

## Variability in Reproduction of Isolates of *Meloidogyne incognita* and *M. javanica* on Resistant Tomato Genotypes

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### ABSTRACT

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Variability in reproduction and root galling of eight isolates of *Meloidogyne incognita* and seven isolates of *M. javanica* on *Mi* gene-based resistant tomato (*Lycopersicon esculentum*) was studied in greenhouse experiments. Fresh-market cultivars Castlemart (susceptible); Valerie, Royal Flush, Jackpot, Super Fantastic, Better Boy, Cavalier, President, Carmen, and Duchess (all resistant); and processing tomato cultivars and advanced lines UC82 (susceptible) and VFN8, GS27, Hy9889, XPH671, CX8202, MOX3076, and MOX3078 (all resistant) were tested. The *M. incognita* isolates did not vary in pathogenicity. The resistant tomatoes, except Valerie, were highly resistant to *M. incognita*, supporting egg production in most combinations at less than 2% of that on susceptible controls. Valerie was a mixture of fully susceptible and highly resistant individual plants, indicating segregation for resistance in this cultivar. Five *M. javanica* isolates also reproduced on resistant tomatoes, except Valerie, at less than 2% of their reproduction on susceptible controls; some of these isolates reproduced more on CX8202 and MOX3078 than on other resistant tomatoes. However, two additional *M. javanica* isolates reproduced more than the other isolates on resistant cultivars and lines; their egg production varied significantly ( $P \leq 0.05$ ) with cultivar from low (highly resistant) to intermediate (moderately resistant) compared with that on susceptible controls for each isolate. No resistant tomato cultivar or line was immune to any nematode isolate.

Additional key words: root-knot nematodes

The *Mi* gene resistance in tomato (*Lycopersicon esculentum* (L.) Mill.) derived from *L. peruvianum* (L.) Mill. (15) is the only source of resistance to

root-knot nematodes in currently available fresh-market and processing tomato cultivars (5). *Mi* gene resistance is composed of two or more closely linked dominant genes (13), although the number and the nature of genes involved is not yet clearly defined. This gene(s) confers resistance to *Meloidogyne incognita* (Kofoid & White) Chitwood, *M. javanica* (Treub) Chitwood, and *M. arenaria* (Neal) Chitwood but not to *M.*

*hapla* Chitwood (1,3).

Variability in reproduction of different populations of *M. incognita*, *M. javanica*, and *M. arenaria* has been demonstrated on different tomato cultivars and under different experimental conditions (1,3,6-8,14,17). The nature of this variability can be expressed as full susceptibility to a certain *Meloidogyne* population in one or more tomato cultivars that are resistant to other *Meloidogyne* populations of the same or other species (6,8,14,17). It can also be expressed as partial resistance in an otherwise highly resistant cultivar that allows some reproduction of a variant *Meloidogyne* isolate (1,3,7). These resistance-breaking populations of *Meloidogyne* spp. may occur naturally, apparently without previous exposure to or selection by tomatoes with *Mi* gene resistance (8). They may also result from selection after repeated exposure to plants with *Mi* gene resistance under greenhouse or field conditions (7,9).

Because of this complex pattern of interactions between host resistance and nematode virulence, the successful development of new resistant cultivars and their implementation for managing field infestations of root-knot should include assessment of virulence of nematode populations present in a

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growing region (10). In many tomato-breeding programs, the testing of root-knot nematode resistance is made with only one *Meloidogyne* population. Because of the recent availability of root-knot-resistant processing tomato cultivars for machine harvest in California and the wide-scale use of some little-tested fresh-market tomato cultivars, selected resistant cultivars and lines from several breeding programs were screened against isolates of a diverse collection of populations of *M. incognita* and *M. javanica*. Field testing of several processing tomato cultivars on five *M. incognita*-infested sites in California revealed highly resistant interactions (11).

## MATERIALS AND METHODS

**Seed sources.** Seed of cultivars and lines used in this study were obtained from Asgrow Seed Co., San Juan Bautista, CA (XPH671); Ball Seed Co., West Chicago, IL (Better Boy and Super Fantastic); Campbell Soup Co., Davis, CA (CX8202); A. L. Castle Inc., Morgan Hill, CA (Castlemart and UC82); Ferry-Morse Seed Co., Mountain View, CA (Jackpot and Royal Flush); Goldsmith

Seeds Inc., Gilroy, CA (GS27 and Valerie); Moran Seeds Inc., Salinas, CA (MOX3076 and MOX3078); and Peto Seed Co., Inc., Saticoy, CA (Carmen, Cavalier, Duchess, President, VFN8, and Hy9889).

**Nematode isolates.** Original sources of the isolates of *M. incognita* and *M. javanica* are given in Table 1. Isolates were cultured from single egg masses on greenhouse-grown plants of susceptible tomato cultivars Rutgers or Tropic in 4-L plastic pots containing steam-sterilized (full steam for 1 hr at 100 C) loamy sand. Isolates were identified morphologically and by the North Carolina differential host test (12).

**Test procedures.** All tests were conducted in the greenhouse. Tomato seedlings (1 mo old) showing vigorous growth were used in these tests. Plants were grown singly in 600-cm<sup>3</sup> pots (Western Pulp Products Co., Corvallis, OR) containing the steam-sterilized loamy sand. Initially, the young plants were irrigated with Hoagland's solution. Subsequently, they were fertilized with Osmocote (Sierra Chemical Co., Milpitas, CA) (18:12:16 NPK).

Inocula were prepared by the method of Hussey and Barker (4). A suspension of 10,000 eggs in 5 cm<sup>3</sup> of water was pipetted into the root zone via three holes around the plant in each pot.

During the experiments, treatments were arranged in a randomized complete block design and replicated five times on benches with temperature-regulated bases that maintained pot soil at 26–27 C. Two months after inoculation, roots were gently washed free of soil, damp-dried and weighed, and assessed for root galling. Root systems were then stored in 5% formalin until they were assessed for egg content per gram (fresh weight) of root.

The galling index (GI) was determined as follows: 0 = no galls, 1 = 1–24% of the roots galled, 2 = 25–49%, 3 = 50–74%, and 4 = 75–100% of roots galled. Recovery of eggs from the total root system was done by a modification of the method of Hussey and Barker (4). The index of resistance (IR) (3) was calculated from the numbers of eggs per gram of fresh root of a nematode isolate produced on a test cultivar or line expressed as a percentage of those produced on the standard susceptible cultivar Castlemart (for fresh-market tomatoes) or UC82 (for processing tomatoes). The numbers of eggs per gram of fresh root produced by each isolate on Castlemart and UC82, from which IR values were calculated, are summarized as means of five replicates in Table 1.

## RESULTS

All isolates of *M. incognita* and *M. javanica* reproduced well (final egg numbers [P<sub>r</sub>]; initial egg numbers [P<sub>i</sub>] > 1) on the standard susceptible cultivars Castlemart and UC82 (Table 1). Some isolates reproduced relatively less well, notably *M. incognita* MI-8 and *M. javanica* MJ-5; however, the reproduction of these two isolates was still at a level considered a susceptible response (P<sub>r</sub>:P<sub>i</sub> > 1).

The GI was generally complementary to the IR in distinguishing resistant from susceptible reactions to both *M. incognita* and *M. javanica*. The GI of the susceptible checks was significantly

**Table 1.** *Meloidogyne incognita* and *M. javanica* isolates and their egg production on susceptible cultivars Castlemart and UC82

Isolate	Race	Origin	Mean eggs per gram of fresh root <sup>a</sup>	
			Castlemart	UC82
<i>M. incognita</i>				
MI-1	1 <sup>b</sup>	Fig (Riverside, CA, 1955)	13,571	20,185
MI-2	1	Peach (Tustin, CA, 1966)	43,478	40,958
MI-3	1	Fig (Riverside, CA, 1982)	19,093	10,403
MI-4	3	Cotton (Tulare, CA, 1981)	75,172	110,229
MI-5	2	Tomato (North Carolina State University Collection, 1980)	16,573	8,301
MI-6	1	Mulberry (Riverside, CA, 1982)	16,527	22,178
MI-7	1	Squash (Riverside, CA, 1982)	23,850	16,535
MI-8	2	Grapevine (Thermal, CA, 1982)	8,571	7,517
<i>M. javanica</i>				
MJ-1	...	Cowpea (Chino, CA, 1954)	91,446	86,527
MJ-2	...	Sweet Orange (Indio, CA, 1973)	39,072	28,008
MJ-3	...	Date Palm (Indio, CA, 1973)	50,427	47,374
MJ-4	...	Okra (Mecca, CA, 1982)	12,904	8,496
MJ-5	...	Grapevine (Coachella, CA, 1982)	3,904	6,273
MJ-6	...	Grapevine (Dinuba, CA, 1982)	24,062	20,766
MJ-7	...	Watermelon (Mecca, CA, 1982)	44,495	57,670

<sup>a</sup> Values for susceptible checks represent index of resistance scores of 100 against which resistant tomato cultivars and lines are ranked in Tables 2–5.

<sup>b</sup> *M. incognita* race designations based on North Carolina differential host test (12).

**Table 2.** Relative resistance (IR) and root galling (GI) indices of eight isolates of *Meloidogyne incognita* on selected fresh-market tomato cultivars<sup>w</sup>

Cultivar	Isolate															
	MI-1		MI-2		MI-3		MI-4		MI-5		MI-6		MI-7		MI-8	
	IR <sup>x</sup>	GI <sup>y</sup>	IR	GI	IR	GI	IR	GI	IR	GI	IR	GI	IR	GI	IR	GI
Castlemart	100.0 a <sup>r</sup>	4.0 a	100.0 a	4.0 a	100.0 a	3.4 a	100.0 a	4.0 a	100.0 a	3.4 a	100.0 a	4.0 a	100.0 a	4.0 a	100.0 a	2.2 a
Valerie	62.9 a	2.2 b	32.4 b	1.6 b	87.2 a	3.2 a	55.6 b	1.8 b	54.5 b	1.4 b	80.8 a	2.8 b	32.5 a	2.0 b	30.4 b	1.0 b
Royal Flush	1.9 b	1.0 c	1.2 b	1.0 b	1.2 b	0.2 b	2.5 c	1.0 bc	0.1 c	0.0 c	0.7 b	0.2 c	0.3 a	0.4 c	2.9 c	0.2 bc
Jackpot	1.5 b	0.8 c	0.6 b	1.0 b	1.8 b	0.2 b	2.5 c	0.4 c	0.7 c	0.2 c	0.6 b	0.2 c	0.7 a	0.2 c	0.4 c	0.0 c
Super Fantastic	0.9 b	0.8 c	0.7 b	1.0 b	0.4 b	0.6 b	1.3 c	0.0 c	0.3 c	0.0 c	0.4 b	0.0 c	0.1 a	0.2 c	0.5 c	0.0 c
Better Boy	1.2 b	0.8 c	1.1 b	1.0 b	0.5 b	0.5 b	2.1 c	0.4 c	0.1 c	0.0 c	0.3 b	0.2 c	0.1 a	0.4 c	0.8 c	0.4 bc
Cavalier	2.0 b	0.8 c	1.3 b	1.0 b	5.1 b	1.0 b	1.0 c	0.4 c	0.2 c	0.0 c	0.2 b	0.2 c	0.4 a	0.0 c	0.8 c	0.4 bc
President	0.6 b	0.8c	1.3 b	1.0 b	1.0 b	0.8 b	1.9 c	0.4 c	0.3 c	0.6 c	0.7 b	0.4 c	0.3 a	0.2 c	0.3 c	0.2 bc
Carmen	1.8 b	1.0 c	0.5 b	1.0 b	0.5 b	0.2 b	1.0 c	0.2 c	0.2 c	0.0 c	0.7 b	0.0 c	0.3 a	0.8 c	0.1 c	0.2 bc
Duchess	2.1 b	0.8 c	0.8 b	1.0 b	1.8 b	0.8 b	1.3 c	0.6 c	0.5 c	0.2 c	1.2 b	0.2 c	121.6 a	0.6 c	13.7 bc	0.8 bc

<sup>w</sup> Values are means of five replicates.

<sup>x</sup> IR (index of resistance): eggs per gram of fresh root produced on a resistant cultivar expressed as a percentage of those produced on susceptible cultivar Castlemart.

<sup>y</sup> GI (galling index): 0 = no galls, 1 = 1–24%, 2 = 25–49%, 3 = 50–74%, and 4 = 75–100% of roots galled.

<sup>r</sup> Values within a column followed by the same letter are not significantly different ( $P \leq 0.05$ ) according to Duncan's multiple range test.

higher than that of resistant tomatoes in all isolate × tomato combinations, except for some isolates on Valerie (Tables 2–5).

Most resistant reactions produced at least a trace of galling (GI > 0) on roots, but in some test combinations, no galling was found on any of the five root systems (GI = 0). However, in all test combinations including those with no galling, some egg production was detected. An absence of root galling, though indicative of a resistance reaction, cannot be interpreted as evidence of immunity because these roots still allowed some egg production. Immunity, defined as a complete lack of nematode reproduction, was not found in any isolate × tomato combinations.

**Reactions to *M. incognita* isolates.** Each of the eight isolates of *M. incognita*

developed poorly on the highly resistant fresh-market tomatoes Royal Flush, Jackpot, Super Fantastic, Better Boy, Cavalier, President, and Carmen, represented by significantly reduced ( $P \leq 0.05$ ) IR values that ranged from 0.1 to 5.1 and mostly less than 2.0 (Table 2). These results show a lack of variability in egg production of the *M. incognita* isolates on these resistant tomatoes. Six *M. incognita* isolates reproduced poorly on Duchess; however, isolates MI-7 and MI-8 reproduced well (IR = 121.6) and moderately well (IR = 13.7), respectively, on this cultivar. On Valerie, IR values for the eight *M. incognita* isolates were intermediate (IR = 30.4–87.2) (Table 2).

Low IR values (<0.1–1.5) for the eight *M. incognita* isolates were recorded on all

processing tomato advanced lines and cultivars (Table 3), except isolate MI-5 on MOX3078 (IR = 4.8), MI-6 on CX8202 (IR = 21.6), and MI-8 on CX8202 (IR = 39.7). These intermediate IR values were each significantly less than that on susceptible UC82. The GI ratings overall were complementary to the IR values, being mostly less than GI = 1.0 for resistant reactions (Table 3).

**Reactions to *M. javanica* isolates.** The IR values of *M. javanica* isolates on fresh-market tomato cultivars were more variable than those of *M. incognita* (Table 4). On Royal Flush, Jackpot, Super Fantastic, Better Boy, Cavalier, President, Carmen, and Duchess, low IR values (0.1–0.7) were recorded for isolates MJ-2, MJ-3, MJ-4, MJ-5, and MJ-7. The

**Table 3.** Relative resistance (IR) and root galling (GI) indices of eight isolates of *Meloidogyne incognita* on selected processing tomato advanced lines and cultivars<sup>1</sup>

Cultivar	Isolate															
	MI-1		MI-2		MI-3		MI-4		MI-5		MI-6		MI-7		MI-8	
	IR <sup>w</sup>	GI <sup>x</sup>	IR	GI	IR	GI	IR	GI	IR	GI	IR	GI	IR	GI	IR	GI
UC82	100.0 a <sup>y</sup>	4.0 a	100.0 a	4.0 a	100.0 a	3.0 a	100.0 a	3.6 a	100.0 a	2.4 a	100.0 a	4.0 a	100.0 a	4.0 a	100.0 a	2.0 a
VFN8	0.6 b	0.6 bc	0.2 c	1.0 b	1.5 b	0.4 b	0.9 b	0.2 b	0.6 c	0.0 c	0.1 c	0.0 c	0.1 b	0.4 b	1.2 b	0.4 bc
GS27	0.8 b	1.0 b	0.9 b	1.0 b	1.4 b	0.4 b	1.0 b	0.2 b	0.3 c	0.2 bc	0.9 c	0.0 c	0.7 b	0.4 b	2.2 b	0.4 bc
Hy9889	0.2 b	0.8 b	0.5 b	1.0 b	1.1 b	0.6 b	0.5 b	0.2 b	0.2 c	0.0 c	0.3 c	0.5 c	0.2 b	0.3 b	0.3 b	0.0 c
XPH671	0.2 b	0.2 c	0.2 c	0.8 b	1.5 b	0.4 b	0.3 b	0.0 b	0.3 c	0.2 bc	0.4 c	0.2 c	0.3 b	0.2 b	1.3 b	0.0 c
CX8202	NT <sup>z</sup>	NT	0.1 c	0.2 c	0.3 b	0.0 b	1.0 b	0.4 b	0.6 c	0.8 b	21.6 b	1.6 b	0.6 b	0.0 b	39.7 b	1.0 b
MOX3076	NT	NT	<0.1 c	0.0 c	<0.1 b	0.0 b	0.3 b	0.0 b	0.2 c	0.2 bc	0.1 c	0.0 c	0.3 b	0.0 b	0.4 b	0.0 c
MOX3078	NT	NT	<0.1 c	0.0 c	0.5 b	0.2 b	0.7 b	0.4 b	4.8 b	0.4 bc	0.4 c	0.0 c	0.9 b	0.0 b	1.0 b	0.0 c

<sup>w</sup> Values are means of five replicates.

<sup>x</sup> IR (index of resistance): eggs per gram of fresh root produced on a resistant line or cultivar expressed as a percentage of those produced on susceptible cultivar UC82.

<sup>y</sup> GI (galling index): 0 = no galls, 1 = 1–24%, 2 = 25–49%, 3 = 50–74%, and 4 = 75–100% of roots galled.

<sup>z</sup> Values within a column followed by the same letter are not significantly different ( $P \leq 0.05$ ) according to Duncan's multiple range test.

<sup>z</sup> Not tested.

**Table 4.** Relative resistance (IR) and root galling (GI) indices of seven isolates of *Meloidogyne javanica* on selected fresh-market tomato cultivars<sup>1</sup>

Cultivar	Isolate													
	MJ-1		MJ-2		MJ-3		MJ-4		MJ-5		MJ-6		MJ-7	
	IR <sup>x</sup>	GI <sup>y</sup>	IR	GI	IR	GI	IR	GI	IR	GI	IR	GI	IR	GI
Castlemart	100.0 a <sup>z</sup>	4.0 a	100.0 a	3.0 a	100.0 a	2.6 a	100.0 a	3.2 a	100.0 a	2.2 a	100.0 a	4.0 a	100.0 a	3.8 a
Valerie	23.1 b	1.6 b	35.8 b	1.8 b	18.3 b	1.6 b	143.0 a	2.3 b	117.9 a	1.0 b	101.3 a	3.0 b	58.0 b	1.4 b
Royal Flush	16.6 bc	1.0 b	0.4 c	0.6 c	0.1 c	0.4 c	0.2 b	0.2 c	0.2 a	0.0 c	12.5 b	1.4 c	0.9 c	0.4 bc
Jackpot	15.6 bc	1.2 b	0.2 c	0.0 c	0.1 c	0.4 c	0.1 b	0.2 c	0.3 a	0.0 c	31.4 b	1.4 c	0.7 c	0.2 c
Super Fantastic	10.1 c	1.2 b	0.3 c	0.2 c	0.1 c	0.2 c	0.1 b	0.0 c	0.3 a	0.2 bc	12.8 b	1.0 c	0.2 c	0.6 bc
Better Boy	17.5 bc	1.2 b	0.4 c	0.2 c	0.1 c	0.0 c	0.2 b	0.0 c	0.2 a	0.2 bc	10.7 b	1.0 c	1.1 c	0.4 bc
Cavalier	15.0 bc	1.4 b	0.4 c	0.2 c	0.1 c	0.6 c	0.1 b	0.2 c	59.7 a	0.4 bc	15.7 b	1.2 c	0.7 c	0.4 bc
President	15.8 bc	1.4 b	0.7 c	0.6 c	0.3 c	0.6 c	0.3 b	0.6 c	0.6 a	0.2 bc	26.1 b	1.6 c	1.5 c	0.6 bc
Carmen	18.0 bc	1.2 b	0.4 c	0.6 c	0.1 c	0.2 c	0.5 b	0.6 c	0.6 a	0.0 c	8.4 b	1.0 c	1.7 c	0.2 c
Duchess	16.3 bc	1.4 b	0.5 c	0.6 c	0.3 c	0.6 c	0.2 b	0.0 c	1.2 a	0.0 c	18.2 b	1.0 c	1.3 c	0.8 bc

<sup>w</sup> Values are means of five replicates.

<sup>x</sup> IR (index of resistance): eggs per gram of fresh root produced on a resistant cultivar expressed as a percentage of those produced on susceptible cultivar Castlemart.

<sup>y</sup> GI (galling index): 0 = no galls, 1 = 1–24%, 2 = 25–49%, 3 = 50–74%, and 4 = 75–100% of roots galled.

<sup>z</sup> Values within a column followed by the same letter are not significantly different ( $P \leq 0.05$ ) according to Duncan's multiple range test.

**Table 5.** Relative resistance (IR) and root galling (GI) indices of seven isolates of *Meloidogyne javanica* on selected processing tomato advanced lines and cultivars<sup>1</sup>

Cultivar	Isolate													
	MJ-1		MJ-2		MJ-3		MJ-4		MJ-5		MJ-6		MJ-7	
	IR <sup>w</sup>	GI <sup>x</sup>	IR	GI	IR	GI	IR	GI	IR	GI	IR	GI	IR	GI
UC82	100.0 a <sup>y</sup>	3.8 a	100.0 a	3.0 a	100.0 a	2.4 a	100.0 a	3.0 a	100.0 a	2.6 a	100.0 a	4.0 a	100.0 a	3.4 a
VFN8	7.2 c	1.0 b	0.4 b	0.0 b	0.1 c	0.0 c	0.1 b	0.0 b	0.1 b	0.2 b	8.6 c	1.6 b	<0.1 c	0.0 b
GS27	24.2 b	1.2 b	0.4 b	0.2 b	0.2 c	0.4 bc	0.2 b	0.0 b	0.2 b	0.0 b	15.1 bc	1.2 b	0.8 bc	0.2 b
Hy9889	23.8 b	1.0 b	0.3 b	0.4 b	0.2 c	0.2 c	0.2 b	0.0 b	0.1 b	0.4 b	37.8 b	1.2 b	0.6 bc	0.4 b
XPH671	5.3 c	1.0 b	0.2 b	0.0 b	0.1 c	0.2 c	0.2 b	0.2 b	0.1 b	0.2 b	12.3 bc	1.2 b	0.3 bc	0.0 b
CX8202	NT <sup>z</sup>	NT	23.1 b	0.6 b	34.6 b	1.4 b	6.0 b	0.6 b	43.8 b	0.6 b	7.7 c	1.4 b	0.1 bc	0.2 b
MOX3076	NT	NT	0.6 b	0.4 b	0.6 c	0.2 c	0.1 b	0.0 b	0.1 b	0.0 b	3.8 c	1.2 b	0.2 bc	0.0 b
MOX3078	NT	NT	1.2 b	0.4 b	1.9 c	0.4 bc	0.1 b	0.0 b	21.1 b	0.6 b	28.9 bc	1.2 b	1.0 b	0.2 b

<sup>w</sup> Values are means of five replicates.

<sup>x</sup> IR (index of resistance): eggs per gram of fresh root produced on a resistant line or cultivar expressed as a percentage of those produced on susceptible cultivar UC82.

<sup>y</sup> GI (galling index): 0 = no galls, 1 = 1–24%, 2 = 25–49%, 3 = 50–74%, and 4 = 75–100% of roots galled.

<sup>z</sup> Values within a column followed by the same letter are not significantly different ( $P \leq 0.05$ ) according to Duncan's multiple range test.

<sup>z</sup> Not tested.

one exception was the intermediate reaction of isolate MJ-5 on Cavalier (IR = 59.7). These five isolates each showed an intermediate IR value on Valerie (Table 4).

The *M. javanica* isolates MJ-1 and MJ-6 reproduced more on each of the resistant fresh-market cultivars than did the above-mentioned five isolates with IR values ranging from 8.4 to 31.4. However, these were all significantly less than on susceptible Castlemart (Table 4).

The IR values of *M. javanica* isolates on processing tomato advanced lines and cultivars showed a similar pattern to their reactions on fresh-market tomatoes (Table 5). Isolates MJ-2, MJ-3, MJ-4, MJ-5, and MJ-7 produced very low IR values on most resistant tomatoes, except MJ-2, MJ-3, MJ-4, and MJ-5 on CX8202 and MJ-5 on MOX3078.

Isolates MJ-1 and MJ-6 produced IR values on resistant tomatoes all significantly ( $P \leq 0.05$ ) lower than that produced on susceptible UC82 but provided significant ( $P \leq 0.05$ ) ranges in IR values depending upon the tomato line or cultivar. For example, isolates MJ-1 and MJ-6 had lower IR values on VFN8 and XPH671 than on GS27 and Hy9889, and isolate MJ-6 had a lower IR value on MOX3076 than on MOX3078. Summarizing by tomato line or cultivar, GS27, Hy9889, and MOX3078 allowed more reproduction of these two *M. javanica* isolates than VFN8, XPH671, CX8202, and MOX3076, whereas CX8202 allowed more reproduction than other tomatoes of *M. javanica* isolates MJ-2, MJ-3, MJ-4, and MJ-5 but not MJ-7 (Table 5).

## DISCUSSION

Our results confirm other reports that the *Mi* gene resistance in different tomato genotypes does not confer immunity to *M. incognita* and *M. javanica* (1,3). However, various levels of resistance were found in the nematode isolate  $\times$  cultivar combinations. With few exceptions, the eight *M. incognita* isolates reproduced equally poorly on all resistant tomato cultivars. These reactions can be considered highly resistant. The few exceptions from a highly resistant reaction were intermediate or partially resistant reactions but not full susceptibility. The consistent intermediate IR values of isolates on Valerie are due to a mixture of highly resistant and fully susceptible individual plants inoculated with each isolate, indicating the presence of genetic segregants for resistance in this cultivar.

The *M. incognita* isolates were collected from differing geographical and host backgrounds, but as far as is known, they were not exposed previously to *Mi* gene resistance. Thus, lack of ability to circumvent *Mi* gene resistance might be expected. Five *M. incognita* populations tested under field conditions in various

California locations also generally failed to reproduce significantly on processing tomato lines and cultivars (11). Greenhouse tests on about 40 resistant tomato genotypes including Better Boy and VFN8 also failed to differentiate populations representing the four host races of *M. incognita* (3). However, Viglierchio (17) compared galling reactions of 10 *M. incognita* isolates from California on VFN8 and LA1221 and found two isolates that induced a fully susceptible reaction, and a resistance-breaking or B-race of *M. incognita* on tomato was reported from West Africa (6).

The overall lack of ability in *M. incognita* populations to develop on resistant tomatoes in these greenhouse tests and in our field tests (11) provides confidence in the potential use of resistant processing tomato cultivars for managing *M. incognita* field infestations. However, the few reports of ability in *M. incognita* to circumvent *Mi* gene resistance do suggest that resistance-breaking populations could be encountered.

Variability in reproduction of *M. javanica* was found on resistant tomatoes. Five isolates generally reproduced poorly, similar to *M. incognita* isolates, whereas two isolates (MJ-1 and MJ-6) reproduced at a moderate level on many resistant cultivars. Isolate MJ-1 was previously shown to reproduce to some extent on other resistant *Lycopersicon* spp. accessions and cultivars (1) and also on resistant lines of cowpea (*Vigna unguiculata* L. (Walp.)) (16) and lima bean (*Phaseolus lunatus* L.) (1. J. Thomason, *personal observation*), whereas MJ-6 was previously untested.

Reactions of tomato cultivars to a more virulent isolate of *M. javanica* differed significantly ( $P \leq 0.05$ ), ranging from highly resistant (e.g., MJ-1 on VFN8 and XPH671; IR = 7.2 and 5.3, respectively) to moderately resistant (e.g., MJ-1 on GS27 and Hy9889; IR = 24.2 and 23.8, respectively) (Table 5). A population of *M. javanica* from India differentiated resistant VFN8 and VFN368 as fully susceptible while failing to develop significantly on another eight resistant tomatoes in the same experiment (14). This variation between lines and cultivars could result in part from the existence in different genotypes of different resistance genes (13) from the *Mi* gene base. However, differentiation of *Meloidogyne* populations on tomato lines bearing these different *Mi* resistance genes has not been demonstrated. The range of egg production levels suggests that other genetic modifying factors may be involved that are determined by the genotype into which the *Mi* gene resistance is incorporated. Fassuliotis (2) suggested that modifying genetic factors derived from the *L. esculentum*-susceptible parent increased the expression of resistance of the *Mi* gene in the offspring compared with the original *L.*

*peruvianum*-resistant parent.

The existence of *M. javanica* populations that show limited reproduction on different resistant tomato cultivars emphasizes the need for preliminary field testing of cultivars on infested fields before use in large-scale plantings. Nevertheless, our results suggest that the newly developed machine-harvested processing tomato cultivars will have a wide application in the management of field populations of *M. incognita* and *M. javanica* and that preferred fresh-market tomato cultivars with good root-knot resistance are available.

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