugar content in the leaves (Maciel, Maluf, Silva, Gonçalves Neto, & Gomes, 2011), and LA-1401 is a wild accession of *S. galapagense*, with a high type IV glandular trichome density, a high leaf acyl sugar content, and resistance to arthropod pests (Lucatti et al., 2013).

For evaluation of resistance to green peach aphids, bioassays with and without choice were set up using seven genotypes of the BPX-486 population, the Santa Clara cultivar the TOM-584 commercial line, and the LA-1401 accession, which were sown in 128-cell expanded polystyrene trays filled with the commercial substrate Tropstrato HA® and covered with a thin layer of vermiculite.

Thirty days after sowing in the greenhouse, the genotypes were transplanted to polyethylene pots with a 5 dm³ capacity for substrate, which was obtained from a mixture of subsurface soil, coarse sand, and the commercial compound Provaso® at a 2:1:1 ratio. Other crop treatments were performed as recommended for the tomato crop, except for chemicals for plant health control.

Sixty days after transplanting, when plants were of good size, a leaflet was collected from the fourth definitive upper leaf of each plant for evaluation of the densities (mean number per mm⁻²) and types of trichomes present. The leaflets were initially placed in a plastic container with 200 mL of 70% ethanol. After 72 hours, paradermic cuts were made in the abaxial and adaxial surfaces of the leaflets with a steel razorblade.

The sections were clarified in a 50% sodium hypochlorite solution for approximately one minute and then washed twice in distilled water. Then, the sections were stained in a 0.01% safranin solution for 20 seconds and washed twice in distilled water to remove excess stain. Semi-permanent slides were prepared as mounts in glycerinated water (Kraus & Arduim, 1997); six sections of each surface were placed on a slide for analysis of the types of leaf trichomes.

The slides were photographed with a Zeiss Axio Cam Erc 5s camera connected to the Zeiss Axio Lab. A1 microscope, and the phytomicrographs were evaluated using the image analysis software ImageTool version 3.00 (Department of Dental Diagnostic Science, University of Texas Health Science Center, San Antonio, Texas). The types of trichomes were classified and quantified in three different 1 mm² areas on each surface of the epidermis (abaxial and adaxial) based on the presence or absence of a gland at the apical tip of the trichome, on its length, and on the type of gland, according to the classification established by Luckwill (1943).

After the analysis described above, the genotypes were cloned from the axillary buds for use in the bioassays, with and without choice, with the green peach aphid. Approximately 30 days after the beginning of rooting of the clones and after sowing the commercial controls in 72-cell expanded polystyrene trays, the seedlings were transplanted to pots, as described above.

The green peach aphid population was maintained in the laboratory on leaves from *Nicandra physalodes* plants in 15-cm-diameter Petri dishes with the abaxial surface of the leaf turned upward over a 1% agar/water layer. Before fastening the plant leaves on the Petri dishes, they were washed in 5% sodium hypochlorite solution and then rinsed for 45 seconds in running water. After aphids were released, the dishes were closed with fine voile fabric and stored in a climate-controlled chamber at a temperature of $25 \pm 2^\circ\text{C}$, relative humidity of $70 \pm 10\%$, and 12-hour photophase. Approximately every three days, when the leaves showed the first signs of senescence, the aphids were transferred to dishes with new leaves by means of a fine bristle brush.

Forty days after transplanting the seedlings to pots in a greenhouse, a trial with choice was set up with the green peach aphid *M. persicae* and with different tomato genotypes. The genotypes (BPX-486-17, BPX-486-62, BPX-486-46, BPX-486-08, BPX-486-313, and BPX-486-383), the accession LA-1401, and the controls Santa Clara and TOM-584 were used for this test.

Leaflets from the middle of the upper third of the plant were collected and placed in paper bags with identification. In the laboratory, these leaflets were fastened on 20-cm-diameter Petri dishes with the abaxial surface turned upward over a 1% agar/water layer. Leaflets of a similar size from each of the nine treatments were arranged in a circle at the same distance from the center, forming an arena. Twenty-four wingless adult aphids at the beginning of the reproductive period were released in the center of each dish. The dishes were closed with a PVC film, perforated with an entomological needle, and stored in a climate-controlled chamber at a temperature of $25 \pm 2^\circ\text{C}$, relative humidity of $70 \pm 10\%$, and 12-hour photophase. The trial was set up in a randomized block design with nine treatments and eighteen replications.

The test without choice was set up 46 days after transplanting the genotypes to pots. Ten genotypes were evaluated: BPX-486-17, BPX-486-62, BPX-486-10, BPX-486-46, BPX-486-08, BPX-486-313, and BPX-486-383; the accession LA-1401; and the controls Santa Clara and 'TOM-584'.

Leaflets of the third completely expanded leaf, from the apex down, of the different tomato genotypes were detached and placed in paper bags with identification. In the laboratory, they were fastened with the abaxial surface turned upward in a 1% water/agar layer in 5-cm-diameter Petri dishes. Three wingless adult aphids at the beginning of the reproductive period were removed from the place they were being raised and transferred to dishes with leaflets corresponding to each treatment. The dishes were sealed with PVC film perforated with a needle to avoid excessive moisture inside and stored in a climate-controlled chamber at $25 \pm 2^\circ\text{C}$, RH of $70 \pm 10\%$, and 12-hour photophase. The trial was set up in a completely randomized design, with ten treatments and eighteen replications.

Both tests were evaluated 24, 48, and 72 hours after the release of the aphids by counting the number of nymphs and adults on the tomato leaflets of each treatment arranged on the dishes. In the first two evaluations, the nymphs were removed with a brush, leaving only the adults.

After verifying the normality and homogeneity of the variances by the Shapiro-Wilk and Bartlett tests, respectively, the data were subjected to the Sisvar statistical program, and analysis of variance was performed; the mean values were clustered by the Scott & Knott test ($p \leq 0.05$) (Ferreira, 2011). The data were transformed in $\sqrt{X+0.5}$. Correlations between the density of type IV glandular trichomes and nonglandular trichomes with the preference of *M. persicae* were also calculated using the SAS (1995).

Results and discussion

Among the glandular trichomes, type IV was predominant on both surfaces of the leaflets evaluated of the genotypes BPX-486-17, BPX-486-62, BPX-486-10, BPX-486-46, and BPX-486-08 and of the accession LA-1401. The genotypes BPX-486-313 and BPX-486-383 and the controls Santa Clara and TOM-584 did not exhibit this type of trichome (Table 1).

The other types of glandular trichomes (I, VI, and VII) were absent from the abaxial surface of the leaflets of all the genotypes analyzed. On the abaxial surface of the leaflets of the genotypes TOM-584, BPX-486-313, BPX-486-17, BPX-486-62, BPX-486-10, and LA-1401, the presence of these types of trichomes was observed, however, in very small numbers. Analyzed together (I+VI+VII), there was an average of 0.45 trichomes per mm^{-2} (Table 1).

Regarding nonglandular trichomes, types II+III+V were observed on the leaflets, with a greater density on the controls Santa Clara and TOM-584 and on genotypes BPX-486-313 and BPX-486-383 than on the others evaluated, on both the abaxial and adaxial surfaces, except for genotype BPX-486-383 on the adaxial

surface, which did not differ from the other genotypes of the BPX-486 population. LA-1401 exhibited the smallest number of nonglandular trichomes among the genotypes evaluated (Table 1).

Table 1. Number (mean \pm standard error) of glandular trichomes (mm^{-2}) of types IV and types I+VI+VII, as well as nonglandular types II+III+V, on the abaxial (ab) and adaxial (ad) surfaces of the tomato genotypes selected and correlations between the types of trichomes and surfaces of the leaflets.

Genotype	Glandular				Nonglandular	
	IV ab	IV ad	I+VI+VII ab	I+VI+VII Ad	II+III+V Ab	II+III+V ad
Santa Clara	0.0 \pm 0.00 c	0.0 \pm 0.00 b	0.0 \pm 0.00 a	0.0 \pm 0.00 a	69.0 \pm 1.64a	35.0 \pm 1.55 b
TOM-584	0.0 \pm 0.00 c	0.0 \pm 0.00 b	0.0 \pm 0.00 a	0.8 \pm 0.46 a	53.9 \pm 1.84 a	31.3 \pm 1.48 b
BPX-486-313	0.0 \pm 0.00 c	0.0 \pm 0.00 b	0.0 \pm 0.00 a	0.3 \pm 0.13 a	44.3 \pm 2.72 b	13.0 \pm 1.15 c
BPX-486-383	0.0 \pm 0.00 c	0.0 \pm 0.0 b	0.0 \pm 0.00 a	0.0 \pm 0.00 a	59.7 \pm 1.76 a	49.6 \pm 6.69 a
BPX-486-17	43.0 \pm 5.51 a	5.0 \pm 3.52 a	0.0 \pm 0.00 a	0.3 \pm 0.13 a	2.6 \pm 2.18 f	16.6 \pm 4.66 c
BPX-486-62	21.1 \pm 3.84 b	8.3 \pm 0.57 a	0.0 \pm 0.00 a	0.3 \pm 0.18 a	31.0 \pm 7.50 c	10.0 \pm 2.51 c
BPX-486-10	16.7 \pm 2.60 b	8.0 \pm 4.51 a	0.0 \pm 0.00 a	0.6 \pm 0.23 a	22.3 \pm 5.89 d	11.3 \pm 1.20 c
BPX-486-46	33.3 \pm 8.41 a	5.0 \pm 1.99 a	0.0 \pm 0.00 a	0.0 \pm 0.00 a	9.3 \pm 2.40 e	16.3 \pm 1.45 c
BPX-486-08	32.3 \pm 6.64 a	4.3 \pm 1.33 a	0.0 \pm 0.00 a	0.0 \pm 0.00 a	15.7 \pm 4.97 d	13.3 \pm 1.45 c
LA-1401	20.3 \pm 1.66 b	7.1 \pm 2.00 a	0.0 \pm 0.00 a	0.2 \pm 0.11 a	2.1 \pm 1.21 f	3.5 \pm 1.53 d

Mean values followed by the same letter in the same column belong to the same group by the Scott-Knott test at 5% probability.

In general, genotypes BPX-486-17, BPX-486-62, BPX-486-10, BPX-486-46, and BPX-486-08 and the accession LA-1401 exhibited high a density of glandular trichomes and low density of nonglandular trichomes; on average, 59.0% of all the trichomes on the leaflets are type IV. Nevertheless, in genotypes BPX-486-313 and BPX-486-383 and in the commercial controls Santa Clara and TOM-584, the opposite was found, with 99.6% of the total trichomes of the nonglandular types (II+III+V).

These results agree with those found by Simmons, Mcgrath, and Gurr (2005), who evaluated the trichome density of F_1 hybrids derived from the cross of a commercial cultivar of *S. lycopersicum* with the accession LA-1410 of *S. galapagense* and found frequent and abundant occurrence of type IV glandular trichomes and scarcity of the other types of glandular trichomes (II, VI, and VII) on both surfaces of the plant leaflets.

Genotypes BPX-486-17, BPX-486-62, BPX-486-10, BPX-486-46, and BPX-486-08, due to their high density of type IV glandular trichomes, may have higher leaf contents of acyl sugars derived from accession LA-1401. There are reports in the literature that this accession, which was used in the present study as one of the parents in the cross that gave rise to the BPX-486 population, has high acyl sugar contents, strongly associated with a high density of type IV glandular trichomes present on plant leaflets (Firdaus et al., 2013; Lucatti et al., 2013).

F_2 genotypes selected for high and low density of type IV glandular trichomes, obtained from crossing tomato with the accession LA-716 of the wild species *S. pennellii*, similar to like LA-1401 of *S. galapagense*, has high leaf contents of acyl sugars, also showed high a association between this type of trichome and leaf content of acyl sugars (Lucini et al., 2015).

Both in the nonpreference test with choice and in the test without choice, a significantly smaller number of *M. persicae* nymphs were found on the leaflets of the tomato genotypes selected for a high density of type IV glandular trichomes (BPX-486-17, BPX-486-62, BPX-486-10, BPX-486-46, and BPX-486-08) and on the accession LA-1401 than on the genotypes selected for a low density of glandular trichomes, such as BPX-486-313 and BPX-486-383, as well as the controls Santa Clara and TOM-584, which also have low density of glandular trichomes in all the evaluations (Tables 2 and 3).

In relation to adult aphids, in both tests, the tomato genotypes selected for high density of type IV trichomes (BPX-486-17, BPX-486-62, BPX-486-10, BPX-486-46, and BPX-486-08), as well as accession LA-1401, exhibited a smaller mean number of *M. persicae* than the genotypes selected for low density of

glandular trichomes, BPX-486-313, BPX-486-383, and the genotypes Santa Clara and TOM-584, at 24, 48, and 72 hours after release of the aphids on the dishes (Tables 2 and 3).

The linear correlations estimated between the density of type IV glandular trichomes with the number of nymphs and adults for the free choice and without choice tests were high and negative in all the periods evaluated (Tables 2 and 3). This indicates the association between the high density of type IV glandular trichomes and the lower preference of *M. persicae*.

Table 2. Mean number of nymphs and adults of *M. persicae* on leaflets of tomato genotypes with different densities of type IV glandular trichomes and types II+III+V nonglandular trichomes on the abaxial surface, and linear correlations between trichome density and preference 24, 48, and 72 hours after the release of aphids in the free choice test (T = 25 ± 2°C, RH = 70% ± 2°C, and 12-hour photophase).

Genotype	Number of nymphs			Number of adults		
	24h	48h	72h	24h	48h	72h
Santa Clara	10.0 ± 1.77 a	12.0 ± 1.55 a	15.3 ± 1.16 a	4.1 ± 0.94 a	6.2 ± 0.96 a	4.5 ± 0.88 a
TOM-584	9.9 ± 1.47 a	10.5 ± 1.42 a	14.0 ± 1.16 a	4.4 ± 0.94 a	6.2 ± 0.88 a	4.5 ± 0.67 a
BPX-486-313	7.9 ± 1.78 a	8.9 ± 1.36 a	13.6 ± 1.06 a	3.5 ± 0.97 a	4.9 ± 0.95 a	4.0 ± 0.75 a
BPX-486-383	7.7 ± 1.67 a	8.1 ± 1.59 a	11.3 ± 1.33 a	3.6 ± 1.01 a	4.8 ± 0.99 a	3.7 ± 0.76 a
BPX-486-17	1.2 ± 0.46 b	1.2 ± 0.27 b	1.2 ± 0.45 b	1.0 ± 0.27 b	1.2 ± 0.36 b	1.5 ± 0.46 b
BPX-486-46	1.6 ± 0.63 b	1.5 ± 0.51 b	1.6 ± 0.48 b	1.3 ± 0.35 b	1.3 ± 0.33 b	1.5 ± 0.54 b
BPX-486-62	1.5 ± 0.54 b	1.2 ± 0.44 b	2.9 ± 0.81 b	0.9 ± 0.22 b	1.5 ± 0.26 b	1.5 ± 0.39 b
BPX-486-08	1.2 ± 0.38 b	1.2 ± 0.43 b	1.6 ± 0.42 b	1.3 ± 0.29 b	2.0 ± 0.49 b	1.2 ± 0.42 b
LA-1401	1.2 ± 0.46 b	1.2 ± 0.34 b	1.2 ± 0.24 b	1.3 ± 0.41 b	1.3 ± 0.34 b	1.2 ± 0.34 b
Correlations (r)						
Type IV trichomes vs Preference	-0.91**	-0.89**	-0.92**	-0.91**	-0.90**	-0.89*
Nonglandular trichomes (II+III+V) vs Preference	0.92**	0.92**	0.93**	0.89*	0.92**	0.90**

Mean values followed by the same letter in the column belong to the same group by the Scott-Knott test at 5% probability. *, ** significant at 1% and 5%, respectively, by the F test.

Table 3. Mean number of nymphs and adults of *M. persicae* on leaflets of tomato genotypes with different densities of type IV glandular trichomes and type II+III+V nonglandular trichomes on the abaxial surface and linear correlations between trichome density and preference 24, 48, and 72 hours after the release of aphids in the test without choice (T = 25 ± 2°C, RH = 70% ± 2°C, and 12-hour photophase).

Genotype	Number of nymphs			Number of adults		
	24h	48h	72h	24h	48h	72h
Santa Clara	9.3 ± 0.96 a	8.8 ± 0.92 a	10.2 ± 0.84 a	2.6 ± 0.18 a	2.5 ± 0.14 a	2.2 ± 0.15 a
TOM-584	8.2 ± 0.68 a	9.0 ± 0.89 a	8.3 ± 0.98 a	2.2 ± 0.21 a	2.3 ± 0.19 a	2.2 ± 0.22 a
BPX-486-313	8.6 ± 0.8 a	8.8 ± 0.78 a	8.5 ± 0.86 a	2.2 ± 0.23 a	2.0 ± 0.18 a	2.0 ± 0.18 a
BPX-486-383	8.4 ± 0.76 a	9.0 ± 0.77 a	8.3 ± 0.73 a	2.2 ± 0.22 a	2.0 ± 0.2 a	1.9 ± 0.23 a
BPX-486-17	1.2 ± 0.23 b	1.5 ± 0.27 b	1.0 ± 0.18 b	1.0 ± 0.23 b	1.5 ± 0.21 b	1.4 ± 0.22 b
BPX-486-46	1.1 ± 0.17 b	0.9 ± 0.27 b	1.2 ± 0.16 b	0.7 ± 0.13 b	0.8 ± 0.21 b	0.8 ± 0.17 c
BPX-486-62	0.8 ± 0.2 b	1.2 ± 0.23 b	0.8 ± 0.21 b	0.7 ± 0.15 b	1.2 ± 0.22 b	0.7 ± 0.15 c
BPX-486-08	1.2 ± 0.28 b	1.3 ± 0.24 b	1.0 ± 0.22 b	0.9 ± 0.17 b	1.2 ± 0.18 b	0.8 ± 0.18 c
BPX-486-10	0.9 ± 0.18 b	1.5 ± 0.18 b	1.2 ± 0.28 b	0.8 ± 0.18 b	1.2 ± 0.17 b	0.8 ± 0.20 c
LA-1401	1.7 ± 0.22 b	0.8 ± 0.21 b	0.7 ± 0.21 b	0.9 ± 0.18 b	0.9 ± 0.22 b	0.6 ± 0.14 c
Correlations (r)						
Type IV trichomes vs Number of aphids	-0.89**	-0.89**	-0.88**	-0.85*	-0.78*	-0.73*
Nonglandular trichomes (II+III+V) vs Number of aphids	0.89**	0.91**	0.92**	0.88**	0.90**	0.83**

Mean values followed by the same letter in the column belong to the same group by the Scott-Knott test at 5% probability. *, ** significant at 1% and 5%, respectively, by the F test.

The adverse effect of tomato genotypes selected for a high density of type IV glandular trichomes on the host selection response of *M. persicae* may have been caused by the presence of higher acyl sugar contents in the leaflets of these genotypes. Acyl sugars are produced and exudated mainly by glands located at the tip of type IV trichomes in the accession LA-1401 of *S. galapagense* (Lucatti et al., 2013), which was used in this study as one of the parents of the cross that gave rise to the genotypes evaluated. Thus, it is presumed that the genotypes of the BPX-486 population selected for high a density of type IV glandular trichomes also have higher leaf contents of acyl sugars, similar to LA-1401. This may explain the fact of that genotypes selected for a high density of this type of trichome have shown the same level of resistance by the mechanism of nonpreference for feeding and production of nymphs/reproduction of the aphid as found for the wild accession LA-1401, both in the test with choice and in the test without choice.

The results of this study are analogous to those found by Simmons and Gurr (2005), who evaluated F1 hybrids with a high type IV trichome density obtained from the cross between tomato and the wild accession LA-1410 of *S. galapagense* and found that these genotypes, similar to LA-1410, were less preferred for feeding by the aphid *M. persicae* than the commercial cultivar of *S. lycopersicum* with a low density of glandular trichomes.

Tomato lines of the second backcross to *S. lycopersicum*, obtained from crossing tomato with the accessions LA-716 of *S. pennelii* and LA-407 of *S. habrochaites* var. *glabratum*, which have a high density of type IV and VI glandular trichomes, respectively, were evaluated under field conditions in regard to resistance to *M. persicae* and *Macrosiphum euphorbiae* (Thomas) aphids (Hemiptera: Aphididae). These lines, similar to what was observed in the present study, exhibited higher levels of nonpreference for feeding and production of nymphs/reproduction of aphids than two commercial tomato cultivars with low density of glandular trichomes (Kohler & Clair, 2005).

Rodríguez López et al. (2011) investigated resistance to another important Hemiptera pests of tomato and found that in genotypes obtained from the cross of *S. lycopersicum* with accession TO-937 of the species *S. pimpinellifolium*, the preference for feeding of the silverleaf whitefly *Bemisia tabaci* biotype B was negatively correlated with the density of type IV trichomes and with the acyl sugar leaf content.

Firdaus et al. (2013) found negative correlations between the density of type IV trichomes and the preference for oviposition/reproduction of silverleaf whitefly *B. tabaci* biotype B in evaluating genotypes of an F2 population obtained from crossing *S. lycopersicum* x *S. galapagense* 'PRI91117'. In addition, the authors detected the occurrence of high positive correlations between the density of type IV trichomes and the leaf acyl sugar content.

The genotypes of the F₂ population (BPX-482) derived from the cross with accession LA-1401 of *S. galapagense* also showed resistance through nonpreference when subjected to tests with the caterpillar *Helicoverpa armigera*. The lower preference and leaf consumption of this insect pest was associated with high a density of type IV glandular trichomes present on the leaflets of the plants (Silva et al., 2016).

The correlations between the number of nymphs and adults of *M. persicae* and the total number of nonglandular trichomes (II+III+V) were high and significant, but positive, in all the time periods evaluated, both for the free choice test and for the test without choice (Tables 2 and 3). These correlations seem to simply reflect the lower proportion (or absence) of glandular trichomes in the genotypes, with higher density of nonglandular trichomes.

Andrade et al. (2017) studied the inheritance of type IV glandular trichomes and their association with resistance to silverleaf whitefly *B. tabaci*, using populations derived from the cross of tomato with the accession LA-1401 of *S. galapagense*. The authors observed that the type IV trichome has relatively simple inheritance, which facilitates its introgression in the domesticated tomato and the association between this type of trichome and the lower preference for reproduction and feeding of silverleaf whitefly. The authors also found high positive correlations between the density of nonglandular trichomes of types II and III with the number of eggs and adults of silverleaf whitefly, indicating that nonglandular trichomes do not grant resistance to insects.

In general, indirect selection for pest resistance based on the density of type IV trichomes derived from the cross of *S. lycopersicum* x *S. galapagense* LA-1401 was effective in obtaining genotypes with high levels of resistance to the green peach aphid *M. persicae* by the mechanism of nonpreference. Therefore, it can be recommended to facilitate the selection process because direct selection in the field or in the laboratory, in most cases, is unfeasible in large plant populations, such segregating populations. The genotypes of the BPX-486 population with a high density of glandular trichomes are promising to provide continuity to the tomato breeding program with a view toward obtaining commercial genotypes resistant to green peach aphids. Other factors not studied in the present study, such as the leaf content of acyl sugars, may be involved in the resistance to insects of tomato plants derived from *S. galapagense* LA-1401 and may also be recommended for future studies of indirect selection of plants resistant to arthropod pests.

Conclusion

Genotypes of tomatoes from the cross between *S. lycopersicum* and *S. galapagense* 'LA-1401' with a high density of glandular trichomes show high resistance to green peach aphids associated with type IV trichomes.

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