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Resistance in *Lycopersicon peruvianum* to Isolates of *Mi* Gene-compatible *Meloidogyne* Populations

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Abstract: Root-knot nematode resistance of F₁ progeny of an intraspecific hybrid (*Lycopersicon peruvianum* var. *glandulosum* Acc. No. 126443 × *L. peruvianum* Acc. No. 270435), *L. esculentum* cv. Piersol (possessing resistance gene *Mi*), and *L. esculentum* cv. St. Pierre (susceptible) was compared. Resistance to 1) isolates of two *Meloidogyne incognita* populations artificially selected for parasitism on tomato plants possessing the *Mi* gene, 2) the wild type parent populations, 3) four naturally occurring resistance (*Mi* gene)-breaking populations of *M. incognita*, *M. arenaria*, and two undesignated *Meloidogyne* spp., and 4) a population of *M. hapla* was indexed by numbers of egg masses produced on root systems in a greenhouse experiment. Artificially selected *M. incognita* isolates reproduced abundantly on Piersol, but not ($P = 0.01$) on resistant F₁ hybrids. Thus, the gene(s) for resistance in the F₁ hybrid differs from the *Mi* gene in Piersol. Four naturally occurring resistance-breaking populations reproduced extensively on Piersol and on the F₁ hybrid, demonstrating ability to circumvent both types of resistance. *Meloidogyne hapla* reproduced on F₁ hybrid plants, but at significantly ($P = 0.01$) lower levels than on Piersol.

Key words: *Lycopersicon esculentum*, *Lycopersicon peruvianum*, *Meloidogyne arenaria*, *Meloidogyne hapla*, *Meloidogyne incognita*, *Meloidogyne javanica*, resistance, root-knot nematode, tomato.

Early attempts to identify sources of resistance to root-knot nematodes in wild *Lycopersicon* species revealed several resistant accessions of *L. peruvianum* (L.) Mill. (7,18). Smith (21) used embryo culture after crossing *L. esculentum* Mill. cv. Michigan State Forcing and resistant *L. peruvianum* USDA Acc. No. 128657 and obtained one F₁ plant, cuttings from which were backcrossed to *L. esculentum* (24). All currently available root-knot resistant tomato cultivars are derived from this source (12).

Resistance is controlled by a major gene (*Mi*) located on chromosome six (3,8); however, the exact number and nature of genes conferring resistance to root-knot is not known (17,19). The *Mi* gene confers resistance to *Meloidogyne incognita* (Kofoid & White) Chitwood, *M. javanica* (Treub) Chitwood, and *M. arenaria* (Neal) Chitwood, but not *M. hapla* Chitwood (2,9). Resistance is diminished at temperatures above 28 C (1,6).

Variability for parasitism of tomato cultivars bearing the *Mi* gene has been re-

ported for populations of *M. arenaria*, *M. incognita*, and *M. javanica* (17). Variability can be in the form of partial or moderate resistant reactions and may reflect an influence of the *L. esculentum* background (cultivar) containing the *Mi* gene (9,16,17). Complete susceptibility also may occur (17,20,23). Some populations able to parasitize plants bearing the *Mi* gene appear to occur naturally, without the selection pressure of contact with the *Mi* gene (13,14,17). Several studies have shown that resistance-breaking populations of these *Meloidogyne* spp. also can arise after continual exposure to *Mi* gene-bearing plants in relatively few generations (4,13,15,22). However, the effect of the *Mi* gene may not be overcome completely (4) and not all populations can be selected (13).

Additional sources of resistance, in *L. peruvianum* Acc. No. 270435 and *L. peruvianum* var. *glandulosum* C. H. Mull. Acc. No. 126443, have been identified. These accessions were highly to moderately resistant to isolates of four host races of *M. incognita* and to *M. arenaria*, but they were less resistant to an aggressive isolate of *M. javanica* (2). Both accessions were resistant to *M. hapla* (2), and the resistance to *M. incognita* was stable at high temperature (1), suggesting the existence of a gene(s) other

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than *Mi*. To further characterize the specificity of resistance to *Meloidogyne* spp. in cultivated tomato (*Mi* gene) and in these wild *Lycopersicon* accessions, parasitism by isolates of nematodes known to infect plants bearing the *Mi* gene was assessed.

MATERIALS AND METHODS

Plant material: Cultivars of *L. esculentum* used in this study included St. Pierre, a susceptible standard, and the near-isogenic Piersol, possessing the *Mi* gene for root-knot nematode resistance. Hybrid F_1 seed was obtained from *L. peruvianum* var. *glanulosum* USDA Acc. No. 126443 \times *L. peruvianum* USDA Acc. No. 270435—clone 3MH (*L. p. g.* 126443 \times *L. p.* 270435), with both parents grown from stem cuttings.

Nematode isolates: The two *M. incognita* isolates used in the selection study were collected in Calissane, France, and Adiopodoume, Cote d'Ivoire, and characterized according to perineal pattern, caryotype, and isoesterase phenotype (10). The selection procedure was performed in Antibes as follows: The subculture of each isolate from wild-type populations maintained on St. Pierre in the greenhouse was cultured on resistant Piersol, with rhizosphere soil and roots of resistant plants periodically transferred to young Piersol transplants at 20–25 C for ca. 30 generations.

All other isolates were maintained on St. Pierre in the greenhouse. Isolates *M. incognita* "Valbonne" (France), *M. arenaria* "Le-Grau-du-Roi" (France), and *Meloidogyne* sp. "Senegal-VSS" (Senegal, West Africa), also have been characterized (10). These and an isolate of *Meloidogyne* sp., "Concarneau" (France), are all known to parasitize tomato cultivars bearing resistance gene *Mi*. An isolate of an *M. hapla* population, "Angleterre" (England), was also included in the study.

Experimental procedure: Seeds were germinated in sterilized soil in flats maintained in a greenhouse at 20–25 C. Two-week-old seedlings were transplanted singly into 10-cm-d plastic pots containing sterilized sandy soil and allowed to establish for 2 weeks

before inoculation. Inoculum of second-stage juveniles (J2) of each nematode isolate was collected from infected roots held in a mist chamber. Hatched J2 were collected daily and stored at 4 C before use within 5 days. Each test plant received 500 J2 of each isolate pipetted in a water suspension onto the soil surface around the stem base followed by light watering. Five plants of each tomato test line were inoculated with each isolate, and the 15 pots with one isolate were completely randomized in a block. Completely randomized blocks of other isolates were arranged side by side on a single greenhouse bench and separated with splash screens. Plants were maintained at 20–25 C for 7 weeks and then washed free of soil in water, and the whole root system was placed in cold Eosin Yellow (0.1 g/liter H_2O) and stirred for 30 minutes to stain egg masses. Numbers of egg masses per root system were counted. An egg mass index was assigned to each count using a rating of 1 = no egg masses, 2 = 1–3 egg masses, 3 = 4–10 egg masses, 4 = 11–30 egg masses, 5 = 31–100 egg masses, and 6 = > 100 egg masses per root system. Egg mass indices were analysed using analysis of variance and means compared by Duncan's multiple-range test.

RESULTS

Isolates selected on plants with *Mi* gene: High reproduction rates based on egg mass index were recorded for all wild-type and selected isolates of *M. incognita* Calissane and Cote d'Ivoire on susceptible St. Pierre (Table 1). Egg mass indices of the two isolates of *M. incognita* Calissane and Cote d'Ivoire selected for 30 generations on Piersol bearing the *Mi* gene were lower ($P = 0.01$) on the resistant F_1 hybrid (*L. p. g.* 126443 \times *L. p.* 270435) than on Piersol and St. Pierre (Table 1). Egg mass indices for these two populations were high on both Piersol and St. Pierre. The wild-type population of Calissane had reduced egg mass indices on Piersol. Reproduction on Piersol by the Cote d'Ivoire wild-type parent also was lower ($P = 0.01$) than that of its selected isolate. Both wild-type parent iso-

lates reproduced poorly on the resistant F_1 hybrid.

Naturally occurring resistance-breaking populations: The egg mass indices of isolates of the naturally occurring resistance-breaking populations *M. incognita* Valbonne, *M. arenaria* Le-Grau-du-Roi, *Meloidogyne* sp. Senegal-VSS (similar to *M. arenaria* and *M. incognita*), and *Meloidogyne* sp. Concarneau (undescribed species) were high on Piersol, the F_1 hybrid, and St. Pierre (Table 1). There was no significant difference in egg mass index among these nematode isolates on the three tomato test lines (Table 1). Within tomato test lines, only *M. arenaria* Le-Grau-du-Roi (index of 5.0) and *M. incognita* Valbonne (index of 6.0) differed ($P = 0.01$) slightly on resistant Piersol. The *M. hapla* Angleterre isolate had an egg mass index of 5.8 on Piersol. On F_1 hybrid plants it had an intermediate egg mass index of 4.2, lower ($P = 0.01$) than naturally occurring resistance-breaking isolates and higher ($P = 0.01$) than *M. incognita* wild-type Calissane and Cote d'Ivoire isolates and the selected Cote d'Ivoire isolate (Table 1).

DISCUSSION

The results with isolates of the two *M. incognita* populations Calissane and Cote d'Ivoire, confirm other reports (4,13,15,22) that selection for parasitism on tomato plants bearing the root-knot resistance gene *Mi* can occur in some *Meloidogyne* spp. populations by repeated exposure of nematode isolates to plants with the *Mi* gene. The high reproduction of the selected *M. incognita* isolates on Piersol was similar to their reproduction (and that of their wild-type parent populations) on the susceptible genotype St. Pierre. Some studies have indicated that full compatibility is not achieved by repeated selection (4). Although we did not test the stability of the selected trait, other studies have revealed that selected parasitic ability on plants carrying the *Mi* gene is genetically stable (15,22).

Comparisons of the selected *M. incognita* isolates on the F_1 hybrid of *L. peruvianum*

TABLE 1. Reproduction (egg mass index†) of wild type and artificially selected isolates of *Meloidogyne* spp. on root-knot resistant and susceptible *Lycopersicon esculentum* cultivars and a *L. peruvianum* F_1 hybrid.

Nematode culture	F_1 hybrid <i>L. peruvianum</i> var. <i>glandulosum</i> 126443 × <i>L. peruvianum</i> 270435-3MH	<i>L. esculentum</i> cv. Piersol (+ <i>Mi</i> gene)	<i>L. esculentum</i> cv. St. Pierre (susceptible control)
<i>M. incognita</i>			
'Cote d'Ivoire'	2.2 de	4.4 d	5.0 b
Wild type	B	A	A
<i>M. incognita</i> ‡			
'Cote d'Ivoire'	2.6 d	5.6 abc	6.0 a
<i>Mi</i> - selected	B	A	A
<i>M. incognita</i>			
'Calissane'	1.2 e	1.0 e	6.0 a
Wild type	B	B	A
<i>M. incognita</i> ‡			
'Calissane'	3.2 cd	4.8 cd	5.8 ab
<i>Mi</i> - selected	B	A	A
<i>M. incognita</i>			
'Valbonne'	5.2 ab	6.0 a	5.8 ab
	A	A	A
<i>M. arenaria</i>			
'Le-Grau-du-Roi'	5.2 ab	5.0 bcd	5.6 ab
	A	A	A
<i>Meloidogyne</i> sp.			
'Senegal-VSS'	5.8 a	5.6 abc	6.0 a
	A	A	A
<i>Meloidogyne</i> sp.			
'Concarneau'	5.8 a	5.6 abc	6.0 a
	A	A	A
<i>M. hapla</i>			
'Angleterre'	4.2 bc	5.8 ab	4.7 c
	B	A	B

Values within columns followed by same lower case letter are not significantly different ($P = 0.01$) according to Duncan's multiple-range test.

Values within rows followed by same capital letter are not significantly different ($P = 0.01$) according to Duncan's multiple-range test.

† Index based on numbers of egg masses per root system: 1 = 0 egg masses, 2 = 1-3 egg masses, 3 = 4-10 egg masses, 4 = 11-30 egg masses, 5 = 31-100 egg masses, 6 = > 100 egg masses. Values are means of five replicate root systems.

‡ Isolates artificially selected for reproduction on *Mi* gene-bearing Piersol.

showed that these isolates had an incompatible interaction with the F_1 hybrid plants, even though they reproduced fully on Piersol carrying the *Mi* gene. This result is substantiated by the similar reaction of isolates of both the Calissane and Cote d'Ivoire *M. incognita* populations. These results indicate that the specificity of resistance in the hybrid, contributed by one or both of its parents, is different from that

conferred by the *Mi* gene originally derived from *L. peruvianum* PI 128657.

The F_1 hybrid parents *L. peruvianum* var. *glandulosum* 126443 and *L. peruvianum* 270435 were resistant to *M. incognita* at high temperature (32 C), unlike plants possessing the *Mi* gene (> 28–30 C) (1,6). Furthermore, both the parents of the F_1 hybrid are highly resistant to *M. hapla*, in addition to *M. arenaria*, *M. incognita*, and *M. javanica*, whereas the *Mi* gene does not confer resistance to *M. hapla* (2). Thus we have several lines of evidence for distinct resistance specificities within these wild *L. peruvianum* genotypes.

Isolates of the four naturally occurring *Mi* gene resistance-breaking populations of *M. incognita* Valbonne, *M. arenaria* Le-Grau-du-Roi, and two undesignated *Meloidogyne* spp. (Senegal-VSS and Concarneau) showed a fully compatible reaction with the F_1 hybrid, similar to that on Piersol carrying the *Mi* gene. Apparently these four populations have not been exposed to *Mi* gene selection pressure in tomato production systems, nor to the resistance in the parents of the F_1 hybrid. Ancestral forms of these nematode and plant types may or may not have been associated in the past. These results indicate that the naturally occurring resistance-breaking populations have a compatibility mechanism(s) that facilitates circumvention of resistance genes of different background in *Lycopersicon*. This mechanism differs at least in part from the compatibility mechanism selected in populations such as Calissane and Cote d'Ivoire for parasitism of *Mi* gene-bearing plants. A gene-for-gene system, as suggested for other phytoparasitic nematodes (11), could explain these compatible-incompatible combinations.

The agricultural significance of these results is twofold. We have shown that root-knot resistance that differs from the *Mi* gene is present in *Lycopersicon peruvianum*; this resistance is effective on nematode populations that might be selected for parasitism of tomato cultivars with the *Mi* gene due to repeated cropping with such cultivars (17). Currently all commercial cultivar

resistance to root-knot nematode is based on the *Mi* gene (12). We also have revealed the existence of populations of *M. arenaria*, *M. incognita*, and nondesignated *Meloidogyne* spp. that are naturally parasitic on plants possessing the new genes and on plants with the *Mi* gene; thus sources of resistance to these populations are not known in *Lycopersicon*. Other studies with *M. incognita* Valbonne and *M. arenaria* Le-Grau-du-Roi and some other populations have identified potentially useful resistance sources in other solanaceous plants such as *Solanum torvum*, *S. sisymbriifolium*, and *S. wercewiczii* (5).

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