Resistance of Tomato, Bean, Southern Pea, and Garden Pea Cultivars to Root-Knot Nematodes Based on Host Suitability

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ABSTRACT

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Tomato, common bean, lima bean, southern pea, and garden pea were evaluated for resistance to species and races of root-knot nematodes (*Meloidogyne* spp.). Many of the tomato cultivars tested were highly or very resistant to certain species and races, but none was immune. All tomato cultivars were susceptible to *M. hapla*. Resistance of Anahu, Atkinson, Healani, Nemared, Patriot, Rossol, and VFN-8 to *M. incognita* and *M. javanica* was confirmed. Beef Master, Manalucie, Marmande, Money Maker, Ponderosa, and Roma—previously reported to be resistant—were susceptible in our tests. Tomato cultivars Better Boy, 662 VFN, Monte Carlo, Marmar, Royal Chico, and Rutgers ranged in susceptibility from highly resistant to susceptible based on egg mass indices. They were studied to determine final population, index of reproduction, and egg mass indexes. *M. incognita* race 4 was more aggressive than races 1, 2, and 3 when Oostenbrink's reproductive factor was used. Penetration of *M. incognita* race 1 into tomato roots increased with increasing degree of susceptibility. Bean and southern pea differed in susceptibility to species and races of *Meloidogyne*. *M. incognita* race 4 was least aggressive on bean and lima bean. Southern pea varied in resistance to races 1, 2, and 3 of *M. incognita*. All cultivars of southern pea were either highly or very resistant to race 4.

Root-knot nematodes (*Meloidogyne* Goeldi) are of economic importance in temperate (3), subtropical and Mediterranean (10), and tropical climates (15). One of the most effective, economical, and environmentally safe ways to minimize losses from diseases caused by nematodes is to use nematode-resistant plant cultivars. More than 235 cultivars have resistance to one or more *Meloidogyne* species (2). A summary of crop cultivars resistant to root-knot nematodes has been complied from published reports or from individuals through personal communications (17).

A worldwide survey of root-knot nematode species in agricultural soils (conducted in the International *Meloidogyne* Project) demonstrated the widespread existence of four races of *M. incognita* (Kofoid & White) Chitwood and two races of *M. arenaria* (Neal) Chitwood (15). These races are distinguishable by use of the North Carolina differential host test (14).

The approximate distribution of *Meloidogyne* species in agricultural soils of the world is *M. incognita*, 52%; *M. javanica* (Treub) Chitwood, 31%; *M. arenaria*, 8%; *M. hapla* Chitwood, 7%; and other species, about 2% (Sasser, *unpublished*). Host response data (16) indicate that populations of a given species or race from widely separated regions behave similarly on the differential hosts. This suggests that resistance identified in one region against a particular species would probably also be resistant to the same species in another region. These host genes could then be used to develop horticulturally adapted cultivars suitable for the region.

The objectives of our research included a reevaluation of resistance reported in selected cultivars using known species and races of *Meloidogyne*, an evaluation of other cultivars for resistance, and a study of the relationship of penetration and development of the nematode in cultivars of varying degrees of resistance.

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MATERIALS AND METHODS

Host and inoculum culture. Populations of *M. incognita* host races 1, 2, 3, and 4; *M. arenaria* host races 1 and 2; *M. javanica;* and *M. hapla* were maintained in the greenhouse on tomato (*Lycopersicon esculentum* Mill. 'Rutgers'). Fifty cultivars of tomato, seven of common bean (*Phaseolus vuglaris* L.), two of southern pea (*Vigna unguiculata* (L.) Walp.), and one cultivar each of garden pea (*Pisum sativum* L.) and lima bean (*Phaseolus limensis* Macf.) were evaluated. All plants were grown in a steam-sterilized mixture of fine sandy loam soil and river sand (1:1, v/v).

Seeds of all cultivars except tomato were planted singly into 4-cm-diameter clay pots. Tomatoes were germinated in seedling flats containing steam-sterilized peat moss and transplanted to 4-cm-diameter clay pots at the one- to two-true-leaf stage. A solution of VHPF (Miller Chemical and Fertilizer Corp., Hanover, PA) supplemented with 1.2×10^{-3} mM of potassium nitrate, 1.9×10^{-3} mM of magnesium sulfate, and 1.6×10^{-5} mM of boric acid was supplied as needed to each plant.

Inoculum in all experiments was eggs collected from tomato roots (5) or second-stage juveniles collected by a modified Baermann funnel technique. Each plant was transferred intact to an 11-cm-diameter clay pot and inoculated with a suspension of a known concentration of eggs or juveniles by applying inoculum uniformly over the root mass with an Oxford pipette. Pots were then filled with the soil mix, watered lightly, and arranged on greenhouse benches in a completely randomized design.

Host suitability. Plants were inoculated with 2,500 eggs per pot. Tomato cultivar Rutgers was also inoculated in the same manner, as a check of inoculum viability. The plants were grown in greenhouses with average minimum and maximum temperatures of 22 and 30 C for *M. incognita, M. arenaria,* and *M. javanica* and 21 and 23 C for *M. hapla.* Each treatment was replicated four times. After 55 days, plants were removed from the pots and the root systems were gently washed free of soil and stained with Phloxine B (0.15 g/L of tap water) for 15 min. The egg mass index (EI) was calculated as follows: 0 = no egg masses, 1 = 1–2 egg masses, 2 = 3–10, 3 = 11–30, 4 = 31–100, and 5 = more than 100 egg masses.

Nematode survival and reproduction. Six tomato cultivars—Better Boy, 662 VFN, Monte Carlo, Marmar, Royal Chico, and Rutgers—were used in this test. Plants of each cultivar were inoculated with 500 freshly hatched, second-stage juveniles of the species and races of *Meloidogyne* and maintained in the greenhouse at average temperatures of 26 C for *M. incognita, M. javanica,* and *M. arenaria* and 22 C for *M. hapla.* Each treatment was replicated six times. After 55 days, we determined final population (Pf), expressed as the total number of eggs and larvae recovered from the roots and soil; index of reproduction (IR), defined as the Pf on the resistant cultivar expressed as a percentage of the Pf on the susceptible cultivar (23); and EI, calculated as in the host suitability studies.

Although we were measuring host suitability of these cultivars to the various species and races of *Meloidogyne* (rather than resistance in the classical sense), we decided to utilize Taylor's (21) resistance designations to quantify this suitability. For example, the designation S (susceptible) was used for plants in which reproduction was more than 50% on the susceptible cultivar Rutgers, where reproduction is considered normal (100%); SR (slightly resistant), for plants in which reproduction was 25–50%; MR (moderately resistant), when reproduction was 10–25%; VR (very resistant), when reproduction was 1–10%; HR (highly resistant), when reproduction was less than 1%; and IM (immune), plants in which the nematodes entered the roots but did not reproduce or were killed.

Final population densities of juveniles in the soil were determined by processing a 100-cm^3 subsample from each pot by a combination of elutriation (1) and centrifugal flotation (8). Eggs were extracted from the roots by a combination of maceration and sodium hypochlorite (NaOCl) (5). Each root system was washed free of soil, cut into 1-cm pieces, and comminuted in a Waring Blendor with about 200 ml of 0.5% NaOCl solution for 10–20 sec. The solution and roots were decanted into a 500-ml container and shaken for 2.5 min. The suspension was then poured through a 75-mm sieve nested on a 26-mm sieve. Eggs on the 26-mm sieve were washed free of NaOCl and counted.

Based on the range of actual EI values and the corresponding DR designations for the six cultivars, the following scale was established for use in estimating degree of resistance (DR) values for those cultivars in which Pf and IR values were not determined: EI range of 0.0–1.0 = HR; 1.10–3.00 = VR; 3.10–3.50 = MR;

Table 1. Egg mass indexes (EI) and degree of resistance (DR) designations of selected cultivars to the species and races of *Meloidogyne*[x]

	M. incognita								*M. arenaria*							
	Race 1		Race 2		Race 3		Race 4		Race 1		Race 2		*M. javanica*		*M. hapla*	
Cultivar	EI[y]	DR[z]	EI	DR	EI	DR	EI	DR	EI	DR	EI	DR	EI	DR	EI	DR
					Tomato											
Ace Hy	4.7	S	5.0	S	4.0	SR	5.0	S	4.7	S	4.5	S	4.2	S	5.0	S
AMEX-VFN	1.7	VR	1.2	VR	1.5	VR	3.0	VR	3.5	MR	3.2	MR	3.0	VR	5.0	S
Anahu	0.5	HR	0.7	HR	1.0	HR	2.2	VR	0.2	HR	0.2	HR	1.0	HR	3.7	SR
Atkinson	0.5	HR	0.2	HR	0.7	HR	3.2	MR	0.5	HR	1.5	VR	0.5	HR	5.0	S
Auburn 76	1.0	HR	1.0	HR	0.7	HR	1.7	VR	1.2	VR	2.2	VR	2.2	VR	4.2	S
Beef Eater VFN	3.5	MR	3.0	VR	4.0	SR	3.7	SR	4.0	SR	3.5	MR	4.2	S	4.0	SR
Beef Master	4.5	S	5.0	S	4.7	S	5.0	S	4.7	S	5.0	S	4.7	S	5.0	S
Better Boy	0.0	HR	0.2	HR	0.5	HR	2.2	VR	0.0	HR	0.2	HR	1.0	HR	4.5	S
Big Set	0.5	HR	0.2	HR	1.5	VR	3.5	MR	1.5	VR	1.5	VR	0.7	HR	4.5	S
Bonus VFN	0.5	HR	0.2	HR	1.2	VR	3.2	MR	0.2	HR	2.0	VR	1.7	VR	4.7	S
BWN-21	1.0	HR	1.0	HR	2.0	VR	3.0	VR	1.7	VR	1.7	VR	2.5	VR	3.5	MR
Fengshan Manuli	2.7	VR	2.5	VR	3.0	VR	3.5	MR	4.5	S	4.7	S	3.2	MR	5.0	S
Healani	1.2	VR	1.2	VR	1.0	HR	3.5	MR	0.2	HR	0.5	HR	2.7	VR	3.7	SR
Hope 1	2.0	VR	1.5	VR	1.7	VR	3.5	MR	4.0	SR	4.0	SR	3.0	VR	4.0	SR
718 K. Goko	3.0	VR	3.0	VR	2.5	VR	3.7	SR	1.7	VR	2.0	VR	2.5	VR	4.2	S
LAR 2	4.0	SR	4.0	SR	4.5	S	4.5	S	4.5	S	4.5	S	4.2	S	5.0	S
Manalucie	4.2	S	3.7	SR	4.2	S	5.0	S	4.0	SR	4.5	S	4.5	S	5.0	S
Marmande	3.5	MR	5.0	S	4.2	S	5.0	S	4.7	S	5.0	S	4.7	S	5.0	S
Marmar	3.5	MR	3.0	VR	1.2	VR	3.0	VR	1.2	VR	1.0	HR	1.5	VR	4.5	S
Master No. 2	2.0	VR	1.2	VR	2.7	VR	2.7	VR	3.2	MR	3.5	MR	3.0	VR	4.5	S
Meltine	1.5	VR	1.0	HR	1.5	VR	2.2	VR	3.7	SR	4.5	S	2.2	VR	4.0	SR
Moneydor	4.5	S	4.2	S	4.0	SR	5.0	S	4.7	S	4.5	S	4.7	S	5.0	S
Money Maker	4.2	S	5.0	S	5.0	S	5.0	S	5.0	S	5.0	S	5.0	S	5.0	S
Monte Carlo	2.7	VR	2.0	VR	2.0	VR	3.5	MR	1.5	VR	2.5	VR	4.0	SR	4.0	SR
Nemared	1.0	HR	0.5	HR	1.5	VR	2.5	VR	0.5	HR	0.5	HR	1.7	VR	3.5	MR
Nemato	1.5	VR	1.5	VR	2.0	VR	2.2	VR	4.5	S	3.5	MR	2.7	MR	5.0	S
Park's Whopper	1.7	VR	2.0	VR	2.2	VR	3.2	MR	4.0	SR	3.2	MR	3.5	MR	4.5	S
Patriot	0.7	HR	0.5	HR	2.0	VR	2.0	VR	1.2	VR	1.0	HR	1.0	HR	3.2	MR
Pelican	1.2	VR	2.0	VR	2.2	VR	3.0	VR	3.5	MR	3.7	SR	2.5	VR	4.5	S
Pink Saturn	1.0	HR	1.0	HR	1.5	VR	3.0	VR	4.2	S	3.7	SR	3.0	VR	5.0	S
Ponderosa	4.2	S	4.2	S	4.0	SR	5.0	S	5.0	S	5.0	S	5.0	S	5.0	S
Resaplus	1.7	VR	2.0	VR	1.2	VR	2.7	VR	4.0	SR	3.5	MR	3.0	VR	4.2	S
Roma	4.5	S	5.0	S	4.7	S	5.0	S	4.5	S	4.5	S	4.5	S	5.0	S
Rootstock KNVF	3.0	VR	1.5	VR	3.0	VR	4.0	SR	3.5	MR	4.0	SR	3.0	VR	5.0	S
Rossol	1.2	VR	0.7	HR	1.0	HR	2.0	VR	0.2	HR	1.2	VR	2.5	VR	3.7	SR
Royal Chico	3.7	SR	2.0	VR	2.0	VR	3.7	SR	2.5	VR	2.0	VR	2.5	VR	4.0	SR
Rutgers	5.0	S	5.0	S	5.0	S	5.0	S	5.0	S	5.0	S	5.0	S	5.0	S
Small Fry VFN	1.0	HR	1.0	HR	1.0	HR	2.7	VR	2.7	VR	2.5	VR	2.7	VR	4.5	S
Stacos VF	4.0	SR	4.5	S	4.2	S	5.0	S	4.7	S	4.5	S	5.0	S	5.0	S
Saint Pierre	4.0	SR	4.5	S	4.5	S	5.0	S	4.5	S	5.0	S	3.7	SR	5.0	S
Terrific VFN	2.0	VR	2.2	VR	2.2	VR	4.0	SR	2.5	VR	1.2	VR	2.5	VR	4.7	S
UH N-11	2.0	VR	1.2	VR	1.7	VR	2.5	VR	4.0	SR	3.5	MR	2.7	VR	4.0	SR
UH N-64	2.2	VR	2.0	VR	2.0	VR	4.0	SR	3.5	MR	3.2	MR	3.2	MR	4.0	SR
UH N-65	1.2	VR	1.2	VR	2.0	VR	4.0	SR	3.5	MR	3.0	VR	2.5	VR	4.0	SR
Ultra Boy VFN	4.0	SR	3.5	MR	3.2	MR	4.0	SR	1.5	VR	1.2	VR	2.0	VR	3.2	MR
Ultra Girl VFN	4.5	S	4.2	S	4.5	S	4.5	S	3.0	VR	3.2	MR	3.7	SR	4.5	S
VFN-8	0.5	HR	0.5	HR	1.0	VR	3.5	MR	0.5	HR	1.0	HR	1.2	VP	2.2	VR
662 VFN	1.7	VR	1.0	HR	3.5	MR	3.7	SR	2.5	VR	1.2	VR	1.2	VR	3.0	VP
Vineripe VFN	3.7	SR	3.7	SR	2.5	VR	4.2	SR	3.2	MR	3.0	VR	2.0	VR	2.5	VR
Wonder Boy VFN	3.7	SR	3.5	MR	3.2	VR	4.0	SR	2.5	VR	1.5	VR	2.0	VR	3.5	MR
LSD ($P = 0.05$)	0.6		0.6		0.5		0.5		0.6		0.6		0.6		0.5	
CV	18.1		17.2		15.8		11.2		15.3		14.6		14.8		8.0	

(*continued on next page*)

Table 1. *(continued from preceding page)*

	M. incognita								*M. arenaria*							
	Race 1		Race 2		Race 3		Race 4		Race 1		Race 2		*M. javanica*		*M. hapla*	
Cultivar	EI[y]	DR[z]	EI	DR	EI	DR	EI	DR	EI	DR	EI	DR	EI	DR	EI	DR
Common bean																
Big Boy	2.7		3.5		3.7		1.2		3.2		4.2		1.75		4.2	
Contender	3.2		1.0		1.7		1.0		2.2		3.0		2.0		3.7	
INRA 223	3.0		3.5		3.0		2.2		2.0		2.0		1.5		3.7	
Kentucky Wonder	2.5		3.5		4.2		0.7		4.5		2.7		3.0		5.0	
Manoa Wonder	4.5		4.2		3.5		3.0		1.2		1.2		1.5		1.7	
Saginaw	4.7		3.7		3.7		2.5		4.2		3.5		4.0		5.0	
SV. 223	5.0		4.7		4.2		0.7		2.0		1.7		1.5		4.2	
Lima bean																
White Ventura N	4.5		5.0		3.2		2.2		3.5		1.5		1.5		4.5	
LSD ($P = 0.05$)	0.4		0.7		0.6		0.7		0.7		0.7		0.7		0.7	
CV	10.6		17.5		19.0		11.3		13.0		14.5		14.7		28.2	
Southern pea																
B.C. Miss. Silver	1.2		3.5		2.0		0.7		1.5		1.5		0.5		1.2	
Black Eye	1.5		2.7		1.5		0.5		1.2		1.0		1.0		1.2	
Brabham Victor	0.5		4.5		3.5		1.5		1.7		1.5		0.7		1.2	
Calif. Black Eye	1.2		3.5		3.5		1.2		1.0		1.0		0.5		2.2	
Clay	4.2		4.7		4.5		0.2		1.5		1.7		0.7		2.5	
Colessus	0.5		1.2		4.5		1.2		1.0		1.0		1.0		1.5	
Floricream	1.2		1.7		4.2		1.0		1.2		1.5		0.7		1.2	
Magnolia Black Eye	1.5		2.0		3.2		0.7		1.5		1.0		1.0		1.7	
Miss. Purple	2.0		1.7		3.2		0.7		1.2		1.0		0.7		1.2	
White Crowder	4.7		5.0		3.2		2.2		3.2		3.5		2.7		5.0	
Zipper Cream	1.5		1.5		3.7		0.2		1.0		1.2		1.0		1.5	
Garden pea																
Wando	4.0		4.0		3.7		4.7		2.5		2.7		2.5		3.2	
LSD ($P = 0.05$)	0.7		0.5		0.5		0.6		0.7		0.7		0.8		0.7	
CV	31.1		25.2		36.7		21.0		26.0		16.2		15.7		49.9	

[x]Means of four replicates, each inoculated with an initial population of 2,500 eggs per plant and harvested 55 days later.
[y]0 = no egg masses, 1 = 1–2 egg masses, 2 = 3–10, 3 = 11–30, 4 = 31–100, and 5 = more than 100 egg masses (22).
[z]Degree of resistance designation for tomato cultivars based on reproduction.

3.60–4.00 = SR; and 4.10–5.00 = S.

Postinfection development. Tomato cultivars used in this study were Better Boy (highly resistant), Royal Chico (slightly resistant), and Rutgers (susceptible). Inoculations were made with 200 freshly hatched, second-stage juveniles of *M. incognita* race 1 per plant. Each treatment was replicated eight times. Plants were placed in a greenhouse maintained at approximately 26 C. Roots were washed free of soil at 4, 6, 8, 10, 14, 18, and 20 days inoculation, immersed for 3 min in boiling 0.05% acid fuchsin-lactophenol, rinsed in cold tap water, and destained in lactophenol for at least 24 hr. The roots were later cut into about 1-cm lengths, pressed between microscope slides, and examined for larval penetration with a dissecting microscope at ×30.

RESULTS

Host suitability. None of the 50 tomato, 8 common bean and lima bean, and 12 southern pea and garden pea cultivars tested were immune to any species or race of *Meloidogyne* tested (Table 1). Host races 1, 2, and 3 of *M. incognita* generally reproduced at similar rates on the tomato cultivars. More egg masses were produced on many of the cultivars by race 4 than by the other three races of *M. incognita*. *M. arenaria* races 1 and 2 had about the same EI on all the tomato cultivars. *M. javanica* reproduced at slightly lower rates than *M. incognita* and *M. arenaria*. All tomato cultivars were susceptible to *M. hapla*.

Common bean Contender was very resistant to *M. incognita* races 2, 3, and 4, but it was only moderately resistant to race 1. Other common bean cultivars supported higher reproduction. A lower level of reproduction by race 4 occurred on common bean and lima bean. Common bean Manoa Wonder was very resistant to all *Meloidogyne* species, including *M. hapla*. The other common bean cultivars ranged from moderately resistant to susceptible to *M. hapla*; they were less susceptible to *M. javanica* than to either race of *M. arenaria* or to *M. hapla*. Lima bean White Ventura N was very resistant to *M. arenaria* race 2 and to *M. javanica*, and it was moderately resistant to *M. arenaria* race 1 and susceptible to *M. hapla* (Table 1).

Minor differences in resistance levels were found among races 1, 2, and 3 of *M. incognita* on southern pea cultivars, but all cultivars were either highly resistant or very resistant to race 4. All southern pea cultivars were very resistant or highly resistant to *M. arenaria*, *M. javanica*, and *M. hapla*, except White Crowder, which ranged from very resistant to *M. javanica* to susceptible to *M. hapla*. Garden pea Wando was only slightly resistant to any race of *M. incognita*, very resistant to *M. arenaria* and *M. javanica*, and moderately resistant to *M. hapla*.

Nematode survival and reproduction. Six tomato cultivars were evaluated for Pf, IR, and EI values when inoculated with the eight nematode isolates (Tables 2 and 3). The values increased with in increase in susceptibility of the tomato cultivars. Better Boy had an EI of 0 for *M. incognita* race 1; however, 96 eggs and larvae were recovered from roots following maceration, giving an IR of 0.2. Consequently, better Boy was classified as highly resistant to this race rather than immune. Tomato 662 VFN was very resistant to *M. incognita* races 1 and 4 but highly resistant to races 2 and 3. Monte Carole was very resistant to all four races; Marmar was highly resistant to race 3 and very resistant to the other races. Royal Chico was moderately resistant to races 1 and 4 but very resistant to races 2 and 3. Rutgers was susceptible to all races.

All tomato cultivars were susceptible to *M. hapla*. (Table 3) Better Boy was highly resistant to all other species. Monte Carlo was very resistant to *M. incognita*, highly resistant to *M. arenaria*, but moderately resistant to *M. javanica*. Marmar was very or highly resistant and Royal Chico was moderately resistant to species other than *M. hapla*. The estimates of degree of resistant shown in

Table 2. Final population (Pf), index of reproduction (IR), degree of resistance (DR), and egg mass index (EI) of selected tomato cultivars inoculated with four races of *Meloidogyne incognita*[t]

	Race 1				Race 2				Race 3				Race 4			
Cultivar[u]	**Pf**[v]	**IR**[w]	**DR**[x]	**EI**[y]	**Pf**	**IR**	**DR**	**EI**	**Pf**	**IR**	**DR**	**EI**	**Pf**	**IR**	**DR**	**EI**
Better Boy	96 e[z]	0.2 f	HR	0.0 d	135 b	0.3 f	HR	0.3 d	147 b	0.4 f	HR	0.3 c	698 d	1.4 f	VR	2.3 c
662 VFN	665 de	1.4 e	VR	2.2 c	367 b	0.8 e	HR	0.7 d	350 b	0.8 d	HR	0.7 bc	851 d	1.7 e	VR	2.5 c
Monte Carlo	1,546 d	3.3 d	VR	2.2 c	581 b	1.3 d	VR	1.2 c	811 b	2.0 c	VR	1.3 b	4,416 c	9.0 c	VR	2.8 bc
Marmar	2,712 c	5.7 c	VR	2.8 b	1,408 b	3.2 b	VR	2.5 b	217 b	0.5 e	HR	0.5 c	2,505 c	5.1 d	VR	2.7 bc
Royal Chico	6,880 b	14.5 b	MR	3.0 b	975 b	2.2 c	VR	1.3 c	1,348 b	3.3 b	VR	1.2 b	7,246 b	14.8 b	MR	3.2 b
Rutgers	47,620 a	100.0 a	S	4.2 a	44,450 a	100.0 a	S	4.0 a	41,490 a	100.0 a	S	4.0 a	48,920 a	100.0 a	S	4.3 a

[t] Means of six replicates, each inoculated with 500 larvae per plant and harvested 55 days later.
[u] Listed in descending order of susceptibility to *M. incognita* race 1 as determined from ratings of experiment 1.
[v] Total number of eggs and larvae recovered from root, plus larvae extracted from soil.
[w] Defined as PF on resistant variety expressed as a percentage of the Pf on the susceptible cutivar (22).
[x] Based on percentage of reproduction. Reproduction in susceptible Rutgers is considered normal (100%). S = susceptible plants, in which reproduction is normal; SR = slightly resistant, with reproduction of 25–50%; MR = moderately resistant, with reproduction of 10–25%; VR = very resistant, with reproduction of 1–10%; HR = highly resistant, with reproduction of less than 1%; and IM = immune, with nematodes entering the roots but not reproducing or being killed (21).
[y] 0 = no egg masses, 1 = 1–2 egg masses, 2 = 3–10, 3 = 11–30, 4 = 31–100, and 5 = more than 100 egg masses.
[z] Within columns, values followed by the same letter are not significantly different according to LSD test ($P = 0.05$).

Table 3. Final population (Pf), index of reproduction (IR), degree of resistance (DR), and egg mass index (EI) of selected tomato cultivars inoculated with four species of *Meloidogyne*[t]

	M. incognita race 1				*M. arenaria* race 1				*M. javanica*				*M. hapla*			
Cultivar[u]	**Pf**[v]	**IR**[w]	**DR**[x]	**EI**[y]	**Pf**	**IR**	**DR**	**EI**	**Pf**	**IR**	**DR**	**EI**	**Pf**	**IR**	**DR**	**EI**
Better Boy	96 e[z]	0.2 f	HR	0.0 d	147 c	0.3 d	HR	0.2 d	238 c	0.5 e	HR	0.5 e	38,890 b	90.2 c	S	4.0 a
662 VFN	665 de	1.4 e	VR	2.2 c	426 c	0.9 c	HR	0.7 c	949 c	2.0 d	VR	2.7 c	39,370 b	91.3 c	S	3.5 b
Monte Carlo	1,546 d	3.3 d	VR	2.2 c	308 c	0.7 c	HR	0.7 c	6,490 b	13.5 b	MR	3.5 b	44,730 a	103.7 a	S	4.0 a
Marmar	2,713 c	5.7 c	VR	2.8 b	379 c	0.8 c	HR	0.7 c	335 c	0.7 e	HR	0.7 e	43,640 a	101.2 ab	S	4.2 a
Royal Chico	6,880 b	14.5 b	MR	3.2 b	5,890 b	12.8 b	MR	2.0 b	5,670 b	11.8 c	MR	2.2 d	41,850 ab	97.1 b	S	4.0 a
Rutgers	47,620 a	100.0 a	S	4.2 a	45,930 a	100.0 a	S	4.0 a	48,190 a	100.0 a	S	4.0 a	43,120 a	100.0 a	S	4.0 a

[t] Means of of six replicates, each inoculated with 500 larvae per plant and harvested 55 days later.
[u] Listed in descending order of susceptibility to *M. incognita* race 1 as determined from ratings of experiment 1.
[v] Total number of eggs and larvae recovered from root, plus larvae extracted from soil.
[w] Defined as Pf on resistant variety expressed as a percentage of the Pf on the susceptible cultivar (22).
[x] Based on percentage of reproduction. Reproduction in susceptible Rutgers is considered normal (100%). S = susceptible plants, in which reproduction is normal; SR = slightly resistant, with reproduction of 25–50%; MR = moderately resistant, with reproduction of 10–25%; VR = very resistant, with reproduction of 1–10%; HR = highly resistant, with reproduction of less than 1%; and IM = immune, with nematodes entering the roots but not reproducing or being killed (21).
[y] 0 = no egg masses, 1 = 1–2 egg masses, 2 = 3–10, 3 = 11–30, 4 = 31–100, and 5 = more than 100 egg masses.
[z] Within columns, values followed by the same letter are not significantly different according to LSD test ($P = 0.05$).

Table 1 are projections based on the IR and EI values shown in Table 2 and the corresponding assigned DR designations.

Tomato cultivars with a high degree of resistance to root-knot nematodes species and races except to *M. hapla* were AMEX-VFN, Anahu, Atkinson, Auburn 76, Better Boy, Big Set, Bonus VFN, BWN-21, Healani, Marmar, Master No. 2, Nemared, Patriot, Rossol, Small Fry VFN, VFN-8, and 662 VFN. Cultivars with a low degree of resistance or with susceptibility were Ace Hy, Beef Eater VFN, Beef Master, LAR 2, Manalucie, Marmande, Moneydor, Money Maker, Ponderosa, Roma, Stacos VF, and Saint Pierre (Table 1). Other tomato cultivars had varying degrees of resistance to one ore more species and races.

The reproductive factor (R) values of the nematodes increased with susceptibility of the cultivars (Table 4). In general, the R values for *M. hapla* on "resistant" cultivars were much higher and differed significantly from those for other species of *Meloidogyne*. *M. incognita* race 4 had slight higher R values when compared with the other species and races on Better Boy and 662 VFN, but the difference was not significant ($P = 0.05$). *M. incognita* races 1 and 4 on Marmar and Royal Chico had R values significantly higher than the values on the other species and races on the same cultivars. *M. incognita* race 4 had the highest R value of the races of *M. incognita*. *M. javanica* had highest R values, differing significantly from the other species and races except *M. hapla*. In the susceptible tomato cultivar Rutgers, *M. incognita* race 4 had the highest R values, followed by *M. javanica*, *M. incognita* race 1, *M. arenaria* races 1 and 2, *M. incognita* race 2, *M. hapla*, and *M. incognita* race 3.

Postinfection development. Penetration rate of *M. incognita* race 1 increased with degree increasing of host susceptibility. After 4 days, the mean numbers of larvae that had penetrated the roots of Better Boy, Royal Chico, and Rutgers were 75, 83, and 89, respectively (Fig. 1). The rate of penetraiton was significantly higher in Rutgers than in Better Boy but not different from Royal Chico ($P = 0.05$). After 6 days, the mean numbers of larvae that had penetrated Better Boy, Royal Chico, and Rutgers roots were 109, 116, and 132, respectively. After 8 days, the mean numbers of nematodes in the roots of Better Boy, Royal Chico, and Rutgers were 53, 97, and 153, respectively. These differences were highly significant and correlated positively with the susceptibility of the tomato cultivar. The differences became progressively greater with time up to 20 days, when the test was terminated.

DISCUSSION

Some plants may have numerous galls caused by *Meloidogyne* spp. with little or no reproduction; conversely, much reproduction can occur on some plants that have few or no galls (2). An evaluation of host suitability (resistance or susceptibility) should therefore be based on the level of reproduction on a host plant under specific conditions and over a specified period of time.

An evaluation based on egg-mass index is better than one based on gall index, but even ET does not measure nematode reproduction adequately because it does not quantify the eggs produced. To measure more accurately, we used an index of reproduction (23). Thus, degree of resistance can be determined based on the classification system suggested by Taylor (21). To illustrate the higher level of accuracy of this system vs. the egg-mass index system, we compared data on IR and EI of tomato Better Boy (Table 2). Based on EI alone, Better Boy should be classified as immune to *M. incognita* race 1, but the IR value was 0.2. Better Boy is then more realistically classified as highly resistant than as immune.

Because the degree of resistance designations are based on IR values, and IR and EI values are related, it seemed reasonable to assume that DR designations can be assigned based on EI values alone. Two basic assumptions were made in assigning DR designations to cultivars shown in Tables 1 and 2. First, we assumed that differences in inoculum levels—2,500 eggs per plant for experiment 1 and 500 larvae for experiment 2—were not a factor. Evidence in favor of this assumption was the degree of infection on Rutgers (5.0) for experiment 1 and 4.0 or greater for experiment 2. Second, we assumed that the relationship between IR, DR, and EI values shown in Tables 2 and 3 could be applied to the EI values shown in Table 1 for the purpose of assigning DR designations. IR and EI values were significantly correlated (r = 0.81) for values in Tables 2 and 3 for the various species and races.

Regression analysis of IR values on egg mass indexes justified the use of DR designations for the tomato cultivars shown in Table 1. If additional tests on other crops substantiate these relationships, then more reliance can be placed on the use of EI values in rating crops for resistance. Because much more time is needed to establish IR values, compared with EI ratings, it would be worthwhile to study these relationships further.

Oostenbrink's (13) R factor provides a basic measurement of nematode reproductive capabilities, and in this study R is used to determine the relative rates of reproduction on a given cultivar. For *Meloidogyne* species and races, R was greatly influenced by degree of resistance. On the basis of the R values of nematodes on suscpetible tomato cultivar Rutgers, *M. incognita* race 4 was the most "aggressive," followed by *M. javanica,* M. incognita race 1, *M. arenaria* race 1, *M. arenaria* race 2, *M. incognita* race 2, and *M. hapla.* The least aggressive nematode on tomato cultivar Rutgers was *M. incognita* race 3.

Our results confirmed that Anahu (24), Atkinson (20), Healani (18), Nemared (11), Patriot (4), Rossol (12), and VFN-8 (19) are resistant to *M. incognita* and *M. javanica*. On the other hand, there were some inconsistencies with literature reports. Beef Master (listed as resistant to *M. incognita* [7]); Marmande, Money Maker, and Roma (resistant to *Meloidogyne* spp. [C. M. Messiaen, Manalucie (resistant to *M. incognita, M. javanica,* and *M. arenaria* [20]); *personal communication*, 1978]); and Ponderosa (moderately resistant to *M. incognita* [9]) were found to be susceptible to all nematode species and races tested.

Equal penetration rates of juveniles in roots of resistant and susceptible tomato cultivars have been reported by several workers. Jatala and Russell (6), however, found significantly lower rates of penetration in resistant sweet potato lines. Our results showed that after 4 days of exposure to *M. incognita* race 1, there was no significant difference (P= 0.05) in tomato in penetration between the highly resistant cultivar Better Boy and the moderately resistant cultivar Royal Chico, nor between the moderately resistant Royal Chico and the susceptible Rutgers. The difference between Better Boy and Rutgers was significant, however. After 6 days, nematode penetration of resistant roots increased less rapidly than in the susceptible plants. The number of nematodes in the roots of resistant plants was significantly lower than in Rutgers after 8 days and for each additional observation. Resistance may have been expressed by failure of the larvae to develop into adults, prolongation of the developmental cycle, larval death within root tissues, alteration of sex ratio toward maleness, or larval egress soon after penetration (2).

We found positive correlation between time and the number of nematodes that penetrated the roots of Rutgers and a negative correlation for Better Boy and Royal Chico. This strongly suggests that, shortly after the initial contact of the nematode with the root, the physiology of the resistant plant is altered to the disadvantage of the nematode; or that the initial penetration of the nematode immediately stimulates a defense reaction in resistant plants that may cause a decrease in the rate of penetration by larvae. These limited studies on penetration and development of *M. incognita* larvae in the roots of resistant, moderately resistant, and susceptible tomato cultivars agree in general with the work of other investigators. It appears that resistance is not so much related to penetration of the roots as it is to factors affecting the development of the larvae following penetration.

These studies have shown that several kinds of data can be used to assess host suitability (resistance) of various crop cultivars to *Meloidogyne* species and races and that cultivars can be assigned to classes of host suitability based on results of parameters measured. If furtherstudies confirm the relationship between the

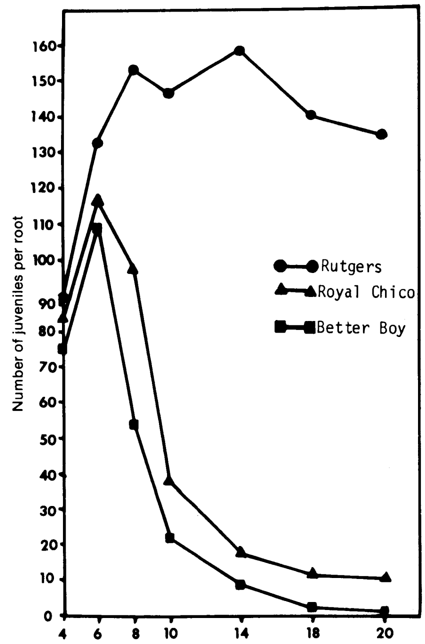

Fig. 1. Number of nematodes detected in roots of susceptible tomato cultivar Rutgers, moderately resistant Royal Chico, and highly resistant Better Boy after inoculation with 200 juveniles of *Meloidogyne incognita* race 1.

Table 4. Reproductive factors of root-knot nematode species and races on selected tomato cultivars[x]

Nematode species Race	Reproductive factor (R)[y] Better Boy	662 VFN	Marmar	Monte Carlo	Royal Chico	Rutgers
M. incognita						
Race 1	0.2 b[z]	1.3 b	5.4 b	3.1 d	13.8 bc	95.2 ab
Race 2	0.3 b	0.7 b	2.8 c	1.2 de	1.9 e	88.7 cd
Race 3	0.3 b	0.7 b	0.4 d	1.6 de	2.7 e	83.0 d
Race 4	1.4 b	1.7 b	5.0 bc	8.8 c	14.5 b	97.8 a
M. arenaria						
Race 1	0.3 b	0.8 b	0.8 cd	0.6 e	11.8 cd	91.8 abc
Race 2	0.3 b	0.8 b	0.8 cd	0.6 e	9.8 d	90.6 bc
M. javanica	0.5 b	1.9 b	0.7 cd	13.0 b	11.3 d	96.4 ab
M. hapla	77.8 a	78.7 a	87.3 a	89.5 a	83.7 a	86.2 cd

[x] Means of six replicates, each inoculated with 500 newly hatched larvae per plant and harvested 55 days later.
[y] Reproductive factor (R) = Pf/Pi (initial population) (13).
[z] Within columns, values followed by the same letter are not significantly different according to LSD test (P = 0.05).

parameters used to measure host suitability and the classification given to tested cultivars, it will be easier and more reliable to categorize crop cultivars with reference to suitability to root-knot nematodes. In addition, adoption of standards governing levels of inoculum per unit volume of soil, duration of tests, and temperatures used during the test period would greatly enhance the development and ultimate utilization of resistant cultivars for root-knot control. Furthermore, communication among workers concerning relative resistance of cultivars to species and races of root-knot nematodes would be improved.

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