PEST MANAGEMENT

Resistance of Tomato Genotypes to the Greenhouse Whitefly *Trialeurodes vaporariorum* (West.) (Hemiptera: Aleyrodidae)

Alejandro F Lucatti[1, 2], Adriana E Alvarez[2], Cristina R Machado[2], Elsa Gilardón[1]

[1]Cátedra de Genética; [2]Cátedra de Química Biológica. Facultad de Ciencias Naturales, Univ Nacional de Salta, Av Bolivia 5150, CP 4400, Salta, Argentina

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ABSTRACT - The greenhouse whitefly, *Trialeurodes vaporariorum* Westwood, is the most common and abundant whitefly in Argentine horticultural greenhouse crops, especially in tomato (*Solanum lycopersicum*). Resistance in some wild tomato relatives, such as *S. peruvianum, S. habrochaites* and *S. pennellii* to the greenhouse whitefly has been described. The *Mi* gene confers effective resistance against several species of insects, among them the sweet potato whitefly, *Bemisia tabaci* Gennadius. Resistance to *T. vaporariorum* was found in the prebreeding line FCN 93-6-2, derived from a cross between *S. lycopersicum* cultivar Uco Plata INTA (*MiMi*) and the wild line FCN 3-5 *S. habrochaites*. The purpose of this study was to evaluate resistance to *T. vaporariorum* in tomato genotypes and to study the relationship between this resistance and the presence of the REX-1 marker, which is linked to the *Mi* gene. In a free-choice assay, the average number of adults per leaf and the number of immatures on the middle and basal plant parts were analyzed. In a no-choice assay, the oviposition rate and adult survival rate were calculated. For all variables analyzed, FCN 3-5 was the most resistant strain. Variations were found in the F_2 progeny between the prebreeding line FCN 13-1-6-1 and cv. Uco Plata INTA. Results from the F_2 progeny indicate that resistance to *T. vaporariorum* may be polygenic with transgressive segregation. Whitefly resistance was found to be independent of the REX-1 marker.

KEY WORDS**:** *Solanum*, *Mi* gene, REX-1 marker, polygenic inheritance, transgressive segregation

Greenhouse tomatoes, *Solanum lycopersicum*, are severely attacked by whiteflies, which are small sucking insects of the Aleyrodidae family (order Hemiptera). Two main species are recognized, *Bemisia tabaci* Gennadius and *Trialeurodes vaporariorum* Westwood. The greenhouse whitefly *T. vaporariorum*, a cosmopolitan species, has been reported in South America in Brazil, Chile, Colombia, Ecuador, Guiana, Peru, Uruguay, Venezuela and Argentina (Arnal *et al* 1993, Basso *et al* 2001, Lourenção *et al* 2008). It is the most common and abundant whitefly in Argentine horticultural greenhouse crops, especially infesting tomato plants (Viscarret 2000, Polack 2005).

The greenhouse whitefly is a generalist and a highly polyphagous pest species. It affects crops directly by phloem feeding, which results in leaf and fruit spotting, plant weakening, irregular ripening of fruits and sooty mold growing on honeydew (Muigai *et al* 2002). It also affects tomatoes indirectly due to the transmission of plant viruses (*Crinivirus* and *Closterovirus*) (Valverde *et al* 2004), and is responsible for several physiological disorders (Francelli & Vendramim 2002). Overall, the direct and indirect damages reduce crop yield (Lindquist *et al* 1972, Johnson *et al* 1992).

Whitefly control is based mainly on pesticide applications, most of which are harmful to the environment and to non-target species. In addition, some whiteflies appear to be resistant to many of the chemicals used. An alternative is the use of whitefly-resistant plants (Bas *et al* 1992, Nombela *et al* 2001). Resistance in some wild tomato relatives, such as *Solanum peruvianum, S. habrochaites* and *S. pennellii* has been described to the greenhouse whitefly (Romanow *et al* 1991, de Ponti & Mollema 1992, Bas *et al* 1992).

The first crosses between cultivated tomato and resistant accessions of *S. habrochaites* (*L. hirsutum glabratum)* and *S. pennellii* were generated in the mid-1970s (de Ponti *et al* 1990). Attempts to introduce resistance to *T. vaporariorum* from *S. habrochaites* into cultivated tomato lines have been hampered by the putative polygenic inheritance of resistance (Bas *et al* 1992).

During the 1940s, a single dominant gene, *Mi*, was transferred from *S. peruvianum* PI 128657 into the cultivated tomato by an embryo rescue technique. At present, all known nematode-resistant *S. lycopersicum* cultivars are descendants from a single F_1 plant (Medina Filho & Stevens 1980, Klein-Lankhorst *et al* 1991, Kaloshian 2004).

The *Mi* gene confers effective resistance against several species of root-knot nematodes (*Meloidogyne* spp.) (Milligan *et al* 1998), some isolates of potato aphid (*Macrosiphum*

euphorbiae Thomas) (Rossi *et al* 1998) ,and the sweet potato whitefly (*B. tabaci*) (Nombela *et al* 2000, 2001, 2003). The *Mi* gene is located in the short arm of chromosome 6 in the tomato and is contained within a large, introgressed chromosomal segment from the corresponding region in *S. peruvianum* (Klein-Lankhorst *et al* 1991, Messeguer *et al* 1991, Ho *et al* 1992, Williamson *et al* 1994).

The *Mi* cluster 1p was found to contain three homologue genes, previously designated as *Mi-1.1*, *Mi-1.2* and *Mi-1.3*. Of these, only *Mi-1.2* confers nematode, aphid and whitefly resistance in tomato (Seah *et al* 2004). *Mi-1.2* produces a transcript of approximately 4 kb that encodes a putative protein of 1,257 amino acids (Rossi *et al* 1998). This protein is a member of a disease resistance-associated plant protein family, characterized by the presence of a nucleotide binding site (NB) and a leucine-rich repeat motif (LRR) (Milligan *et al* 1998). Proteins of the NB-LRR motif structure make up the largest class of cloned plant resistance genes against viruses, bacteria, fungi, nematodes and insects (Dangl & Jones 2001). *Mi-1.2* is the first plant resistance gene with activity against three highly divergent organisms, which are the most important pests of tomato plants worldwide, making *Mi-1.2*-regulated resistance a powerful tool in tomato integrated pest management programs (Nombela *et al* 2003).

There are several molecular markers that are tightly linked to the *Mi* gene, such as the acid phosphatase-1 (*Aps*-1) gene and the RFLP and RAPD markers (Klein-Lankhorst *et al* 1991, Messeguer *et al* 1991). Williamson *et al* (1994) developed a CAPS marker, REX-1, which is tightly linked to the *Mi* gene, making it suitable for routine analysis in breeding programs.

The purpose of this research was to study resistance to *T. vaporariorum* in some tomato genotypes and the relationship between resistance and the presence of the *Mi* gene.

Material and Methods

Plant material. The tomato genotypes used in this study are described in Table 1. The wild line FCN 3-5 was selected from the wild accession PI 134417 (*Solanum habrochaites*) as the source of multiple insect resistances (Farrar & Kennedy 1991, Gilardón 2007).

From the F_2 progeny of the cross between the cultivar Uco Plata INTA and FCN 3-5, a genealogical selection program was performed that was focused on a strong selection for fertility and insect resistance. From F_5 to F_{10}, the aim was to improve yield and certain fruit quality traits. Two F_{10} lines were selected for their good performance: FCN 13-1-6-1 and FCN 93-6-2. FCN 13-1-6-1 was crossed to Uco Plata INTA to obtain 105 F_2 plants.

Free-choice assay. Natural infestation of *T. vaporariorum* was evaluated in a free-choice assay. Seeds from all tomato genotypes were sown in common plastic pots in a greenhouse with open sides until true leaves developed. Plants were then transplanted to 5 kg-black-plastic pots and arranged in a completely random design in a 70 m^2 greenhouse. Four replicates of FCN 3-5, ten or nine replications of the other pure lines and 105 plants for progeny F_2 (FCN 13-1-6-1 x UP) were used.

Whitefly assessments were made on the plants after the first flowers developed (mature plants). The free-choice assay was carried out in the spring, between October and November 2007, as a peak of infestation is observed every year during this period.

The variables considered were the number of adults and immatures of *T. vaporariorum*. Immatures were considered only from nymph 3 and nymph 4 "puparium" classifications, according to Basso *et al* (2001).

Whitefly adults were counted in the first and second fully

Table 1 *Solanum* genotypes used in this study.

Name	Accession description	Characteristics	Origin
Uco Plata (UP)	Cultivar *S. lycopersicum*	Resistant to root-knot nematodes (*Mi* gene) and Tobacco Mosaic Virus (Tm2[2])	INTA[1] La Consulta
LC 138 (LC 330-23-05)	Breeding line *S. lycopersicum*	Resistant to root-knot nematodes (*Mi* gene)	INTA La Consulta
FCN 3-5	Wild line *S. habrochaites*	Resistant to *Trialeurodes vaporariorum*, *Tuta absoluta* Meyrick, and *Tetranychus urticae* Koch	UNSa[2]
FCN 93-6-2	Prebreeding line *S. lycopersicum* x *S. habrochaites*	Long shelf life tomato resistant to *T. absoluta* and *T. urticae*	UNSa[3]
FCN 13-1-6-1	Prebreeding line *S. lycopersicum* x *S. habrochaites*	Long shelf life tomato resistant to *T. absoluta*	UNSa[3]
F_2 (FCN 13-1-6-1 x UP)		Progeny	

[1]INTA La Consulta, Instituto Nacional de Tecnología Agropecuaria, Mendoza, Argentina
[2]UNSa, Universidad Nacional de Salta, Salta, Argentina
[3]Lines F_{10} derived from crossing cv. Uco Plata INTA and FCN 3-5

expanded leaves from the top (plant apical-part) (Basso *et al* 2001, Scotta *et al* 2006). When the number of adults was excessively high, insect counts were made with the aid of digital photographs in the laboratory. Counts were performed in the early morning, when adult whitefly movements are lower. Data were collected four times during the assay, on October 16 and 19 and November 8 and 14. From these data, an average number was calculated.

We used the criterion of tolerance threshold proposed by Polack (2005) of ten adults per leaf as a damage threshold, which is stricter than the damage threshold of fifteen adults per leaf proposed by Lacasa Plasencia & Contreras Gallego (1995).

Whitefly immatures were counted from the third to fifth fully expanded leaves from the top (plant middle-part) and from the sixth to the last fully expanded leaves from the top (plant basal-part). In each stratum, a 4 cm^2 area was evaluated in each of the three terminal leaflets. Data were obtained twice during the assay, on October 25 and November 9. The average number of adults per leaf and the average number of immatures per plant parts were $\log_{10}(x+1)$ transformed and analyzed by one-way ANOVA, followed by a Fisher Protected Least Significant Difference (LSD) test. The normality of the F_2 distribution was tested using the Shapiro-Wilks test. Due to the fact that data from the F_2 progeny did not follow normality, the transgressive segregations method (de Vicente & Tanskley 1993) was modified with a percentile criterion of 99.5%. Correlations between the average number of adults per leaf and the number of immatures on the plant middle-stratum and plant basal-stratum were estimated by the Spearman correlation coefficient. Data were analyzed using the statistical software InfoStat professional (2007).

No-choice assay. Mature plants from the wild line FCN 3-5, the prebreeding lines FCN 93-6-2, FCN 13-1-6-1, the breeding line LC 138 and the cultivar Uco Plata were used in a no-choice assay (Table 2). Two adult females were placed into plastic clip-on cages (2.1 cm in diameter and 1.05 cm high) and were attached to the abaxial surface of a leaf on the middle-stratum. Three cages were placed per plant, one cage per leaf. After five days, the number of eggs and number of surviving females were counted. In each genotype, the oviposition (OR) and adult survival rates (AS) were calculated according to Bas *et al* (1992):

Table 2 Oviposition rate (mean ± SE) and adult survival rate (mean ± SE).

Genotypes	Plant number	OR (eggs/day)	AS (♀/day)
FCN 3-5	8	0.2 ± 0.11 a	0.0 ± 0.00 a
Uco Plata	11	2.4 ± 0.39 bc	0.2 ± 0.10 ab
FCN 93-6-2	10	2.6 ± 0.43 bc	0.4 ± 0.14 ab
FCN 13-1-6-1	5	2.1 ± 0.59 b	0.7 ± 0.18 bc
LC 138	7	4.4 ± 0.58 c	0.8 ± 0.13 c

Numbers in each column followed by different letters are significantly different at $P \leq 0.05$ according to Kruskal-Wallis followed by multiple comparison tests.

$$OR = \frac{2e}{[d(m+n)]}\ day^{-1}$$

$$AS = (m/n)^{\frac{1}{d}}\ day^{-1}$$

where e = number of eggs, d = number of days between redistribution and removal of adult whiteflies (d = 5), m = number of surviving adults after 5 days, and n = number of adults used for inoculation (n = 2).

The OR and AS averages were calculated for each plant and analyzed using Kruskal-Wallis tests followed by a multiple comparison test.

REX-1 marker analysis. Genomic DNA was extracted as described by Fulton (1995) with minor modifications. From each plant and for every genotype, two independent extractions were performed. For F_2 (FCN 13-1-6-1 x UP), 69 plants were analyzed for REX-1. DNA was quantified by spectrophotometry using a Pharmacia Gene Quant Spectrophotometer (Pharmacia, Biotech, Columbus, OH). PCR reactions were carried out in a final volume of 20 µl, containing 40 ng of genomic DNA, 0.1µl of Go*Taq* polymerase (Promega), 4 µl *Taq* polymerase buffer (Promega), 0.1 µM of each dNTP (Promega) and 1 µM of each primer, REX-F1 (5´-TCGGAGCCTTGGTCTGAATT-3´) and REX-R2 (5´-GCCAGAGATGATTCGTGAGA-3´) (Williamson *et al* 1994). Amplification reactions were carried with a TECHNE TC412 thermal cycler, using the following cycling profile: 94°C for 3 min, followed by 35 cycles at 94°C for 30 s, 55°C for 30 s, and 71°C for 2 min, and a final extension step at 72°C for 7 min. Amplification products were assayed with 1.5% agarose gel electrophoresis and visualized with GelStar® staining. Aliquots (10 µl) of the amplified products were digested for one hour at 65°C in a total volume of 20 µl with 0.5 µl of *Taq*I (Promega), using the buffer recommended by the supplier. Digestion products were analyzed by agarose gel electrophoresis (1.5% agarose w/v with TAE 1x buffer) and visualized by GelStar® staining. As reaction controls, the cultivars Rossol (*MiMi*) and Roma (*mimi*) were used.

Results

Free-choice assay. The free-choice test with natural infestation was used to classify the tomato genotypes from resistant to susceptible. The average numbers of whitefly adults on tomato genotypes were clustered into three different groups. The most resistant group included FCN 3-5. The intermediate group included FCN 93-6-2 and Uco Plata, and the susceptible group included FCN 13-1-6-1 and LC 138 (Table 3).

The average number of whitefly adults per leaf on F_2 progeny ranged from 1 to 84. Thirty-four percent of the plants had an average number (de Vicente & Tanskley 1993) of adults below the tolerance threshold of 10 adults per leaf (Polack 2005). Fourteen percent of the plants had an average number of adults that was higher than the susceptible genotype FCN 13-1-6-1 (Fig 1a).

The number of immatures in the plant middle-part on the different tomato genotypes was classified into two

Table 3 Free-choice assay. Mean number (± SE) of whitefly adults per leaf and mean number of whitefly immatures per stratum on the different tomato genotypes.

Genotypes	Plant number	Number of adults per leaf	Number of immatures in middle-stratum	Number of immatures in basal-stratum
FCN 3-5	4	0.5 ± 0.17 a	0.0 ± 0.00 a	0.0 ± 0.00 a
FCN 93-6-2	9	7.6 ± 1.50 b	11.4 ± 1.95 b	9.0 ± 1.37 b
Uco Plata	10	9.9 ± 2.88 b	12.5 ± 3.78 b	17.1 ± 4.01 c
FCN 13-1-6-1	9	39.4 ± 6.79 c	13.8 ± 2.87 b	17.4 ± 1.42 c
LC 138	10	42.7 ± 8.98 c	14.6 ± 2.68 b	20.9 ± 3.27 c

Numbers in each column followed by different letters are significantly different at $P \leq 0.05$ according to one-way ANOVA followed by Fisher Protected Least Significant Difference (LSD) tests.

groups (Table 3): the resistant group, containing the wild line FCN 3-5, with zero immatures per 4 cm^2 of leaf, and the susceptible group, including FCN 93-6-2, Uco Plata, FCN 13-1-6-1 and the breeding line LC138. A great deal of variation was detected in F_2 progeny, ranging from 2.67 to 70.33 immatures/4 cm^2 of leaf. Seven percent of the plants showed an average number of immature below the damage threshold. Sixteen percent of the plants were considered to be transgressive because they had an infestation level higher than the FCN 13-1-6-1 mean, according to the 99.5% percentile criterion (Fig 1b).

The numbers of immatures in the basal part of the tomato plants were classified into three groups (Table 3). FCN 3-5, with zero immature per 4 cm^2 of leaf, was the most resistant genotype. Uco Plata, FCN 13-1-6-1 and LC 138 were the most susceptible. FCN 93-6-2 formed an intermediate infested

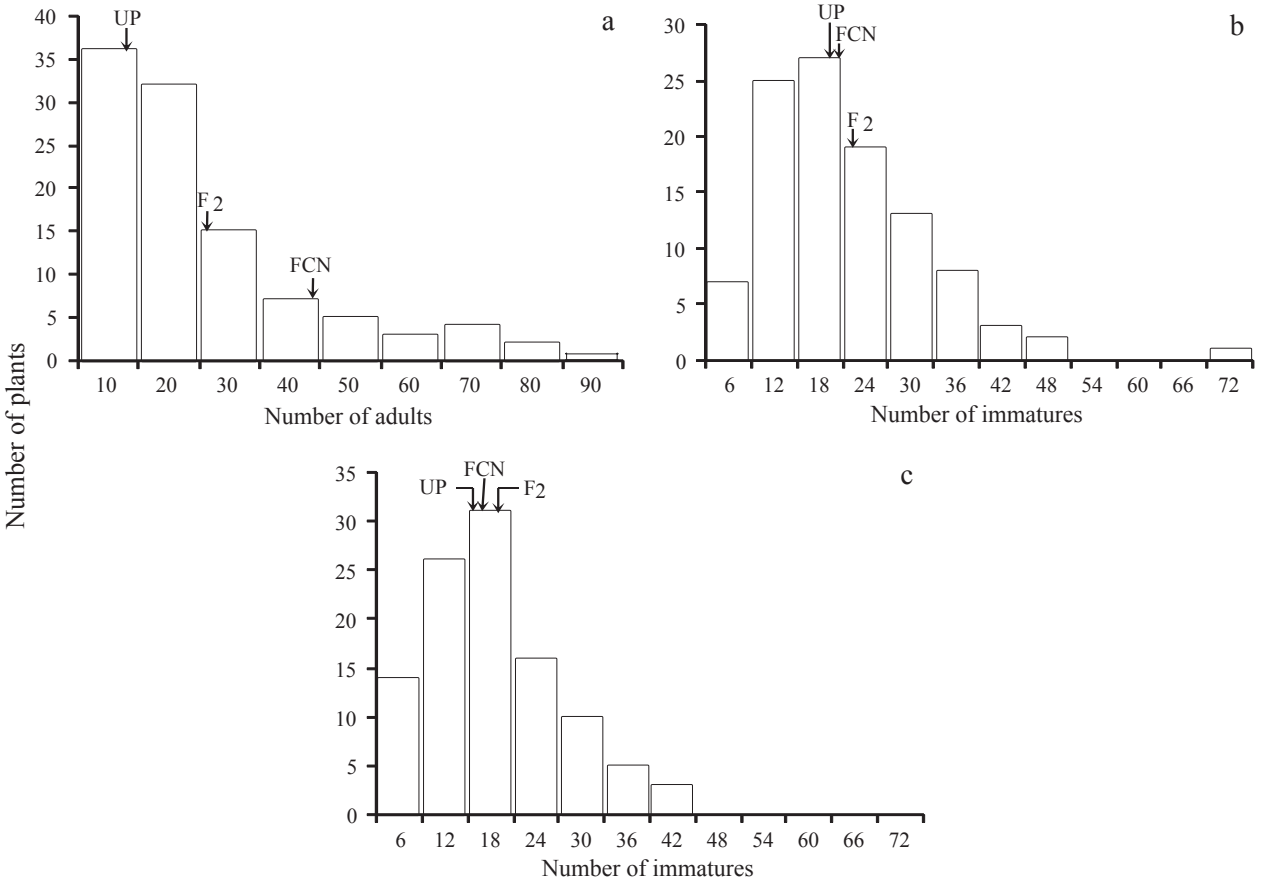

Fig 1 Distribution of phenotypes per *Trialeurodes vaporariorum* variable for F_2 progeny. Averages for parental genotypes (cv. Uco Plata (UP) and prebreeding line FCN 13-1-6-1 (FCN)) and F_2 progeny are indicated by arrows. a) number of adults in plant apical-stratum; b) number of immatures per 4 cm^2 of leaf in plant middle-stratum; c) number of immatures per 4 cm^2 of leaf in plant basal-stratum.

group, with a mean value of 11.4 ± 5.86 immatures/4 cm^2.

A wide range of variation was detected in the F_2 progeny, from 3.6 to 41.1 immatures/4 cm^2 of leaf. Thirteen percent of the plants had a degree of infestation below the threshold of 6 immatures/4 cm^2 (Fig 1c).

A significant correlation of 65% was found between immatures in the middle and basal plant parts, and a 32% correlation was found between adults and immatures in the middle plant part. No correlation was found between adults and immatures in the basal plant part.

No-choice assay. The results of the no-choice assay are shown in Table 2. While *T. vaporariorum* on FCN 3-5 (*S. habrochaites*) had the lowest oviposition rate (OR) (0.2 ± 0.11 eggs laid per day) and zero adult survival (AS) at the end of the experiment, *T. vaporariorum* on LC 138 (*S. lycopersicum*) had the highest oviposition and adult survival rates (4.4 ± 0.58 OR and 0.8 ± 0.13 AS). Uco Plata, FCN 93-6-2, and FCN 13-1-6-1 were classified in an intermediate group.

REX-1 marker. The prebreeding line FCN 13-1-6-1 (*S. lycopersicum*) and the genotypes resistant to root-knot nematodes, Uco Plata and LC 138, carried the cleaved allele of REX-1. The wild line FCN 3-5 (*S. habrochaites*) and the prebreeding line FCN 93-6-2 (*S. lycopersicum*) did not yield amplified bands with the REX primers in either of the two independent DNA extractions (Fig 2). All 69 F_2 (FCN 13-1-6-1 x UP) plants carried the cleaved allele of REX-1. None showed the band linked to the *mimi* genotype.

Discussion

Evaluation of tomato resistance to the whitefly using a choice assay with free infestation was a useful tool to assess and to characterize inbred lines and F_2 progeny in tomato breeding programs for whitefly resistance. Although the nematode-resistant lines LC 138 and Uco Plata have the *MiMi* genotype, they show significant differences in the numbers of whitefly adults. While LC 138 was susceptible, Uco Plata demonstrated a good level of resistance (Table 3). Furthermore, FCN 13-1-6-1, which amplified the allele of the REX-1 marker that is linked to the *Mi* gene, was susceptible to greenhouse whitefly adults. On the contrary, FCN 3-5 and FCN 93-6-2, which did not amplify the REX-1 marker, had the highest levels of resistance to greenhouse whitefly adults. These results suggest that resistance to whitefly adults is independent of the REX-1 marker linked to the *Mi* gene.

Regarding the number of immatures in the middle and basal plant parts on the different tomato genotypes, great variation was found within each tomato line. This variation is expected, because a female can lay up to 300 eggs in its lifetime (Byrne & Bellows 1991).

While the most resistant genotype, FCN 3-5, did not amplify the REX-1 marker, the most susceptible lines, LC 138 and FCN 13-1-6-1, did amplify the REX-1 marker (Table 3). Although the parental lines Uco Plata and FCN 13-1-6-1 had the same infestation levels on plant middle and basal-parts, great variations between plants were found in the F_2 progeny (Table 3). A number of F_2 plants had extreme phenotypes related to the parental phenotype: more resistant than Uco Plata or more susceptible than FCN 13-1-6-1, namely, transgressive segregation (de Vicente & Tanskley 1993).

While no transgressive plants were found in the basal part according to the 99.5% percentile criterion, in the middle plant part transgressive plants were detected. According to de Vicente & Tanksley (1993), the occurrence of transgressive plants could be explained by assuming that the parental genotypes contain different mixtures of positive and negative QTL alleles, which lead to similar phenotypic averages for some traits. With increased similarities of the phenotypes of the parents, the likelihood that transgressive individuals would occur in the F_2 progeny is increased (de Vicente & Tanksley 1993, Rieseberg *et al* 1999). Moreover, Rieseberg *et al* (1999), who reviewed 171 studies in which transgressive traits were detected among plants and animals, proposed that complementary gene action is the primary cause of transgression. The results suggest that the complementary action of additive alleles could be the main cause of transgression with regard to resistance to immatures. The overall appearance of transgressive phenotypes strengthens the hypothesis of polygenic inheritance of whitefly resistance. In Fig 3, a hypothetical model is represented to explain the segregation results observed for whitefly immatures.

Considering the different correlation coefficients found between the number of immatures in the middle and basal plant parts, as well as those found between the adults and immatures in the middle plant part, it can be hypothesized that the resistance factors to whitefly adults for the tomato genotypes analyzed are not exactly the same as those related

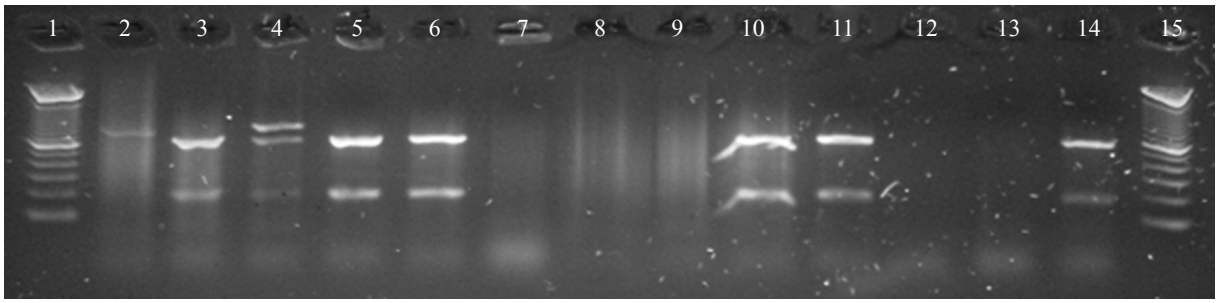

Fig 2 Genotypes patterns of REX-1 amplified products followed by restriction with *Taq1*. Lanes 1 and 15, 100-bp molecular marker; 2, Roma (control *mi*); 3, Rossol (control *Mi*); 4, *Solanum lycopersicum* heterozygote control; 5 and 6, Uco Plata; 7, 8, and 9, FCN 3-5; 10 and 11, FCN 13-1-6-1; 12 and 13, FCN 93-6-2; 14, LC 138.

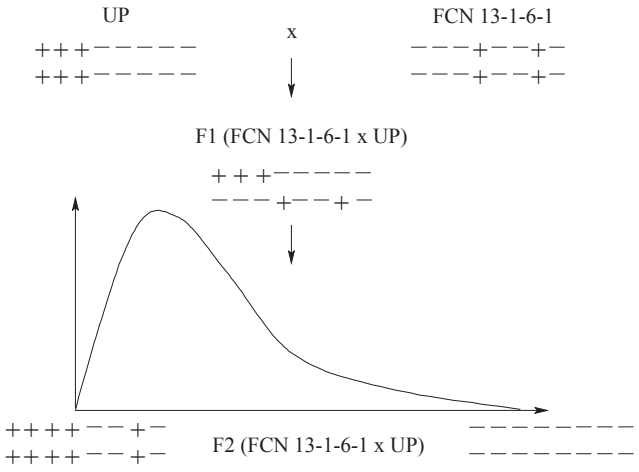

Fig 3 Hypothetical model of transgressive segregation with the complementary action of genes with additive effects in the F_2 progeny between FCN 3-5 and FCN 13-1-6-1.

to whitefly juvenile resistance; however, these traits could share QTL alleles. To test this hypothesis, further analyses with QTL mapping need to be performed.

In the no-choice assay, FCN 3-5 (which showed no amplification of the REX-1 marker) had the lowest number of eggs per female per day as well as the lowest female survival average, suggesting that this genotype possesses mechanisms that limit the development and survival of *T. vaporariorum*. Baldin *et al* (2005), working on two accessions of *S. habrochaites* (PI 134417 and PI 134418), found a lower oviposition rate and a no-preference of *Bemisia tabaci*, which they ascribed to plant volatiles that could prevent whiteflies from landing and ovipositing on leaflets.

These results for *T. vaporariorum* together with the results from Baldin *et al* (2005) regarding *B. tabaci,* suggest that FCN 3-5 *S. habrochaites* is an important source of resistance to whiteflies in tomato breeding programs.

The tomato genotypes evaluated in this study for resistance to *T. vaporariorum*, the results from the free choice assay, no-choice assay, and REX-1 marker analysis altogether suggest that: 1) resistance to *T. vaporariorum* is independent of the REX-1 marker linked to *Mi* gene, and 2) FCN 3-5 and FCN 93-6-2 did not amplify the REX-1 marker. The lack of amplification in FCN 93-6-2 could be explained as an introgression from FCN 3-5 in the marker region or as a physical impediment in the recognition of primer targets due to the different genetic background of *S. habrochaites* with respect to *S. peruvianum*.

In order to clarify the genetic basis of whitefly resistance with respect to the tomato genotypes analyzed here, the resistant wild line FCN 3-5 (*S. habrochaites*) should be crossed with the susceptible breeding line LC 138 (*S. lycopersicum*) to generate a mapping population.

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