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Source: Florida Entomologist, 103(4) : 472-478

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/024.103.00409

Resistance to *Bemisia tabaci* (Hemiptera: Aleyrodidae) Mediterranean (Q biotype) in landrace and wild tomato populations from Mexico

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Abstract

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae) Mediterranean (Q biotype) is a major pest of tomato (*Solanum lycopersicum* L.; Solanaceae) globally. To our knowledge, no whitefly resistant cultivar has been released commercially, and breeding programs are hampered by the lack of resistance sources to this insect which are related closely to the cultivated tomato. Two non-free-choice experiments on *B. tabaci* with 22 landrace (*S. lycopersicum*) and wild tomato (*S. lycopersicum* var. 'cerasiforme') populations from Mexico were performed to find sources of antibiosis resistance to this insect. Plants were infested with 20 insects per 1 leaflet of each plant using plastic micro-cages. In both assays, the number of adults and eggs were counted at 4 d post infestation, the number of nymphs (12 d post infestation), new adults, and non-glandular trichomes at 28 d post infestation. The highest *B. tabaci* resistance was detected in the UTC-SV13 population followed by UTC-SV12, UTC-SV1, and UTC-SV3 with a range of 15.0 to 20.0 dead adults, 0.0 to 16.5 eggs, 0.0 to 12.6 nymphs, 0.0 to 9.7 new adults per leaflet, and with a reproduction index of 0.0 to 21.7. Ten populations showed an intermediate level of resistance significantly lower in the number of dead adults, eggs, nymphs, new adults, and reproduction index compared to the commercial cultivar ('Bonny Best') used as the standard. The remaining 8 genotypes and the commercial cultivar were fully susceptible to *B. tabaci*. The number of non-glandular trichomes correlated significantly with the number of eggs, nymphs, and new adults emerging from the infested plants, suggesting that the density of non-glandular trichomes is favorable for whitefly reproduction. Those genotypes with moderate to high levels of resistance to *B. tabaci* are potential candidates for developing commercial tomato cultivars with some resistance levels to this insect.

Key Words: antibiosis; non-glandular trichomes; *Solanum lycopersicum*; whitefly

Resumen

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae) Mediterranean (biotipo Q) es una importante plaga del tomate (*Solanum lycopersicum* L.; Solanaceae) a nivel mundial. Hasta donde sabemos, ningún cultivar resistente a la mosca blanca ha sido liberado comercialmente y los programas de mejoramiento se ven obstaculizados por la falta de fuentes de resistencia a este insecto estrechamente relacionadas con el tomate cultivado. Se realizaron dos experimentos de no libre elección sobre *B. tabaci* con 22 poblaciones de tomates criollos (*S. lycopersicum*) y tomates silvestres (*S. lycopersicum* var. 'cerasiforme') de México para encontrar fuentes de resistencia tipo antibiosis a este insecto. Se infestaron las plantas con 20 insectos por 1 foliolo de cada planta utilizando microjaulas de plástico. En ambos ensayos se contó el número de adultos y huevos a los 4 d post infestación, el número de ninfas (12 d post infestación), nuevos adultos, y tricomas no glandulares a 28 d post infestación. La mayor resistencia a *B. tabaci* se detectó en la población UTC-SV13, seguida de UTC-SV12, UTC-SV1, y UTC-SV3 con un rango de 15,0 a 20,0 adultos muertos; 0,0 a 16,5 huevos; 0,0 a 12,6 ninfas; 0,0 a 9,7 adultos nuevos por hoja; y con un índice de reproducción de 0,0 a 21,7. Diez poblaciones mostraron un nivel intermedio de resistencia significativamente menor en el número de adultos muertos, huevos, ninfas, nuevos adultos y índice de reproducción en comparación con el cultivar comercial ('Bonny Best') utilizado como el estándar. Los 8 genotipos restantes y el cultivar comercial fueron totalmente susceptibles a *B. tabaci*. El número de tricomas no glandulares se correlacionó significativamente con el número de huevos, ninfas, y nuevos adultos que emergieron de las plantas infestadas, lo que sugiere que la densidad de tricomas no glandulares es favorable para la reproducción de la mosca blanca. Los genotipos con niveles de resistencia moderados a altos a *B. tabaci* son candidatos potenciales para desarrollar cultivares comerciales de tomate con algún nivel de resistencia a este insecto.

Palabras Clave: antibiosis; mosca blanca; *Solanum lycopersicum*; tricomas no-glandulares

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The whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), harbors a complex of cryptic species composed of at least 36 morphologically undistinguishable species, within 11 genetic groups (Firdaus et al. 2012). This insect is highly polyphagous and feeds on several hundred species within 86 botanical families, causing severe damage globally due to direct feeding on the phloem vessels and secretion of sugary compounds that promote the formation of sooty mold (*Capnodium* spp.; Capnodiaceae), limit photosynthesis of leaves, and reduces the quality of fruits. Secondly, whiteflies introduce plant disorders such as irregular ripening of fruits (Schuster et al. 1995), and transmit plant viruses, including Begomovirus, Crinivirus, Carlavirus, Torradovirus, and Ipomovirus (Navas-Castillo et al. 2014), which are devastating and threaten food security in several regions of the world (Brown 2007).

The most invasive and globally distributed species within the *B. tabaci* complex are the Mediterranean (MED, described as biotype Q) and the Middle East Asia Minor 1 (MEAM1, previously known as biotype B). These species are among the most important globally because they remain in quarantine status in several countries (De Barro & Ahmed 2011). Different whitefly control methods are used currently, among them chemical and applied biological control (Neiva et al. 2018). Other control tactics like genetic resistance may be used to complement the integrated management of this insect. Genetic resistance has been identified as one of the most important component of integrated pest management programs (Morales 2006).

Plants possess different defense mechanisms that may repel or reject herbivores or suppress the growth of a pathogen, and in some cases cause mortality. Resistance mechanisms were described by Painter (1951), who classified them in 3 categories, non-preference or antixenosis, antibiosis, and tolerance.

A wide range of genetic variability has been reported in the wild and landrace relatives of *Solanum lycopersicum* L. (Solanaceae) from Mexico (Mazzucato et al. 2008). This country is considered the domestication center of tomato cultivation (Peralta et al. 2005), which implies a great potential to use a wide range of variability in tomato breeding programs, as well as to search for resistance sources to *B. tabaci*. The negative effects of whitefly have been observed in Mexico since 1960 (Sánchez-Peña et al. 2006). Similarly, tomato landraces and wild populations of *S. lycopersicum* var. 'cerasiforme' (Dunal) Spooner, G. J. Anderson et R. K. Jansen (Solanaceae) occur in abandoned fields, formerly tropical dry forest within coastal sites, and in the Pacific slopes (about. 300–1100 masl) of different regions of Mexico. These populations constitute a natural source of potential resistance genes to control whitefly. The wild and landrace relatives of the tomato are genetic resources that have been used successfully to find resistance sources to different whitefly species (Gentile et al. 1968; Nombela et al. 2000; Baldin et al. 2005; Sánchez-Peña et al. 2006; Maruthi et al. 2008; Firdaus et al. 2012). Different species of tomatoes like *Solanum pimpinellifolium* L., *Solanum chilense* (Dun.) Reiche, *Solanum habrochaites* S. Knapp & D. M. Spooner, and *Solanum pennellii* Correll (all Solanaceae) have been reported as resistant to *B. tabaci* (Nombela et al. 2000; Baldin et al. 2005; Maruthi et al. 2008; Firdaus et al. 2012) and other whitefly species like *Trialeurodes vaporariorum* (Westwood) (Diptera: Aleyrodidae) (Gentile et al. 1968). However, landraces and wild tomatoes (*S. lycopersicum* var. cerasiforme) from Mexico scarcely have been studied as a source of genetic resistance for cultivated tomato.

The trichomes of the *Solanum* species have been studied in detail because of their role in plant resistance. Typically, 8 different types are distinguished (Channarayappa et al. 1992) of which type I, IV, VI, and VII are glandular capitate trichomes, which can be found mostly in *Solanum galapaguense* S. C. Darwin & Peralta, *S. habrochaites* and *S. penelli*, and the type II, III, V, and VIII that are non-glandular and is found mostly in *Solanum chesmaniae* (Riley) Fosburg, *Solanum arcanum* Peralta, Knapp & Spooner, *Solanum peruvianum* Knapp & Jarvis (all Solanaceae), *S. pimpinellifolium*, *S. lycopersicum* var. cerasiforme, and cultivated *S. lycopersicum* cultivars (Sánchez-Peña et al. 2006; Firdaus et al. 2012; Glas et al. 2012). Studies of the resistance mechanism to the whitefly in wild tomatoes have shown that it is often associated with the physical external characteristics of the leaf surface, including villi and trichomes (Oriani & Vendramim 2010), and with the chemical compounds synthesized by the plant, and present in trichomes like acylglucoses, methyl ketones, and sesquiterpenes that may cause high mortality in whitefly adults, specifically acyl sugars that adhere to the adult, preventing colonization of the insect (Rodríguez-López et al. 2012). On the other hand, a glandular trichome-based resistance mechanism is not the only mechanism in tomato to obtain whitefly resistance. Whitefly resistance also was found in accessions without glandular trichomes such as in *S. arcanum* and *Solanum glandulosum* Banks ex Dun Solanaceae) (Firdaus et al. 2012).

Despite multiple potential resistance sources and the studies on resistance mechanisms to this insect, there are no tomato cultivars currently with any type of resistance to *B. tabaci*. This could be due to various factors including the incompatibility of the wild tomato species with cultivated tomatoes, the lack of studies on the heritability of the resistance trait to this insect, the complexity of the introgression of the resistance trait into commercial tomato background, and the species diversity of the *B. tabaci* complex that may have different responses to the different resistance sources of tomato reported so far. The objective of this study was to identify resistance sources to *B. tabaci* Mediterranean (Q biotype) in wild tomatoes and landraces to support tomato breeding programs and, therefore, to have a greater probability of generating tomato cultivars with some level of resistance to this insect.

Materials and Methods

PLANT MATERIAL

Fruits of about 10 plants (without visible diseases symptoms) of each of the 22 wild and landrace populations were collected during the fall and winter season of 2016 in different states of Mexico (Sinaloa, Nayarit, Jalisco, Michoacán, Guerrero, Oaxaca, and Chiapas; Table 1). The 'Bonny Best' tomato cultivar was used as the susceptible control due to its reported susceptibility to *B. tabaci* (Hanson et al. 2016). Seeds were germinated in polystyrene trays (T.L.M., Salt Lake City, Utah, USA) of 200 cells in a growth chamber at 30 °C ± 2 °C with 100% relative humidity (RH).

WHITEFLY COLONY

Whitefly adults of *B. tabaci* Mediterranean (Q biotype) were collected with an entomological aspirator from a pumpkin (*Cucurbita pepo* L.; Cucurbitaceae) crop under open field conditions at the Palazuelos-Villegas farm located in Aguaruto in the Culiacan Valley, Sinaloa, Mexico. These insects were placed on cotton plants (*Gossypium hirsutum* L.; Malvaceae) in insect-proof wooden rectangle cages (150 cm long × 50 cm wide × 100 m high) covered with 60 × 60 mesh organza fabric (20 × 10 caliber) to avoid contamination of other insect vectors. Insects were maintained for 6 mo (6–9 generations) in a greenhouse at an average temperature of 28 °C and 65% RH for maintenance with the aim to have a large virus-free *B. tabaci* population. Maintaining the whitefly population isolated on plants free of viruses over 3 to 4 generations allows one to keep the vector insect free of viruses. *Gos-*

Table 1. Geographic location of the different genotypes of *Solanum lycopersicum* collected in Mexico.

Genotypes	DD[1]	Coordinates		Altitude (masl)[2]
UTC-SV1	Wild	16.8627778°N	99.8869444°W	30
UTC-SV2	Wild	17.9561111°N	102.1922222°W	10
UTC-SV3	Wild	19.6438889°N	102.0483333°W	1,228
UTC-SV4	Wild	19.4000000°N	102.1333333°W	1,140
UTC-SV5	Wild	18.9166667°N	103.8833333°W	33
UTC-SV6	Wild	19.2500000°N	104.5666667°W	29
UTC-SV7	Wild	20.6500000°N	102.8000000°W	161
UTC-SV8	Wild	20.8694444°N	105.4408333°W	2
UTC-SV9	Wild	22.3972222°N	105.4572222°W	8
UTC-SV10	Wild	21.5397222°N	105.2855556°W	10
UTC-SV11	Wild	17.5091667°N	91.9822222°W	60
UTC-SV12	Wild	15.4333333°N	92.1166667°W	927
UTC-SV13	Wild	16.1161111°N	92.6888889°W	187
UTC-SV14	Wild	23.2833333°N	106.0666667°W	120
UTC-SV15	Wild	24.8000000°N	107.3833333°W	100
UTC-CR1	Landrace	17.5513889°N	99.5008333°W	1,242
UTC-CR2	Landrace	16.5116667°N	96.9794444°W	1,550
UTC-CR3	Landrace	15.8619444°N	97.0716667°W	60
UTC-CR4	Landrace	16.8666667°N	96.7833333°W	1,447
UTC-CR5	Landrace	24.8041667°N	107.4311111°W	124
UTC-CR6	Landrace	25.1402778°N	107.5913889°W	224
UTC-CR7	Landrace	25.6472222°N	108.9255556°W	156
Bonny Best	Commercial	NA	NA	NA

[1]Degree of domestication for each genotype.
[2]Meters above sea level.

sypium hirsutum is not a host for Begomovirus that could infect Solanaceae (Czosnek et al. 1993). The cotton plants were substituted with young plants every 2 mo.

The *B. tabaci* Q biotype was confirmed through polymerase chain reaction in the original samples collected from the field before beginning the experiments, taking 6 samples of 50 adults from the collected field and from the insect colony before the resistance assays for their posterior analysis with biotype F (5'-GGCTTATTTTGTAATAAGAGAGGTGTT) and R (5'-GAATTAAAGGTACATGGACCACTT) primers, which amplify a 400 bp fragment of the mitochondrial gene, carboxylesterase. DNA extraction from the insects was achieved with the method described by Doyle & Doyle (1990), and polymerase chain reaction reactions were made according to Kang et al. (2012). Amplified reactions were performed in a thermocycler Bio-Rad C 1000 TM Thermal Cycler (Bio-Rad Laboratories, Inc., Hercules, California, USA), and the polymerase chain reaction products were analyzed through 1% agarose gel electrophoresis.

EXPERIMENTS OF RESISTANCE TO *BEMISIA TABACI*

Two no-choice experiments were performed under greenhouse conditions. The first experiment was performed in Feb 2017 and consisted of fifteen 30-d-old plants of each genotype, which were transplanted individually into plastic planting pots (Poppelman Plastic, Claremont, North Carolina, USA) following a completely randomized design with 23 treatments (landrace and wild tomato genotypes) with 10 replicates of 1 plant per genotype; 5 plants of each genotype were not infested and were considered as a negative control. To infest the plants with the insects, the methodology reported by Muniz & Nombela (2001) was followed, which consisted of placing 20 adult whiteflies (1 d old) on a leaflet in the apical region of the first fully expanded leaf of each of the plants of the different genotypes, to be evaluated through micro-cages fabricated manually with clear plastic cup (SOLO Cup Co., Chicago, Illinois,USA), foam sheet, organza fabric, and hair clips (5 cm diam × 2 cm high) in a no-choice experiment. The number of dead adults and eggs was assessed using an entomological loupe (30×) at 4 d post infestation, as well as the number of nymphs (12 d post infestation), and new adults per leaflet at 28 d post infestation. Dead and live adults were removed with an entomological aspirator and the microcages put them back in the same place. The number of non-glandular trichomes in an area of 8 mm² was evaluated at 28 d post infestation. These determinations were performed on the abaxial surface of each leaflet with a stereoscope LUXEO 2S (30×) Labo America, Fremont, California, USA. With the data obtained, the reproduction index was calculated to analyze the resistance level of each of the evaluated genotypes. The resistance level to *B. tabaci* was based on the reproduction index reported by Taylor (1967) with some modifications, which was calculated through the following formula: the number of eggs of the assessed genotype divided by the average of eggs of the susceptible cultivar multiplied by 100. Classification of the reproduction index was determined as follows: reproduction index = 0 (immune), reproduction index = 1 to 20 (resistant), reproduction index = 21 to 50 (moderately resistant), and reproduction index > 50 (susceptible), or reproduction index ≥ 100 (highly susceptible).

The second assay was performed in Feb 2018 using the same methodology; the number of plants, experimental design, and the resistance evaluation was done as in the first assay. Both experiments were established under the same greenhouse conditions.

STATISTICAL ANALYSIS

The data did not comply with the statistical assumptions of normality and homogeneity of variances; therefore, they were subjected to a nonparametric variance analysis with the Kruskal-Wallis test and Dunn medians to determine significant differences among genotypes ($P \leq 0.05$). Correlations were made with the Spearman test among the measured variables. All statistical analyses were performed with the SAS software.

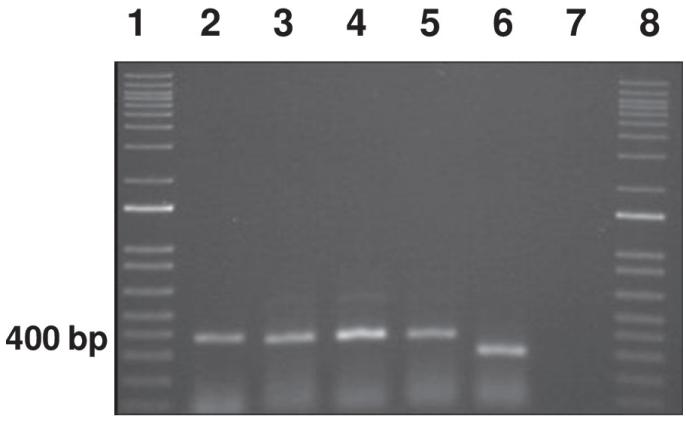

Fig. 1. Polymer chain reaction (PCR) products obtained from the genomic DNA of isolates of *Bemisia tabaci* Mediterranean with the specific primer pair F and R, viewed on a 1.0% agarose gel. Lanes 1 and 8 = 1 kb Plus; lanes 2 to 5 = DNA isolated from whitefly colony of *B. tabaci* MED; lane 6 = DNA isolate of *B. tabaci* MEAM1 (control); lane 7 = negative control.

Results

MOLECULAR IDENTIFICATION OF INSECTS

Polymer chain reaction analysis of all 12 samples (from the field and the insect colony before the experiments) taken during this study generated the expected 400 bp amplicon of the mitochondrial gene, carboxylesterase, indicating that the insects used in this study belong to *B. tabaci* Mediterranean (*Bt*MED) (Q biotype) (Fig. 1).

RESISTANCE ASSAYS

There were no significant differences between experiments 1 and 2 for the number of dead adults, eggs, nymphs, and emerged adults of *Bt*MED ($P > 0.05$); therefore, results were pooled for analysis.

In both experiments, most of the genotypes (12 of 23) were susceptible to *Bt*MED (Table 2). However, the number of dead adults, eggs, nymphs, and emerged adults of *Bt*MED, varied significantly among the tomato genotypes ($P < 0.0001$) (Table 2). Genotype UTC-SV13 showed a significantly higher number of dead adults, a lower number of eggs, nymphs, and emerged adults per leaflet, followed by UTC-SV12, UTC-SV1, UTC-SV3, UTC-CR2, UTC-SV9, UTC-SV5, UTC-SV4, UTC-SV15, UTC-SV11, UTC-CR1, as compared to most of the other genotypes and the commercial cultivar (Table 2). The rest of the 11 genotypes showed no significant difference compared to the commercial cultivar (Table 2).

Regarding the reproduction index, most of the tomato cultivars showed an intermediate reproduction index, although there were significant differences among genotypes ($P < 0.0001$). Based on the reproduction index reported by Taylor (1967), genotype UTC-SV13, UTC-SV12, UTC-SV1, and UTC-SV3 populations were highly resistant, and genotypes UTC-CR2, UTC-SV9, UTC-SV5, UTC-SV4, UTC-SV15, UTC-SV11, and UTC-CR1 showed a moderate resistance to *B. tabaci*. On the other hand, although genotypes UTC-SV2, UTC-SV6, and UTC-SV14 did not show a significant difference compared to the susceptible control, they showed moderate resistance (Table 2). The rest of the 8 populations and the commercial cultivar were fully susceptible to *Bt*MED.

A low positive correlation was identified between the density of non-glandular trichomes and the number of eggs ($R = 0.45$; $P = 0.03$), nymphs ($R = 0.49$; $P = 0.01$), and new adults ($R = 0.52$; $P = 0.01$) of *Bt*MED (Fig. 2a, b, c).

Table 2. Mean ± SD of dead adults, eggs, nymphs, new adults, and reproduction index of *Bemisia tabaci* MED in 23 landrace and wild tomato populations under greenhouse conditions.

Genotypes	Domestication grade	Dead adults*	Eggs	Nymphs	Adults	RI†	DR‡
UTC-SV13	Wild	20.0 ± 0.0^{i}	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}	I
UTC-SV12	Wild	18.8 ± 1.8^{hi}	14.9 ± 11.3^{b}	6.5 ± 5.7^{ab}	2.1 ± 4.0^{ab}	19.5 ± 14.9^{bc}	R
UTC-SV1	Wild	13.2 ± 4.9^{bcdefg}	15.2 ± 16.1^{b}	11.4 ± 11.9^{bc}	7.8 ± 8.1^{bc}	19.9 ± 21.3^{b}	R
UTC-SV3	Wild	15.0 ± 7.0^{defgh}	16.5 ± 11.0^{bc}	12.6 ± 7.6^{bcd}	9.7 ± 7.3^{cdefg}	21.7 ± 14.5^{bcd}	MR
UTC-SV9	Wild	13.0 ± 4.6^{abcdef}	24.8 ± 19.7^{bcd}	14.7 ± 12.1^{bcde}	7.7 ± 8.5^{bcde}	32.6 ± 26.0^{bcde}	MR
UTC-SV5	Wild	9.4 ± 4.7^{ab}	29.5 ± 34.5^{bcd}	19.6 ± 20.6^{bcdef}	7.3 ± 10.2^{bc}	38.8 ± 45.4^{bcde}	MR
UTC-SV4	Wild	11.4 ± 6.9^{abcde}	30.7 ± 37.0^{bcd}	23.4 ± 29.1^{bcde}	13.1 ± 21.2^{bc}	40.4 ± 48.7^{bcde}	MR
UTC-SV15	Wild	17.2 ± 3.1^{fghi}	31.0 ± 12.3^{bcdef}	20.1 ± 9.4^{cdef}	11.0 ± 9.5^{cdefg}	40.7 ± 16.2^{bcdef}	MR
UTC-SV11	Wild	10.9 ± 5.6^{abcd}	31.4 ± 23.6^{bcdef}	26.2 ± 23.2^{cdefg}	16.7 ± 19.8^{cdefg}	41.3 ± 31.1^{bcdef}	MR
UTC-SV2	Wild	16.6 ± 3.5^{efghi}	34.1 ± 32.9^{bcdef}	22.0 ± 31.5^{bcde}	12.3 ± 25.6^{bcd}	44.8 ± 43.4^{bcdef}	MR
UTC-SV6	Wild	7.40 ± 5.7^{a}	35.3 ± 22.1^{bcdef}	21.7 ± 12.9^{cdefg}	9.4 ± 7.5^{cdef}	46.4 ± 29.2^{cdef}	MR
UTC-SV14	Wild	10.3 ± 3.4^{ab}	37.2 ± 25.1^{cdef}	29.0 ± 20.7^{defg}	17.3 ± 11.1^{defgh}	48.9 ± 33.0^{def}	S
UTC-SV7	Wild	9.80 ± 5.0^{ab}	40.8 ± 32.1^{cdef}	27.3 ± 25.1^{cdef}	16.5 ± 19.9^{cd}	53.6 ± 42.3^{def}	S
UTC-SV10	Wild	10.9 ± 4.3^{abc}	44.7 ± 35.8^{def}	36.3 ± 30.2^{efg}	21.0 ± 27.9^{cd}	58.8 ± 47.1^{ef}	S
UTC-SV8	Wild	15.2 ± 5.0^{defgh}	46.1 ± 43.5^{bcdef}	28.9 ± 26.3^{cdefg}	13.6 ± 14.4^{cd}	60.6 ± 57.3^{bcdef}	S
UTC-CR2	Landrace	17.6 ± 3.8^{ghi}	19.1 ± 22.2^{bc}	13.4 ± 19.3^{bc}	8.5 ± 13.5^{bc}	25.1 ± 29.2^{bc}	MR
UTC-CR1	Landrace	12.3 ± 4.0^{abcde}	33.1 ± 40.1^{bcde}	21.0 ± 33.1^{bcd}	16.1 ± 29.2^{cdef}	43.5 ± 52.7^{bcde}	MR
UTC-CR6	Landrace	11.4 ± 7.7^{abcdef}	44.8 ± 24.3^{def}	31.0 ± 23.0^{defg}	20.6 ± 18.4^{efgh}	58.9 ± 31.9^{def}	S
UTC-CR4	Landrace	13.0 ± 4.8^{abcdef}	45.7 ± 44.3^{bcdef}	17.3 ± 12.3^{bcdef}	9.4 ± 8.7^{cdef}	60.1 ± 58.3^{bcdef}	S
UTC-CR5	Landrace	9.6 ± 6.5^{ab}	51.8 ± 44.3^{ef}	39.5 ± 22.5^{fg}	28.7 ± 22.3^{gh}	68.1 ± 34.2^{ef}	S
UTC-CR7	Landrace	10.6 ± 6.0^{abc}	53.7 ± 44.3^{def}	33.9 ± 24.2^{defg}	16.4 ± 16.6^{cdefg}	70.6 ± 52.9^{def}	S
UTC-CR3	Landrace	15.2 ± 6.6^{defgh}	67.0 ± 59.1^{def}	54.0 ± 50.9^{efg}	32.3 ± 29.2^{fgh}	88.1 ± 77.7^{def}	S
Bonny Best	Commercial	8.6 ± 6.2^{ab}	76.0 ± 67.8^{f}	65.5 ± 63.5^{g}	55.9 ± 57.0^{h}	100.00 ± 0.0^{f}	HS

*Means in a column followed by different lowercase letters are significantly different ($P \leq 0.05$; Kruskal-Wallis test followed by sequential Holm adjustment).
†Reproduction index
‡Degree of resistance: I = immune, R = resistant, MR = moderate resistant, S = susceptible, and HS = high susceptible

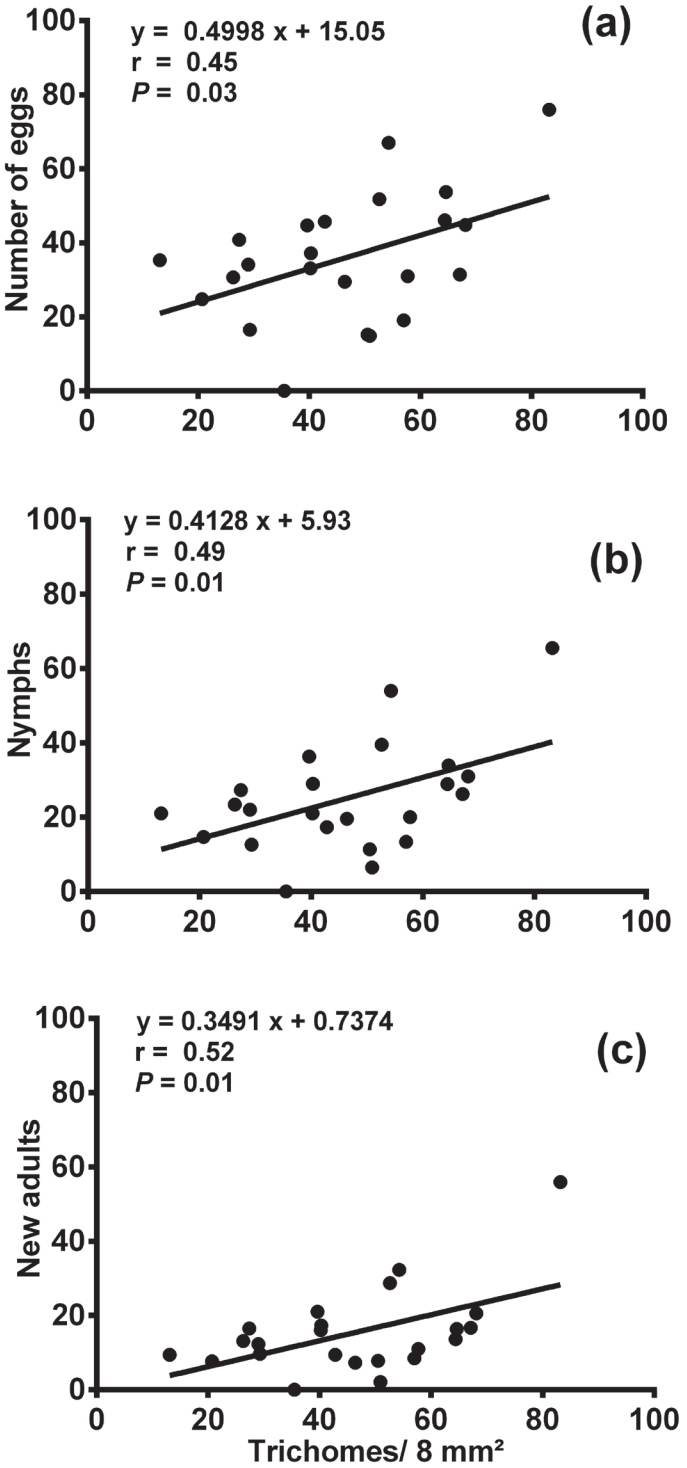

Fig. 2. Linear correlations between whitefly resistance parameters and non-glandular trichomes of wild and landrace tomato populations in non-choice bioassays.

Discussion

The use of resistant cultivars represents an alternative option for the control of *B. tabaci* Mediterranean (*Bt*MED) (Q biotype), which is recognized as an important pest that limits tomato production in diverse regions around the world (Morales 2006). From 22 genotypes of *S. lycopersicum* used in this study, the genotype UTC-SV13 showed 100% dead adults at 4 d post infestation, and 0% new adults at 28 d post infestation. Therefore, this insect could not complete its biological cycle in plants of this genotype, indicating that this wild tomato population has an antibiosis mechanism that impedes the reproduction of this insect in this genotype. According to Taylor (1967), this mechanism is an immunity type, although further studies with nymph infestation are needed to corroborate this issue. These results agree with those of Lucatti et al. (2013) and Rakha et al. (2017), who found immunity to *B. tabaci* in wild genotypes of *S. galapaguense* and *S. penelli*, respectively. Genotype UTC-SV13 is a promising source of resistance for genetic breeding programs of tomato, as well as for studies on the genetic basis of this resistance trait and the development of molecular markers.

Ten genotypes showed high to moderate resistance level to *Bt*-MED in both experiments at 28 d post infestation (Table 2), also suggesting presence of an antibiosis mechanism in these genotypes because they significantly reduced the different biological stages (eggs, nymphs, and new adults) of this insect compared to the commercial cultivar Bonny Best (Table 2). Toscano et al. (2002) and Neiva et al. (2018) have reported similar results regarding moderate and high levels of resistance to whiteflies in wild genotypes of tomato. Therefore, these genotypes are promising sources of resistance that may be used for the development of tomato cultivars with different resistance levels to *Bt*MED. This would be accomplished through the use of these sources of resistance to obtain cultivars with more stable and durable resistance to this agriculturally important insect (Vidavski et al. 2008).

The first step for the development of commercial cultivars resistant to pests or diseases is to scrutinize wild or landrace relatives of the cultivated plants that will allow selection of resistant genotypes to be used in the genetic breeding programs of farm crops. The second step is to analyze the genetic basis of the resistance trait and its heritability to design the best genetic model of the desired introgression trait in the cultivated elite germplasm, and a last step would be to develop the breeding program (Retes-Manjarrez et al. 2018).

The results of the present study indicate that populations of *S. lycopersicum* differ in their level of whitefly resistance and are more resistant than cultivated varieties of tomato with non-free-choice resistance testing under controlled conditions. These results support previous studies indicating that cultivated species are less resistant to herbivores than wild and landrace populations (Sanchez-Peña et al. 2006).

Wild and landrace populations of *S. lycopersicum* have been in contact with whiteflies in the same geographic area as the cultivated tomato in Mexico, at least during the last century. Wild and landrace populations likely have been exposed to the selective pressure imposed by whiteflies. This constitutes a plausible explanation for the different levels of resistance to whitefly that has been detected in wild and landrace populations. At the same time, wild and landrace populations of tomato have not been sufficiently explored as a source of genetic resistance to whitefly. For this reason, it must be incorporated in future breeding programs to increase pest resistance in tomato and to bring new variability that could contribute to improving other agronomical traits such as yield and vigor.

Due to the absence of the glandular trichomes from the *S. lycopersium* landraces and *S. lycopersicum* var. cerasiforme wild populations used in this study, we focused on the relationship of the resistance parameters such as number of eggs, nymphs, and new adults, and the density of non-glandular trichomes. The number of non-glandular trichomes was correlated with the number of eggs,

nymphs, and new adults that emerged from the infested plants (Fig. 2), indicating that the greater the number of this type of trichomes, higher whitefly infestations occurred. This result suggests that the density of non-glandular trichomes observed in the genotypes with different levels of resistance are favorable for the reproduction of whiteflies. Similar results were reported by Butter & Vir (1989), who concluded that non-glandular trichomes provide a favorable microclimate for oviposition, and protection of eggs and nymphs of these insects to their natural enemies. Other authors, including Firdaus et al. (2012), also found resistance in genotypes without glandular trichomes in accessions of *S. arcanum* and *S. glandulosum*. Other mechanisms, such as trichome inclination, density, length, leaf color, leaf surface hardness, and cuticle thickness or mesophilic leaf compounds, may affect whitefly landing, feeding, and oviposition, which also may play a role in the whitefly resistance mechanism (Glas et al. 2012; Riddick & Simmons 2014; Hasanuzzaman et al. 2016). Further studies regarding the chemical exudates of the resistant genotypes of this study are required to characterize the compounds excreted by the cells of the trichomes associated with resistance, such as those reported by Bleeker et al. (2012), who found the presence of zingiberene with a toxic effect in a wild genotype of tomato, and which has been associated with resistance to many insect herbivores (Maluf et al. 2001).

The wild and landrace tomato populations collected in Mexico showed a wide variation in their resistance levels to *Bt*MED. This wide variability enabled us to find and select plants with different resistance levels to this insect. These results agree with the variations observed in landrace and wild tomatoes reported in Mexico (Hoyt 1992; Eingenbrode & Trumble1993; Mazzucato et al. 2008) regarding different morphological traits and different resistance levels to *B. tabaci*.

In conclusion, the wild and landrace tomato populations from Mexico exhibited sufficient genetic variability to find different levels of resistance to *Bt*MED, indicating that these tomato populations are a valuable genetic resource that must be studied to improve their use and conservation.

Acknowledgments

We thank FitoCiencia for the support provided for this research.

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