



A differential interaction study of *Bemisia tabaci* Q-biotype on commercial tomato varieties with or without the *Mi* resistance gene, and comparative host responses with the B-biotype

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Abstract

Three tomato varieties (Motelle, Ronita, and VFN8) bearing the *Mi-1.2* gene providing resistance to nematodes *Meloidogyne* spp. and to the potato aphid *Macrosiphum euphorbiae* Thomas, and three varieties not bearing this gene (Moneymaker, Roma, and Río Fuego), were compared by choice assay for host preference using the Q-biotype of *Bemisia tabaci* (Gennadius). The most preferred hosts, determined by infestation levels and numbers of feeding adults were Moneymaker, Río Fuego and Roma, all of which were not carrying the *Mi* gene. Ronita and Motelle, both of which bore the *Mi* gene, were the least preferred hosts. In a no-choice assay, *B. tabaci* females laid a significantly lower number of eggs on the varieties that carried the *Mi* gene than on those lacking the gene. Differences were more dramatic when plants carrying the *Mi* gene were pooled together and compared with pooled plants without this gene. Significantly greater values were obtained for the *Mi*-lacking group for all parameters tested. Comparing these results with those from a previous study on the B-biotype of *B. tabaci*, Q-biotypes were found to produce higher daily infestation rates on most of the tomato varieties. When results from plants carrying *Mi* were pooled, they showed lower infestation levels of Q-biotypes than B-biotypes. The Q-biotype infested less *Mi*-plants and more non-*Mi* plants than B-biotype. Q-biotype females produced significantly less pupae than the B-biotype females on both groups of plants. These results suggest the existence of an antixenosis and antibiosis-based resistance to the Q-biotype of *B. tabaci* in *Mi*-bearing commercial tomato varieties, which is greater than that previously reported for the B-biotype.

Introduction

The damage caused by *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) to commercial tomato *Lycopersicon esculentum* Mill and other horticultural crops world-wide may be directly through phloem feeding or indirectly by the transmission of plant viruses such as tomato yellow leaf curl viruses (Carnero et al., 1990; Moriones et al., 1993; Bedford et al., 1994; Blua & Toscano, 1994; Brown, 1994; Brown & Bird, 1992, 1996; Markham et al., 1996; Jiang et al., 1999). In Spain, control of *B. tabaci* is based mainly

on the application of insecticides. However, whiteflies appear to be resistant to many of the chemicals employed. Consequently, the utilisation of resistant plants (Russell, 1978), based on detailed insect-plant interaction studies, has recently increased. One of the most important scientific aspects to be addressed in host plant interaction and plant resistance studies, is the behavioural diversity of biotypes within a pest species. Severe infestations of crop plants can result from a failure to recognise the existence of insect biotypes (Smith et al., 1994) and also their different host adaptation capabilities (Bernays, 1999).

A *Bemisia tabaci* species complex has been proposed to encompass all *B. tabaci* (Brown et al., 1995). Although this group exhibits diverse host ranges and much molecular genetic variation, it has not been possible to link distinct morphological features to these diverse characteristics. Recent investigations have shown that the mitochondrial COI gene is useful as a molecular marker for identification of whitefly species and genera (Brown & Torres-Jerez, 1999). Both the B- and Q-biotypes of *B. tabaci* have been described in Spain: the B-biotype has been detected in Canary Islands, Málaga, Almería, Madrid, and Barcelona. The Q-biotype has been observed in Sevilla, Málaga, Almería, Murcia, Valencia, and Mallorca Island (Guirao et al., 1997). More recently, Simón et al. (1999) observed an increase of the Q-biotype in southern Spain, where the B-biotype was almost absent.

Although the need for understanding the fundamental relationships between biotypes of *B. tabaci* has already been documented (Wagner, 1995; Wang & Tsai, 1996) and many studies have been carried out on the A- and B-biotypes (see review by Drost et al., 1998), few studies on host plant selection of the Q-biotype have been undertaken to date (Muñiz & Nombela, 1997a, b).

Several commercial varieties of tomato contain the *Mi-1.2* (*Mi* throughout) gene which provides resistance to nematodes (*Meloidogyne* spp.) and to the potato aphid *Macrosiphum euphorbiae*. In a previous study Nombela et al. (2000) indicated that the *Mi* gene, or another gene in its region, may also be involved in partial resistance to the B-biotype of *B. tabaci*. The study presented in this paper, was undertaken to evaluate the host response of the Q-biotype *B. tabaci* in commercial tomato varieties with and without the *Mi* gene and to compare this to the response already recorded with the B-biotype.

Materials and methods

Plant material. Three commercial tomato varieties carrying the nematode-resistance gene *Mi* (*L. esculentum* cv. Motelle, cv. VFN8, and cv. Ronita) and three other varieties without this gene (cv. Money-maker, cv. Río Fuego, and cv. Roma) were used. Roma and Ronita are near-isogenic lines. Money-maker and Motelle are near-isogenic lines too and differ only in the presence of a 650 kb introgressed region from *L. peruvianum* containing the *Mi* gene, in chromosome

6 of Motelle. VFN8 contains a longer *L. peruvianum* introgressed region including the region present in Motelle (Ho et al., 1992).

Choice assay. Seeds from the six tomato varieties were germinated in a climatic chamber maintained at a temperature regime of 27 °C:16 °C (Light:Dark), a photoperiod of L16:D8 h, and a relative humidity of 68–75%. Plants were grown in perlite in one-litre plastic pots irrigated with a nutritive complex 20-20-20 (Nutrichem 60, Miller Chemical, Hanover, PE, USA) in a proportion of 0.75 l week⁻¹. At 52 days post planting, plants were transferred to an insect-free greenhouse and randomised in a complete block design with ten replicates at 23 °C:15 °C (Light:Dark) and 60–80% r.h. Each plant was equidistant from the adjacent pots and plant leaves did not touch each other. Three days later, plants were infested with Q-biotype *B. tabaci* by releasing approximately 2000 seven-day old mature adults that had been reared on tomato cv. Río Fuego for thirty generations. Adults were released from a plastic tube in the centre of the greenhouse at an equidistant point from the plants. After seven days, the numbers of adult whiteflies (males and females) were counted daily *in situ* on all leaves of every plant until the emergence of new adults (30 days). Counts were made early in the morning before the adults became active. Three days after the beginning of emergence of new adults, the total numbers of pupae and empty pupal cases on all leaves of every plant were recorded.

Numbers of pupae were $\log_{10}(x + 1)$ transformed and analysed with a one-way ANOVA followed by Tukey's HSD test. Proportions (*p*) of *B. tabaci* daily infestation and leaflets infested by pupae were transformed to arcsine $(p/100)^{0.5}$ before analysis (StatSoft, 1994).

No-choice assay. Thirty-day old plants from the six tomato varieties used in the choice assay, were placed in a growth chamber at 23 °C:18 °C, L16:D8 h. When plants were 60 day-old, one 7-day old female was placed into each of 91 plastic truncated cone clip-cages (3.6 cm × 2.6 cm diameter; 4 cm high) attached to the under surface of the leaves (one cage per plant). After three days, the total number of eggs laid by each female was recorded and the daily number of eggs per female was determined. Data were processed as described in the choice assay.

Comparative analysis with the B-biotype. The percentage of all Q-biotype adults (males and females)

Table 1. Daily infestation (average over 30 days) and pupa production of *B. tabaci* (Q-biotype) on six commercial tomato varieties (Mean \pm SE)

Varieties	Daily infestation				Pupa production			
	Plants infested by females (%)	Plants infested by males+females (%)	Females on plants (%)	Males+females on plants (%)	Plants <i>n</i>	Pupae/plant	Pupae/leaflet	Leaflets infested by pupae (%)
Moneymaker (-Mi)	96.7 \pm 1.3 a	98.7 \pm 0.6 a	31.0 \pm 1.3 a	30.5 \pm 1.2 a	10	511.7 \pm 141.8 a	2.9 \pm 0.9 a	14.5 \pm 3.3 a
Río Fuego (-Mi)	85.7 \pm 2.0 b	93.0 \pm 1.5 b	17.3 \pm 1.0 b	17.4 \pm 0.9 b	10	146.7 \pm 30.9 bc	1.8 \pm 0.3 a	11.1 \pm 1.5 a
Roma (-Mi)	81.3 \pm 2.8 bc	87.3 \pm 2.0 b	18.4 \pm 2.1 b	18.3 \pm 2.1 b	10	228.9 \pm 36.4 ab	1.7 \pm 0.2 a	10.4 \pm 1.5 a
Motelle (+Mi)	67.0 \pm 3.4 d	75.3 \pm 3.0 cd	10.4 \pm 0.5 c	10.1 \pm 0.5 c	10	116.5 \pm 45.7 c	0.6 \pm 0.2 b	4.8 \pm 1.0 b
VFN8 (+Mi)	72.3 \pm 4.1 cd	75.3 \pm 3.9 c	17.1 \pm 1.4 b	17.0 \pm 1.5 b	10	376.4 \pm 98.1 a	2.0 \pm 0.6 a	12.3 \pm 3.0 a
Ronita (+Mi)	54.7 \pm 3.6 e	69.0 \pm 2.9 d	6.3 \pm 0.5 d	6.7 \pm 0.6 d	10	32.5 \pm 13.0 d	0.3 \pm 0.1 b	4.1 \pm 0.9 b

Means followed by the same letter in columns do not differ significantly ($P < 0.05$) by Tukey's HSD.

Table 2. Fecundity of *B. tabaci* (Q-biotype) on six commercial tomato varieties (Mean \pm SE)

Varieties	Plants <i>n</i>	Daily eggs per female ¹
Moneymaker (-Mi)	17	3.9 \pm 0.5 ab
Río Fuego (-Mi)	12	4.6 \pm 0.4 a
Roma (-Mi)	16	3.3 \pm 0.4 abc
Motelle (+Mi)	15	3.2 \pm 0.7 bcd
VFN8 (+Mi)	17	2.6 \pm 0.6 cd
Ronita (+Mi)	14	1.9 \pm 0.6 d

¹ Over a period of three days.

Means followed by the same letter do not differ significantly ($P < 0.05$) by Tukey's HSD.

and the percentage of females recorded on the plants from the choice assay were compared with B-biotype data from a previous study (Nombela et al., 2000). The numbers of Q-biotype pupae per plant and per leaflet were standardised prior to comparison since the initial female population in the choice assay was slightly greater than in the B-biotype experiment. The standardisation was made by multiplying each value with the ratio of the initial number of B-females/ initial number of Q-females. Since the infestation rate also depended on the number of insects, and the initial populations were different in the B- and Q-biotype experiments, the relationship between the percentages of infested plants (y) and the number of females or total adults (x) was predicted by a regression analysis where $z = -ax$; $z = \ln[1-(y/100)]$ and a was estimated by least-squared regression (StatSoft, 1994). Estimated data from both biotypes were transformed and compared using the same statistical methods previ-

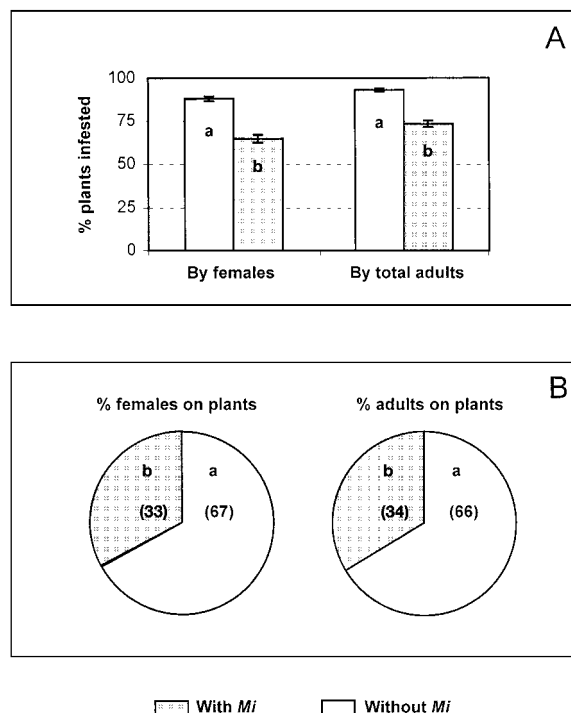


Figure 1. Daily infestation by *B. tabaci* (Q-biotype) on pooled tomato plants with and without the *Mi* gene. (A) Percentage of plants infested by females or total adults. (B) Percentage of insects on plants (females and total adults).

ously described for the independent analysis of the Q-biotype.

Results and discussion

Tomato host response to the Q-biotype of B. tabaci. Significant differences ($P < 0.001$) were obtained under choice conditions for all tested parameters when the six tomato varieties were compared. Mean values of most daily infestation and pupa production para-

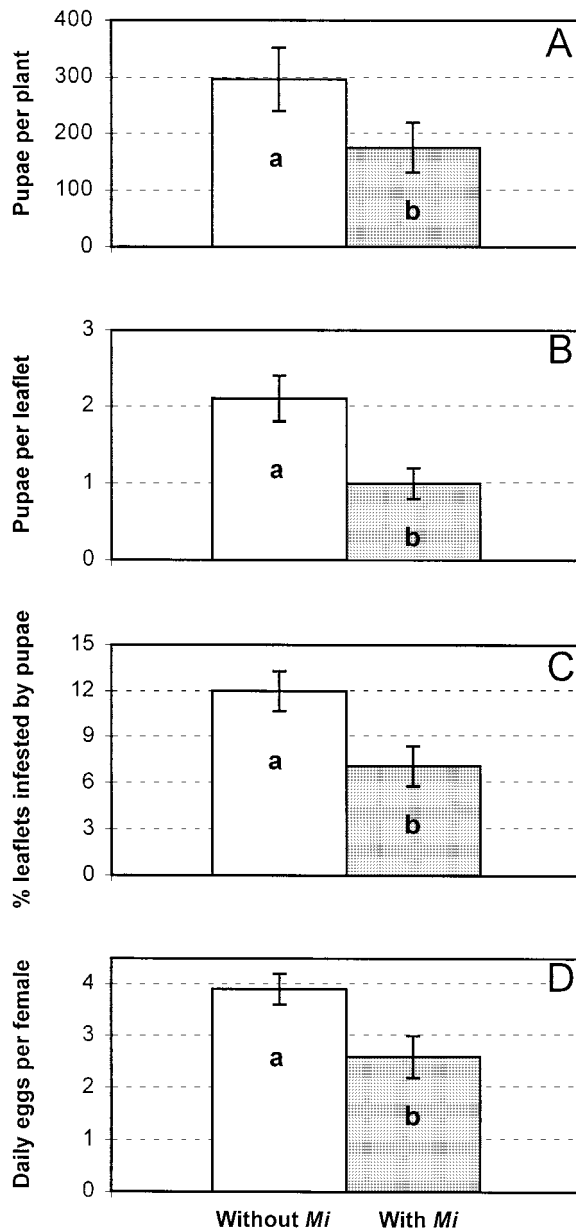


Figure 2. Pupa production and fecundity of *B. tabaci* (Q-biotype) on pooled tomato plants with and without *Mi* gene. (A) Number of pupae per plant. (B) Number of pupae per leaflet. (C) Percentage of leaflets infested by pupae. (D) Daily number of eggs per female.

parameters were lower on Motelle, VFN8, and Ronita (*Mi*-bearing plants) than on Moneymaker, Río Fuego, and Roma (*Mi*-lacking ones, Table 1). The significant differences between near-isogenic lines, specially between Moneymaker and Motelle, give us the best clue for the relationship between the tomato response and the presence/absence of the *Mi* gene or another

gene within the 650 kb region present in Motelle, as this is the smallest fragment of the *L. peruvianum* introgressed region containing *Mi*. The percentage of insects on VFN8 plants, as well as the pupae numbers, did not significantly differ from those recorded on the *Mi*-lacking plants; this could be due to other gene products in the genetic background of VFN8 masking the resistance effect. Similar behaviour was also observed in the initial study with B-biotype *B. tabaci* (Nombela et al., 2000), where lower infestations and pupae numbers were recorded on the tomato varieties with *Mi*, but with some statistical overlap.

When results from plants with the *Mi* gene were pooled together and compared with pooled results from plants lacking this gene, differences between the two groups became very clear and were statistically significant ($P < 0.001$) for all parameters considered. According to Panda & Khush (1995), antixenosis is the resistance mechanism employed by a plant to deter or reduce colonisation by insects and antibiosis is the resistance mechanism that operates after the insects have colonised and started utilising the plant. Our results suggest that *Mi*-bearing tomato plants exhibit a certain level of antixenosis-based resistance to the Q-biotype as the percentage of infested *Mi*-bearing plants was lower (Figure 1A) and they were less infested (Figure 1B) than plants without the gene. Moreover, an antibiosis-based resistance was observed on the group of plants with *Mi* as values of the pupa production parameters were also lower on them (Figures 2A–C). The same findings were previously obtained for the B-biotype (Nombela et al., 2000).

In the no-choice oviposition assay (Table 2), females laid fewer eggs on Ronita, VFN8, and Motelle (*Mi*-bearing plants) than on *Mi*-lacking ones, although the mean values obtained on Roma did not significantly differ from those recorded on Motelle or VFN8. Once again, differences were more dramatic when plants were grouped on the basis of the presence/absence of this gene (Figure 2D), which corroborates the existence of an antibiosis-based resistance to these insects in plants with *Mi*. These results are in accordance with those from aphids reported by Kaloshian et al. (1997), who observed a significant decrease in the fecundity of *M. euphorbiae* due to the presence of the same gene.

Comparative analysis of Q- and B-biotypes. A comparison of the results obtained from this Q-biotype study with those of a previous B-biotype study (Nombela et al., 2000) was possible as no significant

Table 3. Percentages of tomato plants (y) with and without the *Mi* gene infested by B- and Q- biotypes of *B. tabaci*, estimated by the linear regression $z = -ax$, where $z = \ln [1-(y/100)]$; R, correlation coefficient; a, slope. (Mean \pm SE)

Plants	Biotype	By adults			By females		
		a	R	% infested plants (estimated)	a	R	% infested plants (estimated)
With <i>Mi</i>	B	-0.024 ± 0.001	0.9788	64.8 ± 4.7 a	-0.029 ± 0.001	0.9860	76.6 ± 2.1 a
With <i>Mi</i>	Q	-0.013 ± 0.001	0.9370	60.9 ± 3.7 b	-0.018 ± 0.001	0.9588	64.4 ± 1.5 b
Without <i>Mi</i>	B	-0.023 ± 0.001	0.9839	76.0 ± 3.5 b	-0.027 ± 0.001	0.9859	79.9 ± 1.4 b
Without <i>Mi</i>	Q	-0.017 ± 0.001	0.9554	88.6 ± 1.6 a	-0.023 ± 0.001	0.9597	84.1 ± 0.4 a

R was significant ($P < 0.0001$) in all cases. Means followed by different letter, within the same group of plants (with or without *Mi*), differ significantly ($P < 0.05$) by Tukey's HSD test.

differences were observed in plant growing and greenhouse climatic conditions (biotype B: $T = 21.2 \pm 0.3$ °C, r.h. = $68 \pm 0.7\%$; biotype Q: $T = 20.8 \pm 0.2$ °C, r.h. = $68.4 \pm 1.0\%$). Investigations on insect-plant interactions (particularly those related to host plant selection), have demonstrated the existence of marked differences between the B- and Q-biotypes in terms of their reproductive activity and development on different pepper varieties (Muñiz & Nombela, 1997a, b). As in these studies, variation between the six tomato varieties was detected in relation to their host suitability to B- and Q-biotypes. The Q-biotype showed higher daily infestation rates than the B-biotype on most of the tested varieties. These results, as well as those from another comparative study on some common weeds as reservoirs for *B. tabaci* (Muñiz, 2000), could partially explain the putative increase of the Q-biotype recently observed in Southern Spain (Simón et al., 1999).

When pooled together, *Mi*-plants hosted significantly ($P < 0.001$) lower percentages of Q-biotype females (33.4) and total adults (33.8) than B-biotype insects (39.1 and 38.1, respectively). Significant differences between biotypes were also detected in the percentages of infested plants when values were estimated by linear regression (Table 3). The goodness-of-fit of this model to the observed data is shown by its correlation coefficient (*R*) which was significant ($P < 0.0001$) in all cases. In the group of plants with *Mi*, the Q-biotype was shown to have infested a lower number of plants than the B-biotype, although the number of *Mi*-lacking plants infested by the Q-biotype was greater than infested by the B-biotype. These results suggest that *Mi*-bearing plants present greater antixenosis-based resistance to the Q-biotype than to the B-biotype. Q-biotype females had a lower reproductive capacity as they produced significantly

($P < 0.01$) lower numbers of pupae on both *Mi*-bearing (175) and *Mi*-lacking (296) groups of plants than B-biotype females (235 and 392, respectively).

In conclusion, this study suggests the existence of an antixenosis and antibiosis-based resistance in *Mi*-bearing commercial tomato varieties to the Q-biotype of *B. tabaci*, with similar, yet more pronounced effects than those previously reported for the B-biotype. This effect is mediated by *Mi* or another linked gene (Nombela et al., 2000). Differences in host suitability of B- and Q-biotypes on these commercial tomato varieties suggest that this whitefly-resistance is biotype-specific, similarly to the isolate-specific *Mi*-resistances to nematodes (Bost & Triantaphyllou, 1982; Jarquin-Barberana et al., 1991; Milligan et al., 1998) and aphids (Rossi et al., 1998), and strengthen the theory of a gene-for-gene interaction regulating this resistance. The agricultural significance of these findings is based on the fact that the relationship between tomato resistance to whiteflies and *Mi*, or another gene closely linked to it, is of practical interest in breeding programs to simultaneously control *B. tabaci*, *M. euphorbiae*, and *Meloidogyne* spp. More studies are in progress to confirm or reject the direct implication of *Mi* in such a resistance.

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