Variation in tomato host response to *Bemisia tabaci* (Hemiptera: Aleyrodidae) in relation to acyl sugar content and presence of the nematode and potato aphid resistance gene *Mi*

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Abstract

Two commercial cultivars of tomato, Alta and Peto 95, the accession line number LA716 of *Lycopersicon pennellii* and lines 94GH-006 and 94GH-033 (backcrosses between Peto 95 and LA716), with different leaf acyl sugar contents were screened for resistance to *Bemisia argentifolii* Bellows & Perring (corresponding to the Spanish B-biotype of *Bemisia tabaci* (Gennadius)), in greenhouse- and field-no-choice experiments. There was no oviposition on LA716 (with the highest acyl sugar content) while the greatest fecundity and fertility values were observed on the cultivar Alta (no acyl sugar content). However, no clear relationship was found between the low acyl sugar content in the other tomato cultivars tested and whitefly reproduction. Thus, resistance to *B. tabaci* did not appear to correlate with acyl sugar content below a threshold level of 37.8 $\mu\text{g cm}^{-2}$ leaf. In a greenhouse choice-assay, *B. tabaci* exhibited reduced host preference and reproduction on the commercial tomato cultivars Motelle, VFN8 and Ronita all of which carry the *Mi* gene resistance to *Meloidogyne* nematodes and the aphid *Macrosiphum euphorbiae* (Thomas), than on the *Mi*-lacking cultivars Moneymaker, Rio Fuego and Roma. When data of *Mi*-bearing plants were pooled, the mean values for daily infestation and pupal production of *B. tabaci* were significantly lower than those of *Mi*-lacking plants. This reflected a level of antixenosis- and antibiosis-based resistance in commercial tomato and indicated that *Mi*, or another closely linked gene, might be implicated in a partial resistance which was not associated either with the presence of glandular trichomes or their exudates. These findings support the general hypothesis for the existence of similarities among the resistance mechanisms to whiteflies, aphids and nematodes in commercial tomato plants.

Introduction

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae) is a major pest of both greenhouse and open-field horticultural

crops worldwide. It causes serious damage to many plants in different areas of Spain (Carnero *et al.*, 1990). Guirao *et al.* (1997) reported that populations of *B. argentifolii* Bellows & Perring (Perring *et al.*, 1993; Bellows *et al.*, 1994) from California were identical to the Spanish biotype B of *B. tabaci*. Damage by *B. tabaci* is caused by sap removal and transmission of geminiviruses and other viruses to a wide range of plants in tropical, subtropical, and fringe

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temperature zones (Brown & Bird, 1992; Moriones *et al.*, 1993; Bedford *et al.*, 1994; Blua & Toscano, 1994; Brown, 1994; Brown & Bird, 1996; Markham *et al.*, 1996). *Bemisia tabaci* is the vector of the Tomato Yellow Leaf Curl Viruses, one of the most important groups of geminiviruses (Schuster *et al.*, 1996).

Bemisia pest management programmes are usually based on insecticide applications, but these products are often toxic to the environment and to nontarget species. One of the most effective components of disease and pest control is the utilization of resistant plants (Russell, 1978). Resistance to whiteflies and other insects found on the wild species of tomato *Lycopersicon pennellii* (Corr.) D'Arcy (Solanaceae), has been attributed to the presence of sugar esters in the glandular exudate of type IV trichomes (Gentile *et al.*, 1968; Juvik *et al.*, 1994; Heinz & Zalom, 1995). It has therefore been agreed that selection for sugar ester accumulation should be an efficient technique in selecting for general insect resistance in *L. pennellii* (Goffreda *et al.*, 1990) and other tomato plants (Kisha, 1981; Berlinger, 1986). Leaf-trichome densities, presence of acyl sugars in the exudate of glandular trichomes as well as the type of trichomes, are reported to be important factors affecting whitefly–tomato relationships (Williams *et al.*, 1980; Kisha, 1981; Berlinger, 1986; Kishaba *et al.*, 1992; Simmons, 1994); but the actual effect of these, and other factors, on tomato resistance has been broadly questioned (Goffreda *et al.*, 1989; Steffens & Walters, 1991; Liedl *et al.*, 1995).

Field resistance to *B. tabaci* was reported in different lines of the wild species *L. peruvianum* (L.) Mill (Hassan *et al.*, 1982; Channarayappa *et al.*, 1992), a close relative of commercial tomato *L. esculentum* (Solanaceae). This resistance was shown to be due to factors other than the presence of trichomes and their exudates, since Va and Vb non-glandular trichomes were predominant and ViC glandular trichomes absent (Channarayappa *et al.*, 1992). These authors also reported that commercial cultivars of tomato mostly exhibit non-glandular type III and V trichomes and four-lobed glandular ViA trichomes, which are not considered to be important in whitefly control mechanisms (Ponti *et al.*, 1990). Differential host response to insects in these commercial cultivars might be due to alternative mechanisms of resistance regulated by genes as yet unknown. Feeding similarities between piercing-sucking insects, such as aphids and whiteflies, and root-knot nematodes (Byrne & Bellows, 1991; Walker & Perring, 1994; Kaloshian *et al.*, 1995) suggest that a specific gene-for-gene defence response (Flor, 1955) could be highly effective in regulating the prolonged interaction of the stylets of these insects and the plant cell contents (Fernandes, 1990). There are many examples of single-resistance genes conferring gene-for-gene resistance to piercing-sucking insects and nematodes. The *Mi* gene, present in many cultivars of cultivated tomato and introduced into this plant from its wild relative, *L. peruvianum* (Smith, 1944), confers resistance characterized by a hypersensitive reaction, to three species of root-knot nematodes *Meloidogyne* spp. (Roberts & Thomason, 1986). It has recently been demonstrated that *Mi* in tomato also regulates resistance to insects such as the potato aphid *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae) (Kaloshian *et al.*, 1995; Rossi *et al.*, 1998).

In this paper we present the results of both greenhouse and field experiments aimed at clarifying how the acyl

sugar content in several wild and commercial tomatoes and their cultivars affects their capacity to host the Spanish B-biotype of *B. tabaci*. In another greenhouse assay we tested a range of commercial tomato cultivars to investigate whether *Mi*, or another closely linked gene, confers resistance to whiteflies.

Materials and methods

The study to evaluate the influence of acyl sugar content on whitefly reproduction was carried out at the University of California, Davis (USA), using insects collected from a large stock colony of B-biotype of *B. tabaci* reared on poinsettia *Euphorbia pulcherrima* Willd. ex Koltz (Euphorbiaceae) for two years in a greenhouse at 20°C (T max. = 28°C; T min. = 14°C) and 65–70% relative humidity. The *Mi* study was conducted at the Centro de Ciencias Medioambientales (CSIC), Madrid (Spain) using insects of the Spanish B-biotype of *B. tabaci*. This population had been reared on the commercial tomato cultivar Rio Fuego for 20 generations.

Effect of the acyl sugar content

Greenhouse assay

Seeds of *L. esculentum* Alta (an F₁ hybrid commercial cultivar), *L. pennellii*, wild species accession LA 716, Peto 95 (an open pollinated cultivar) and 94GH-006 and 94GH-033 (F₃ backcrosses between *L. pennellii* and Peto 95) were germinated, and the plants grown in 4.6 l plastic pots containing greenhouse potting soil mix. Mean values of total acyl sugar content ($\mu\text{g cm}^{-2}$ leaf of acylglucose + acylsucrose) were 0 on Alta, 5.8 ± 0.5 on Peto 95, 6.1 ± 0.4 on 94GH-006, 7.1 ± 0.6 on 94GH-033 and 37.8 ± 2.8 on LA716 (D. St Clair, personal communication). At 58 days, the plants were transferred to a greenhouse with a day:night temperature of 23°C: 15°C and 70–75% relative humidity. Seven-day-old whitefly adults were collected with an aspirator from the stock colony and two females introduced into each of 72 plastic truncated cone clip-cages (3.6 cm $\times$ 2.6 cm diameter; 4 cm high) (Muñiz & Nombela, 1997), attached to the under surface of the leaves (three cages per plant; 24 plants per *Lycopersicon* line or cultivar). After four days, one leaf per plant was removed, the cage circumferences marked, and the marked area examined using a binocular dissecting microscope to record the number of eggs laid. After 20 and 30 days, respectively, two other leaves were removed to record the number of pupae and empty pupal cases. It was assumed that the T-shaped split in the pupal cases meant that the adult had emerged.

Field assay

In order to validate the previous results under natural conditions, plants of the same lines or cultivars as those in the greenhouse test were transplanted to a field experimental plot. Temperatures in the field ranged on average between 17.5°C and 36.5°C. Three clip-cages per plant (two females per cage) were attached to different leaves on all 18 plants (60 days old) of each *Lycopersicon* line or cultivar. The same methodology as in the greenhouse experiment was followed to record the number of eggs, pupae and adults.

Mi gene study

Seeds of three tomato cultivars carrying the nematode-resistance gene *Mi* (Motelle, VFN8 and Ronita) and three cultivars lacking this gene (Moneymaker, Rio Fuego and Roma) were germinated and the plants grown in perlite in one-litre plastic pots irrigated with 0.75 l per week of a nutritive fertilizer 20-20-20 (Nutrichem 60, Miller Chemical, Hanover, Pennsylvania, USA). When potted plants were 57 days old, they were moved to a greenhouse and randomized in a complete block design with ten replicates at 23:15°C (day:night) and with 70–80% relative humidity. Each plant was equidistant from the adjacent pots so that plant leaves did not touch each other. Three days after being installed in the greenhouse, the plants were infested by releasing approximately 1000 whitefly adults. After seven days, the number of male and female whiteflies were counted daily *in situ* on all leaves of every plant until the emergence of the next generation of adults (25 days). Counts were made early in the morning before the adults became active. Three days after the emergence of new adults, the total number of pupae and empty pupal cases on all leaves of every plant were recorded. In addition, the number of four-lobed type VIa glandular trichomes per cm² of two leaves, selected from the middle part of ten 60-day-old plants of every tomato cultivar, were counted.

Statistical analysis

The number of eggs, pupae and adults, as well as the number of leaf trichomes, were $\log_{10}(x+1)$ transformed and analysed with a one-way ANOVA and subsequently by the Fisher Protected Least Significant Difference (LSD) post-hoc test. Proportions (p) of *B. tabaci* infestation and adult emergence rates were transformed to arcsine $p^{1/2}$ before analysis (Statsoft, 1994).

Results

Effect of the acyl sugar content

Greenhouse assay

Bemisia tabaci oviposition was affected by tomato plants in this no-choice experiment (fig. 1). The mean daily number of eggs laid per female was significantly ($P < 0.5$) greater when Alta (no acyl sugar content) was the host. By contrast, there was no oviposition on LA 716, the line with the highest acyl sugar content ($37.8 \pm 2.8 \mu\text{g cm}^{-2}$ leaf). Significantly more eggs were found on 94GH-033 than on Peto 95 and 94GH-006, although they did not significantly differ in acyl sugar content. Similar results were obtained with respect to the daily average numbers of pupae and adults per female, as well as in the percentage of adult emergence (fig. 1).

Field assay

Although females laid more eggs than in the greenhouse assay (due to the higher average temperature in the field), the mean numbers of pupae and adults were lower, probably owing to a higher mortality rate at the immature stages (fig. 1).

Mi gene study

The average number of type VIa leaf trichomes per cm² was significantly lower on Motelle and VFN8 than on other

tomato cultivars (table 1). Also, there were significant differences ($P < 0.01$) among the six tomato cultivars tested for daily infestation, with *Mi*-bearing cultivars showing lower percentages for both insects and infested plants. Significant differences in infestation rates were found between *Mi*-bearing and *Mi*-lacking plants, except on Roma and Motelle, which yielded similar values. Cultivars with *Mi* also exhibited, in general, lower reproductive values,

Fig. 1. Averaged daily egg, pupa and adult production per female and adult emergence of *Bemisia tabaci* on tomato, represented as bars scaled on the Y1 axis, in greenhouse (grey) and field (white) no-choice experiments. Error bars indicate the SEM. Different letters on bars from the same experiment indicate that corresponding means differ significantly ($P < 0.05$) by Fisher's Protected LSD. Black points connected by discontinuous lines in the first graph represent the total acyl sugar content (TAC = glucose + sucrose) of each cultivar, backcrossing line or wild species accession, scaled on the Y2 axis. A, Alta; P, Peto 95; 06, 94GH-006; 33, 94GH-033; L, LA716.

Table 1. Daily infestation rate and pupal production (mean $\pm$ SEM) of *Bemisia tabaci* B-biotype on six cultivars of tomato of varying trichome density, with and without the *Mi* gene, under greenhouse conditions.

Cultivars	n	Trichomes per cm ²	Daily infestation					Pupal production			
			n	Plants infested by females (%)	Plants infested by adults (%)	Females on plants (%)	Adults on plants (%)	n	Pupae per plant	Pupae per leaflet	Leaflets infested by pupae (%)
Separated											
Moneymaker (− <i>Mi</i>)	20	68 ± 7.0 ab	25	74 ± 3.8 a	82 ± 3.5 a	24 ± 0.9 a	23 ± 0.8 a	10	372 ± 73.1 ac	3 ± 0.6 b	26 ± 2.6 ab
Rio Fuego (− <i>Mi</i>)	20	56 ± 4.9 b	25	70 ± 3.5 a	82 ± 2.9 a	23 ± 1.7 a	25 ± 1.8 a	10	435 ± 68.4 a	5 ± 0.9 a	31 ± 3.1 a
Roma (− <i>Mi</i>)	20	75 ± 5.0 a	25	66 ± 3.9 ab	76 ± 3.4 ab	14 ± 0.6 b	15 ± 0.6 b	10	369 ± 69.6 ac	3 ± 0.6 ab	26 ± 2.7 ab
Motelle (+ <i>Mi</i>)	20	42 ± 4.8 c	25	60 ± 4.7 bc	68 ± 3.9 bc	14 ± 1.0 b	13 ± 0.7 bc	10	230 ± 62.5 b	2 ± 0.5 b	19 ± 2.9 b
VFN8 (+ <i>Mi</i>)	20	35 ± 3.9 c	25	56 ± 4.5 c	62 ± 4.4 c	14 ± 0.9 b	13 ± 0.8 bc	10	191 ± 45.3 bc	2 ± 0.3 b	21 ± 2.0 b
Ronita (+ <i>Mi</i>)	20	68 ± 4.6 ab	25	54 ± 4.3 c	70 ± 3.6 bc	11 ± 0.7 c	12 ± 0.6 c	10	283 ± 75.6 ab	3 ± 0.7 b	22 ± 2.4 b
Pooled											
Without <i>Mi</i>			25	70 ± 18.6 a	80 ± 16.4 a	61 ± 1.7 a	62 ± 1.4 a	30	392 ± 39.6 a	4 ± 0.4 a	28 ± 1.6 a
With <i>Mi</i>			25	57 ± 22.3 b	67 ± 19.9 b	39 ± 1.7 b	38 ± 1.4 b	30	235 ± 35.5 b	2 ± 0.3 b	20 ± 1.4 b

Means followed by the same letter in columns for separated cultivars and pooled plants do not differ significantly ($P < 0.05$) by Fisher's Protected LSD.

although the statistical significance of these differences was variable (table 1).

Differences were more dramatic when the three cultivars of tomato plants carrying the *Mi* gene were pooled and compared with plants without the gene (table 1). Significantly ($P < 0.001$) fewer females (57%) and adults (67%) were observed on plants with *Mi* than on plants lacking this gene (70% and 80%, respectively). Likewise, plants with *Mi* hosted a daily average of 39% females and 38% total adults, compared with 61% females and 62% total adults found on plants without the *Mi* gene.

Significantly fewer pupae per whole plant or per leaflet were found on the group of plants with *Mi* gene ($P < 0.01$). *Bemisia tabaci* pupae were found on 21% of *Mi*-bearing plants but on 28% of the plants lacking *Mi* ($P < 0.01$).

Discussion

Results from the present study are in agreement with those reported from California (Heinz & Zalom, 1995), where significant variability was obtained in a no-choice experiment of susceptibility to the silverleaf whitefly *B. argentifolii* (= B biotype of *B. tabaci*) on several commercial cultivars of processing tomato and wild relatives of tomato under greenhouse conditions. It has been pointed out previously that oviposition is a more reliable indicator of host plant acceptance than feeding in *B. argentifolii* (Walker & Perring, 1994). We observed no oviposition on *L. pennellii* LA 716, in agreement with Heinz & Zalom (1995), who also demonstrated that *B. argentifolii* oviposition across wild relatives of tomato was independent of trichome density. Although in some cases a tomato variety is resistant in the field and susceptible when grown in the greenhouse (Lange & Bronson, 1981), our study showed that the most susceptible cultivars or lines in the greenhouse experiment (Alta and 94GH-033) also proved to be the most susceptible in the field assay.

According to Luckwill's classification (Luckwill, 1943), type IV trichomes (characterized by a minuscule acyl sugar-secreting vesicle) are present on *L. pennellii*, but not on *L. esculentum* varieties (Lemke & Mutschler, 1984; Goffreda & Mutschler, 1989). Commercial tomato cultivars, Alta and Peto 95, do not synthesize acyl sugars since they do not have the appropriate alleles at the 5+ loci involved in the biosynthetic pathway for acyl sugar production (D. St Clair, personal communication), but the analysis of our plants showed a total acyl sugar (acylglucose + acylsucrose) level in Peto 95 similar to those obtained for 94GH-033 and 94GH-006. Moreover, under the experimental conditions of our assay, production of eggs, pupae and adults did not correlate with low amounts of acyl sugars. This indicates that a higher threshold level is required to achieve a significant reduction of *B. argentifolii* eggs on *L. esculentum* leaves. This threshold was established as $27 \mu\text{g cm}^{-2}$ in leaves treated with acyl sugars (Liedl *et al.*, 1995). This value, and the acyl sugar content obtained from *L. pennellii* LA716 in our analysis ($37.8 \mu\text{g cm}^{-2}$), are below the purified acyl sugar range ($50\text{--}70 \mu\text{g cm}^{-2}$) effective for the control of potato aphid (Goffreda *et al.*, 1988), green peach aphid *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) (Rodriguez *et al.*, 1993), leafminer *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae) (Hawthorne *et al.*, 1992), tomato fruitworm *Helicoverpa zea* (Boddie) and beet armyworm *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) (Juvik *et al.*, 1994).

The relationships between acyl sugar content and reproductive parameters in the field were similar to those found in the greenhouse, owing to essentially uniform climatic conditions in both assays. Although the acyl sugar content was measured on plants in the greenhouse, we assume, in accordance with Johnson *et al.* (1981), that acyl sugars are relatively stable compounds, with equivalent amounts accumulating under both greenhouse and field conditions. Shapiro *et al.* (1994) pointed out the high correlations of mean acyl sugars and rank of accessions between a greenhouse study and in each of two field studies; this suggests that accession performance in one environment may provide a fairly reliable indicator of relative performance in another environment.

As observed in the wild relative *L. peruvianum* (Hassan *et al.*, 1982; Channarayappa *et al.*, 1992), our study on commercial tomato cultivars demonstrated a differential antixenosis response to *B. tabaci* not attributable to the presence of glandular exudates of type IV or VIc trichomes, as these were absent in all the plants tested. In this experiment, moreover, whiteflies often showed a preference for plants bearing greater numbers of type VIa glandular trichomes. This suggests the existence of alternative genes regulating the resistance mechanisms in commercial tomato cultivars. One of the candidates could be, in the light of our results, the simple dominant gene, *Mi*. We observed that *Mi*-bearing tomato plants showed poorer host-settling results with significantly fewer females and *B. tabaci* adults per plant than in those lacking the *Mi* gene, which suggests an antixenosis-based resistance. This was confirmed when the percentage of whiteflies sucking the phloem (monitored using an Electrical Penetration Graph technique) was clearly lower on *Mi* bearing tomato plants (M. Muñiz, unpublished data). Moreover, assuming that pupae production and adult emergence rates are indicative of insect reproduction as well as of survival capacity in immature stages, our results show that the reproductive capacity of *B. tabaci* is also reduced on *Mi*-bearing tomato plants compared with those lacking *Mi* (antibiosis-based resistance). For many arthropod species, such as whiteflies or aphids, even low to moderate levels of antixenosis and antibiosis would effectively delay the time required for the population to reach an economic damage threshold (Panda & Khush, 1995). In their entirety, these results reflect a partial resistance in *Mi*-carrying tomato cultivars, which might be increased under field conditions due to a synergistic effect of natural enemies (van Emden, 1990). This partial resistance cannot be related to the presence of four-lobed glandular trichomes type VIa, as *Mi*-bearing plants had significantly lower numbers of these trichomes than those not carrying the gene.

The fact that the same gene could be involved in resistance to such different organisms as whiteflies, aphids and nematodes allows us to hypothesize on the existence of similar recognition and response mechanisms in the tomato plant. The mechanisms of the *Mi*-mediated resistance to these organisms are as yet unknown. The *Mi* gene has recently been cloned (Milligan *et al.*, 1998); it encodes a putative protein with a nucleotide binding site and a leucine-rich repeat region, which are characteristic of proteins that are required for resistance to a wide range of organisms. Most members of the same gene family are clustered in the 650-kb region from *L. peruvianum* that is present in the cultivar Motelle (Milligan *et al.*, 1998).

We conclude that resistance to the B-biotype of *B. tabaci* requires an acyl sugar content above a threshold level, and that a gene in the *Mi* region is responsible for the differential host response of some commercial tomato cultivars to whitefly development. The gene *Mi*, or another closely linked to it, may be involved in the partial resistance shown by *L. esculentum* cultivars, and is distinct from the pathway regulating the acyl sugar content of leaf glandular trichomes. Since *Mi* also mediates resistance to both nematodes (*Meloidogyne* spp.) and aphids (*M. euphorbiae*), it is not unreasonable to conclude that a functional analogy may exist among the resistance mechanisms in tomato plants to these organisms and *B. tabaci*. Further studies are in progress to provide a better understanding of these similarities among mechanisms of resistance in tomato to whiteflies, aphids and nematodes.

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