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Response of tomato rootstocks carrying the *Mi*-resistance gene to populations of *Meloidogyne arenaria, M. incognita and M. javanica*

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Abstract The response of four *Mi*-resistance gene tomato rootstocks to seven populations of *Meloidogyne* was determined in pot tests conducted in a glasshouse. Rootstocks PG76 (*Solanum lycopersicum* × *Solanum* sp.) and Brigeor (*S. lycopersicum* × *S. habrochaites*) and resistant cv. Monika (*S. lycopersicum*) were assessed against one population of *M. arenaria*, three of *M. incognita,* and three of *M. javanica.* Rootstocks Beaufort and Maxifort were assessed against one population of *M. arenaria*, two of *M. incognita* and two of *M. javanica*. Rootstock PG76 was highly resistant (reproduction index <10%) to all the populations, whereas rootstock Brigeor and cv. Monika were highly to moderate resistant. Rootstocks Beaufort and Maxifort showed reduced resistance or inability to suppress nematode reproduction, and their responses varied according to the population tested. Beaufort and Maxifort were susceptible to the two populations of *M. javanica* as Maxifort was to one of *M. incognita.* The reproduction index of the nematode was higher ($P < 0.05$) on Maxifort than Beaufort for all root-knot nematode populations.

Keywords Genetic variability · Resistance · Root-knot nematodes · SCAR-PCR · *Solanum habrochaites* · *Solanum lycopersicum*

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Meloidogyne is the most important plant parasitic nematode genus that causes serious yield losses in tomato (*Solanum lycopersicum*, formerly *Lycopersicon esculentum*) worldwide. *Meloidogyne javanica* and *M. incognita* are the most common root-knot nematodes found in vegetable production areas in Spain whereas *M. arenaria* is found to a lesser extent (Sorribas and Verdejo-Lucas 1994; Verdejo-Lucas et al. 2002).

The use of new control methods against soil pathogens has increased in the last two decades to circumvent the toxicity and environmental impact of traditional pesticides used in agriculture (i.e. methyl bromide). Plant resistance is an economically, sustainable and environmentally friendly alternative to conventional and organic agriculture (Roberts and Thomason 1996; Besri 2003; Sorribas et al. 2005). In tomato, the *Mi*-resistance gene, introgressed from *S. peruvianum* (Smith 1944),

strongly reduces development and reproduction of *M. arenaria, M. javanica* and, *M. incognita* at soil temperatures below 28°C (Dropkin 1969). Tomato cultivars carrying the *Mi*-resistance gene are not immune to root-knot nematodes and support some level of reproduction (Roberts and Thomason 1989). Reproduction on resistant tomatoes has been explained by the interaction between plant genotype and nematode isolate, but not by either factor alone (Jacquet et al. 2005). The inter- and intra-specific genetic variability in the genus *Meloidogyne* contributes to variation in the response of *Mi*-resistance gene tomatoes with introgressions from *S. peruvianum,* which can result in reduced levels of nematode suppression (Roberts and Thomason 1996; Ornat et al. 2001; Castagnone-Sereno 2002).

At present, grafting vegetables is expanding in Europe, and it is primarily used to increase their vigour and yield. In tomato, most commercially available rootstocks are interspecific hybrids of *S. lycopersicum* and *S. habrochaites* (formerly, *L. hirsutum*) or other wild *Solanum* species. They incorporate the *Mi*-resistance gene in addition to other resistance genes to manage diseases caused by bacteria, fungi and viruses. The response of *Mi*-resistance gene tomato rootstocks against root-knot nematodes varies greatly depending on plant genotype and ranges from highly resistant to fully susceptible (Graf et al. 2001; López-Pérez et al. 2006; Cortada et al. 2008; Verdejo-Lucas and Sorribas 2008). However, little is known on the contribution of the nematode genotype-observed variation in levels of nematode suppression. The objective of this study was to determine variation in the resistance response of four tomato rootstocks against different populations of *M. arenaria*, *M. incognita* and *M. javanica.*

Materials and methods

The root-knot nematode populations were held on susceptible cv. Roma, and had never been exposed to the *Mi*-resistance gene. They included one population of *M. arenaria* (code MA-68), three of *M. incognita* (codes MI-ALM, MI-CROS and MI-26), and three of *M. javanica* (codes MJ-IBIZA, MJ-05 and MJQ21). The identity of these populations was confirmed before the start of the study by molecular SCAR-PCR markers according to Zijlstra et al. (2000). The tomato rootstocks were PG76, Brigeor, Beaufort, and Maxifort and the resistant cv. Monika. All had been described as highly resistant to *M. arenaria*, *M. incognita* and *M. javanica* (Marín Rodríguez 2005). The susceptible cv. Durinta was included as a reference standard for comparison. The main characteristics and resistances of the tomatoes are described in Table 1.

Pot tests were conducted to determine nematode reproduction on rootstocks PG76, and Brigeor, and cv. Monika. Seedlings were transplanted singly into 1.5 l pots containing steam-sterilised river sand, and were allowed to grow for one week before inoculation. Nematode inoculum was obtained from infected tomato cv. Roma by macerating the roots in a 0.5% NaOCl solution in a food blender at 1,000 rpm for 5 min. (Hussey and Barker 1973). Macerated roots were then passed through a 74 μm aperture sieve to remove root debris, and the dispersed eggs were collected on a 25 μm sieve. Plants were inoculated with approximately 3,000 eggs of *M. arenaria* MA-68, *M. incognita* MI-ALM, MI-CROS, and MI-26, *M. javanica* MJ-IBIZA, MJ-05, and MJQ21. Each tomato-population combination was replicated eight times. Plants were maintained in a glasshouse for 8 weeks. They were watered as needed and fertilised with a slow-release fertiliser (15% N+10% P_2O_5+ 12% K_2O+2% MgO_2+microelements). At the end of each test, the number of eggs g^{-1} of fresh root was determined by macerating two 10-g root sub-samples in a 0.5% NaCOl solution for 10 min, as described previously. The response of the tomato rootstocks was categorised according to the reproduction index (RI) as highly resistant (RI<10%), moderately resistant (10≤ RI<50%) or susceptible (RI≥50%) (Hadisoeganda and Sasser 1982). The RI was calculated as number of eggs per plant on resistant rootstock or cultivar divided by the number of eggs per plant on the susceptible cv. Durinta×100.

Rootstocks Beaufort and Maxifort were inoculated with populations *M. arenaria* MA-68, *M. incognita* MI-ALM and MI-CROS, and *M. javanica* MJ-IBIZA and MJ-05. It was not possible to test *M. incognita* MI-26 and *M. javanica* MJ-Q21 populations with Beaufort and Maxifort due to insufficient inoculum. Preparation of nematode inoculum and experimental conditions were similar to those described previously except for the combinations Beaufort and Maxifort

Table 1 Main characteristics and resistances of the *Mi*-resistance gene tomatoes used to determine variation in the response to different populations of *Meloidogyne arenaria*, *M. incognita,* and *M. javanica*

Variety	Mi23 profile[a]	Parental Species[b]	Seed Company	Resistances [c]
Rootstock				
PG76	Mi/Mi	*S. lycopersicum*× *Solanum* sp.	Gautier Seeds	HR: TMV/ Fol:2 /For / Va/ Vd/ Pl/ Ma/ Mi/ Mj
Brigeor	Mi/Mi	*S. lycopersicum*× *S. habrochaites*	Gautier Seeds	HR: TMV/ Fol:2/ For/ V/ Ma/ Mi/ Mj
Beaufort	Mi/Mi	*S. lycopersicum*× *S. habrochaites habrochaiteshabrochaiteshabrochaites*	De Ruiter Seeds	HR: ToMV/ Fol:0,1/ For/ Pl/ Va/ Vd/ Ma/Mi/ Mj
Maxifort	Mi/Mi	*S. lycopersicum*× *S. habrochaites*	De Ruiter Seeds	HR: ToMV/ Fol:0,1/ For/ Pl/ Va/ Vd/ Ma/ Mi/ Mj
Cultivar				
Monika	Mi/mi	*S. lycopersicum*× *S. peruvianum*	Syngenta Seeds	HR: ToMV: 0–2/ *Fol:1*/ Va/ Vd IR: Mi/ Ma/ Mj
Durinta	mi/mi	*S. lycopersicum*	Western Seeds	HR: ToMV/ *Fol:1–2*/ Va/ Vd

[a] Mi/Mi (homozygous resistant); Mi/mi (heterozygous resistant); mi/mi (homozygous susceptible).

[b] *S. lycopersicum*× *Solanum* sp. unknown parental species.

[c] Information from the seed companies' descriptions. HR: High resistance; TMV: *Tobacco mosaic virus*; ToMV: *Tomato mosaic virus*; TYLCV: *Tomato yellow leaf curl virus*; Ff: 1–5: *Fulvia fulva* races 1, 2, 3, 4, 5; Fol: 0–2: *Fusarium oxysporum* f. sp. *lycopersici* races 0, 1, and 2; For: *Fusarium oxysporum* f. sp. *radicis-lycopersici*; Pl: *Pyrenochaeta lycopersici;* Sbl*: Stemphylium botryosum* f. sp. *lycopersici,* Va: *Verticillium albo-atrum*; Vd*: Verticullium dahliae*; Ss: *Stemphylium solana;*Si: *Silvering*; Cmm: *Clavibacter* pv. *michiganensis;* Pst: *Pseudomonas syringae pv. tomato*; Mi, Ma, Mj: *Meloidogyne incognita, M. arenaria, M. javanica.*

with *M. incognita* MI-CROS and *M. javanica* MJ-05 that were maintained in the glasshouse for 12 instead of 8 weeks.

The general linear model procedure of the SAS software version 8 (SAS institute Inc., Cary, NC) was used for statistical analysis. The number of eggs g^{-1} of root and eggs per plant were transformed to $\sqrt{x}$ to achieve normality of data, and then subjected to analysis of variance (ANOVA). The Tukey's studentised range test was used to compare means when the ANOVA analysis was significant ($P<0.05$). Soil temperatures were registered daily at 30 min intervals by placing temperatures probes into the potted soil. Temperatures were below 28°C for the duration of the tests and ranged from 11.2 to 24.6°C ($x=19.3$°C).

Results and discussion

Resistant rootstocks PG76 and Brigeor supported a lower number of eggs g^{-1} of root ($P<0.05$) than susceptible Durinta (Table 2). Both rootstocks showed similar ability to inhibit nematode reproduction irrespective of the populations tested. Egg production was similar on rootstock Brigeor and cv. Monika, but differences between rootstock PG76 and cv. Monika were observed with populations *M. incognita* MI-CROS, and *M. javanica* MJ-05 and MJ-Q21. Nematode reproduction (eggs g^{-1} root) on resistant Monika was lower ($P<0.05$) than on susceptible control Durinta for all combinations. Rootstock PG76 was highly resistant to the seven

Table 2 Numbers of eggs g^{-1} of root of three populations of *Meloidogyne javanica* (MJ-IBIZA, MJ-O5, MJQ21), one of *M. arenaria* (MA-68), and three of *M. incognita* (MI-ALM, MI-CROS, MI-26) on *Mi*-resistance gene tomato rootstocks PG76 and Brigeor, and resistant cv. Monika and susceptible Duritna eight weeks after the inoculation of 3,000 eggs per plant

Tomato	*M. javanica*			*M. arenaria*		*M. incognita*	
	MJQ21	MJ-05	MJ-IBIZA	MA-68	MI-ALM	MI-CROS	MI-26
PG76	290±165 c	168±185 c	354±844 b	16±19 b	74±146 b	3±6 c	351±275 b
Brigeor	1182±1291 bc	875±1042 bc	611±794 b	107±100 b	73±67 b	382±672 bc	3216±1837 b
Monika	3189±3670 b	2118±2223 b	1564±1423 b	564± 401 b	159±160 b	1110±1140 b	4294±3974 b
Durinta	10488±5115 a	13696±7104 a	12511±3310 a	6452±3910 a	3570±1602 a	12315±3576 a	14921±8708 a

Values are back-transformed mean±standard deviation of seven replicated plants. Values within the same column sharing the same letter are not significantly different according to Tukey's studentized range test ($P<0.05$).

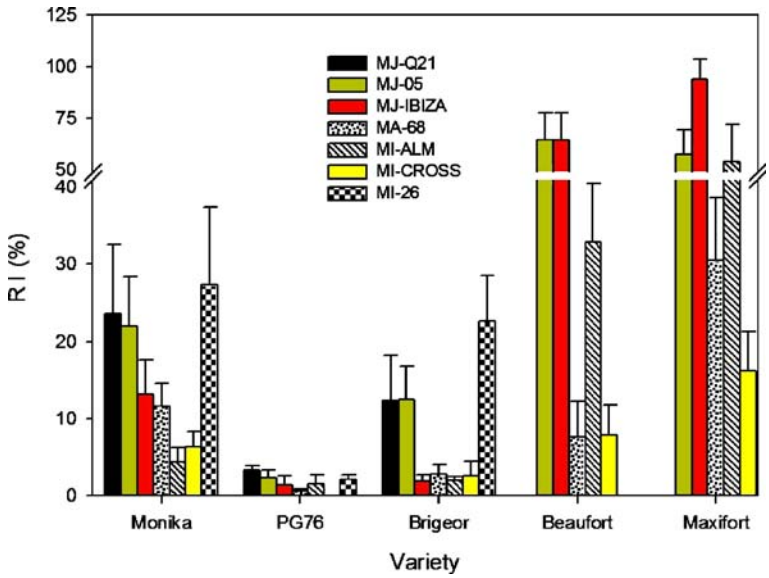

Fig. 1 Reproduction index (RI) of one population of *Meloidogyne arenaria* (MA-68), three populations of *M. incognita* (MI-ALM, MI-CROS, MI-26), and three populations of *M. javanica* (MI-IBIZA, MJ-O5, MJQ21) on *Mi*-resistance gene tomato cv. Monika, and rootstocks PG76, Brigeor, Beaufort, and Maxifort. RI: eggs per plant on a resistant tomato divided by eggs per plant on susceptible control×100

populations of *Meloidogyne* as RI values ranged from 0.02% (MI-CROS) to 3.3% (MJ-Q21) (Fig. 1). Rootstock Brigeor was highly resistant to four nematode populations but moderately resistant to *M. incognita* MI-26, and two *M. javanica* populations. The RI values for cv. Monika ranged from 4.4% (MI-ALM) to 27.3% (MI-26) (Fig. 1).

The number of eggs g^{-1} of root on rootstock Beaufort was lower ($P<0.05$) than on susceptible Durinta inoculated with *M. arenaria* MA-68, and *M. incognita* MI-ALM and MI-CROS, but was not different from the susceptible control when inoculated with *M. javanica* MJ-IBIZA and MJ-05 (Table 3). Egg production on rootstock Maxifort was lower ($P<0.05$) than on susceptible Durinta inoculated with *M. arenaria* MA-68, *M. incognita* MI-CROS and *M. javanica* MJ-05, but the number of eggs g^{-1} of root did not differ from the susceptible tomato with the remaining populations (Table 3). Rootstock Beaufort was highly resistant (RI<10%) to *M. arenaria* MA-68 and *M. incognita* MI-CROS, moderately resistant to *M. incognita* MI-ALM (RI=33%), and fully susceptible to both *M. javanica* populations. Rootstock Maxifort responded as moderately resistant to *M. arenaria* MA-68 and *M. incognita* MI-CROS, and as susceptible (RI>50%) to *M. incognita* MI-ALM, and the two *M. javanica* populations (Fig. 1). Rootstocks Beaufort and Maxifort inoculated with *M. javanica* MJ-IBIZA and MJ-05 resulted in very high RI values that were not significantly different from the susceptible control ($P>0.05$).

Table 3 Numbers of eggs g^{-1} root of two populations of *Meloidogyne javanica* (MJ-IBIZA and MJ-05), one of *M. arenaria* (MA-68), and two of *M. incognita* (MI-ALM and MI-CROS), on *Mi*-resistance gene tomato rootstocks Beaufort and Maxifort and susceptible cv. Durinta eight or twelve weeks after the inoculation of 3,000 eggs per plant

Tomato	Duration of the tests				
	8 weeks			12 weeks	
	M. javanica MJ-IBIZA	*M. arenaria* MA-68	*M. incognita* MI-ALM	*M. javanica* MJ-05	*M. incognita* MI-CROS
Beaufort	9859±2204 a	508±635 c	1197±694 b	6908±3998 ab	2846±4024 b
Maxifort	15669±6865 a	1627±1079 b	1811±1359 ab	6403±3778 b	4658±3671 b
Durinta	12511±3310 a	6436±1034 a	3570±1602 a	12239±4881 a	27697±7847 a

Values are back-transformed mean±standard deviation of seven replicated plants. Values in the same column shearing the same letter are not significantly different according to Tukey's studentized range test ($P<0.05$).

There was a strong effect of tomato genotype on the response to the nematode population. A total of 31 nematode population-tomato genotype combinations was tested in this study. Of these, 15 combinations resulted in a highly resistant response, 11 moderately resistant, and five were susceptible responses: three involved rootstock Maxifort, and two, rootstock Beaufort. Molecular analysis using co-dominant marker REX-1 (Williamson et al. 1994) and the PCR-based co-dominant SCAR marker Mi23 (Seah et al. 2007b) were performed. Both indicated that all tomato rootstocks were homozygous resistant for *Mi-1* locus and that resistant cv. Monika was heterozygous (Cortada et al. 2008). The marker Mi23 was specifically designed for interspecific tomato hybrids lines with *S. habrochaites* as were rootstocks Brigeor, Beaufort and Maxifort. However, the pathogenicity tests showed variable results. Tzortzakakis et al. (1998) and Jacquet et al. (2005) suggested that the *Mi*-1 homozygous locus might better protect against the nematode compared to the *Mi*-1 heterozygous locus, but no consistent effect was found in this study. For instance, rootstocks Beaufort and Maxifort were susceptible to both populations of *M. javanica* whereas cv. Monika was resistant. The molecular markers were unable to distinguish variation in the resistant response, which emphasises the need to use different nematode populations to characterise plant resistance. High soil temperatures as a cause for resistance-breaking were discarded because soil temperatures remained below 28°C during the tests.

Remarkable changes were revealed in some rootstocks depending on the population, and were best illustrated for rootstock Beaufort which was highly resistant to *M. arenaria* MA-68 and *M. incognita* MICROS, moderately resistant to *M. incognita* MIALM, and susceptible to both populations of *M. javanica*. Conversely, highly resistant responses were consistently obtained on PG76 challenged with seven populations.

Several hypotheses could explain the susceptibility of rootstocks Beaufort and Maxifort against the two populations of *M. javanica*. The lack of resistance could be attributed to gene silencing by a methylation process (Liharshka 1998) or a spontaneous mutation in the sequence of *Mi-1.2* gene that could inhibit gene expression (Seah et al. 2007a). The absence or the mutation of genes necessary in the signalling pathway of *Mi-1.2* gene such as *Rme1* (Martínez de Ilarduya et al. 2004), Hsp90 or *Sgt*1 (Bhattarai et al. 2007) could also explain the susceptible phenotype of Beaufort and Maxifort. Nevertheless, the differential responses of both rootstocks were related to the nematode population, which reinforces the concept that each plant-nematode combination has a specific interaction pattern. Changes from resistant to susceptible responses have been reported in tomato cultivars with introgressions from wild *Solanum* species, when a single plant genotype was challenged with different *Meloidogyne* isolates (Sorribas and Verdejo-Lucas 1999; Tzortzakakis et al. 2006). On the other hand, little is known about root-knot nematode avirulence effectors (*Avr*) (Fuller et al. 2008) and the reason why some isolates can reproduce on resistant plants, whereas others never overcome the resistance of the *Mi-1.2* gene (Jarquin- Barbarena et al. 1991). Virulence could be due to a lack of or modification of those nematode gene products that activate plant defence genes against nematodes (*Nem-R* genes) (Williamson and Kumar 2006). To date, the specific interaction of the nematode and the *Mi-1.2* resistance signalling pathway remains to be solved.

As all nematode-rootstock combinations were not tested simultaneously, main effects could not be statistically analysed but differences in the phenotypic expression of the *Mi*-resistance gene were apparent as tomato rootstocks and cultivar were not equally effective in suppressing nematode reproduction. As a general trend, rootstock PG76 was most effective, followed by Brigeor, cv. Monika, Beaufort, and Maxifort. These results are in agreement with those of Cortada et al. (2008) using a single population of *M. javanica* (MJ-05) regarding the differential response of tomato rootstocks and ranking of the resistance levels.

The differences found in the resistant responses of tomato rootstocks have implications in root-knot nematode management. The success of growing resistant tomato rootstocks in nematode-infested soils could vary according to locally-occurring populations of *Meloidogyne*, and this could limit their usefulness as an alternative to chemical control. The susceptibility of Beaufort to populations of *M. incognita* and *M. arenaria* has already been reported (Graf et al. 2001; López-Pérez et al. 2006). The extremely vigorous root system of the rootstocks and the presence of additional resistance genes in their genome may help to counteract other soil-borne diseases, and in turn

contribute to increased tomato yields, but may not be effective enough to control root-knot nematodes.

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