

Interaction of *Meloidogyne javanica* with Different Races of *Meloidogyne incognita*

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Abstract: The interspecific interactions of *Meloidogyne javanica* with races 1, 2, 3, and 4 of *M. incognita* on tomato were determined. Impacts of the interactions on fecundity and morphometrics of females were also examined. Mutually inhibitory interactions occurred between *M. javanica* and the races of *M. incognita*, but the negative interactions did not reflect in plant growth. Numbers of root galls, egg masses, mature females, total population, fecundity, and reproduction factor declined in concomitant treatments, but the morphometrics of the females remained unaltered. In general, mutual suppressive effects in all parameters were smaller for *M. javanica* than *M. incognita*, but some variations occurred among the races of *M. incognita*. Race 2 appeared to be more competitive than other races. The interaction between the species was not intense; therefore, the species coexist in mixed populations in agricultural fields.

Key word: egg mass index, fecundity, gall index, interspecific interaction, *Meloidogyne incognita*, *Meloidogyne javanica*, morphometrics, race.

Sedentary endoparasitic nematodes are highly specialized parasites developing a prolonged complex relationship with the host that greatly alters the host physiology (7). Competition between two sedentary endoparasitic nematode species is generally mutually suppressive because of the competition for available feeding sites and nutrition (10-12,15). Neutral or stimulatory effects may also occur (2,3). *Meloidogyne incognita* (Kofoid & White) Chitwood, *M. javanica* (Treub) Chitwood, *M. arenaria* (Neal) Chitwood, and *M. hapla* Chitwood are the major species of plant-parasitic nematodes found in cultivated fields (16). Mixed infections of the species on plants and field infestations are common. Since the feeding sites of *Meloidogyne* species are similar, theoretically, two or more coexisting species may interact, and it is likely that one may dominate and affect the population density of the other species.

Little attention has been given to the interactions among species of *Meloidogyne*. *Meloidogyne javanica* and *M. incognita* are the two most common species in tropical and subtropical regions of the world (18).

They have similar ecological requirements and thrive together in many different parts of the world. Recent studies indicate that *M. javanica* and *M. incognita* are the most frequent species in mixed populations in Uttar Pradesh, India (5,8,9). The nature of interactions in mixed populations, i.e., whether the Gause principle (4) of exclusion of one species by the other from the community operates or they develop a balanced relationship and coexist together in cultivated fields, and the behavior of races of *M. incognita* have not been determined. When two closely related nematode species with similar modes of parasitism invade the same root system near the same feeding sites and receive nutrition from the same host, influence over each other may occur with respect to development of host-parasite relationship, fecundity, rate of population growth and population density of the species. The objective of this study was to determine interactions between *M. javanica* and the four races of *M. incognita*.

MATERIALS AND METHODS

Interactions of *M. javanica* with races 1, 2, 3, and 4 of *M. incognita* were studied on tomato under greenhouse conditions.

Plant culture: Seedlings of tomato (*Lycopersicon esculentum* Mill. cv. Pusa Ruby) were grown from surface sterilized seeds in trays filled with steamed sandy loam field soil (66% sand, 24% silt, 8% clay; pH 7.7,

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2% OM). One 3-week-old seedling was transplanted into each 15-cm-d clay pot containing a mixture (3:1, v:v) of steamed soil and farmyard cow manure. Three days after transplanting, plants were inoculated with second-stage juvenile (J2) nematodes.

Inoculations: Second-stage juveniles of *M. javanica* and races 1, 2, 3, and 4 of *M. incognita* were obtained by incubating egg masses of each species or race cultured on roots of tomato or eggplant (*Solanum melongena* L. cv. Pusa Kranti) in sterilized distilled water in 9-cm-d petri dishes in the incubator at 25 C. After 72 hours, J2 were collected and numbers of J2 in 10 1-ml samples were recorded. In all tests, each tomato seedling was inoculated with the J2 suspension in depressions made in soil around the seedling. Treatments (J2 per pot) were Control (0), *M. javanica* (1,000), *M. javanica* (2,000), *M. incognita* race x (1,000), *M. incognita* race x (2,000), and *M. javanica* (1,000) + *M. incognita* race x (1,000) (x = race 1, 2, 3, or 4). Treatments were replicated five times. Pots were arranged in a randomized complete-block design and maintained at 25 C \pm 2 for 50 days and watered as needed.

Parameters: Fifty days after inoculation, plant shoots were measured and weighed. Shoots were dried in an oven at 60 C for 3 days and weighed. Root-gall index (GI) and egg-mass index (EMI) were rated on a 0–5 scale (18). Soil population densities of J2 and males in each treatment were estimated by modified Cobb's sieving and decanting method (17). Roots from each replicate were weighed, cut into 1-cm pieces, and mixed thoroughly. A 1-g sample of root pieces was stained with acid fuchsin and lactophenol (17) and examined under a stereoscopic microscope, and numbers of J2 and J3 + J4 were recorded. The total number of J2 and J3 + J4 for the entire root system of the replicate was calculated. A 1-g sample of root pieces was transferred in 5% HNO₃ and incubated at 25 C. After 72 hours, root pieces were gently teased to release the females. The females per gram of root were counted and the total number of females for the entire root system was

calculated. From *M. javanica* + *M. incognita* treatments, 15 females were randomly sampled, perineal patterns prepared, species identified, and relative ratios determined. Reproduction factor (Rf) for each treatment was calculated as $Rf = Pf/Pi$, where Pf = final population density (soil + roots) and Pi = initial inoculum level of the nematode species.

Data were subjected to analysis of variance and the least significant differences ($P = 0.05$, $P = 0.01$) among the treatment means were determined.

Interactive effects on nematodes: The effects of interspecific interactions of *M. javanica* and *M. incognita* races 1, 2, 3, and 4 on fecundity (number of eggs per egg mass) and morphometrics of females were studied separately under greenhouse conditions. Seedlings of Pusa Ruby tomato were produced from surface sterilized seeds in steamed sandy loam soil and 3-week-old seedlings were transferred to 15-cm-d clay pots (1 seedling per pot) filled with steam pasteurized sandy loam field soil and farmyard cow manure (3:1, v:v). Inoculations were made with *M. javanica* and *M. incognita* J2 as follows: Single species inoculum was 2,000 J2 for *M. javanica*, *M. incognita* race 1, *M. incognita* race 2, *M. incognita* race 3, and *M. incognita* race 4. Inoculum for concomitant treatments was 1,000 J2 each for *M. javanica* + *M. incognita* race 1, *M. javanica* + *M. incognita* race 2, *M. javanica* + *M. incognita* race 3, and *M. javanica* + *M. incognita* race 4. Treatments were replicated three times. Inoculated plants were arranged in a randomized complete-block design on benches (25 C \pm 2).

Fifty days after inoculation, plants were uprooted and five uniform egg masses randomly selected from each replicate. Fifteen egg masses from each treatment were used to determine the fecundity. Each egg mass was placed on a slide in two drops of 0.1% NaOCl solution, and the eggs per egg mass for each treatment were counted.

The female producing a given egg mass was dissected. The length and width of the body, neck, and median bulb and the length of the stylet were measured. In the con-

comitant treatments after counting the number of eggs per egg mass and determining the morphometrics, the perineal pattern of each female was prepared for species identification.

The data on fecundity and morphometrics were subjected to analysis of variance test. Means between the two treatments were separated using Student's *t*-test.

RESULTS

Shoot growth: Meloidogyne javanica and *M. incognita* races 1, 2, 3, and 4 in single or concomitant treatments reduced plant growth of tomato when compared with uninoculated plants (Table 1). When tomato seedlings were inoculated with either 1,000 or 2,000 J2 of *M. javanica* or either race of *M. incognita*, reductions ($P = 0.05$) occurred in length and fresh and dry weights of shoots. In concomitant treatments with Pi 1,000 J2 of *M. javanica* + 1,000 J2 of *M. incognita* races reductions ($P = 0.05$) in growth parameters were also recorded. Growth reductions obtained with 1,000 J2 or 2,000 J2 of each nematode species and race in single inoculations were not different ($P = 0.05$) from those in concomitant inoculations with Pi 1,000 J2 of each. The reductions in shoot growth obtained with 1,000 J2 and 2,000 J2 of either nematode species did not differ. The percentage of reduction in plant growth parameters was greater for *M. javanica* than for *M. incognita*, regardless of race, at both the inoculum levels in single species treatments. The percentage of reduction in concomitant treatments of Pi 1,000 J2 was less than single inoculation of either species and race at the same inoculum level.

Root gall and egg mass production: Root gall and egg mass production was adversely affected by interactions in concomitant treatments as indicated by GI and EMI values (Table 1). In concomitant treatments GI and EMI were reduced when compared with single inoculations at similar Pi. At Pi 2,000 J2, respective GI and EMI were 4.50 and 4.50 for *M. javanica* and 4.50 and 4.00 for *M. incognita* race 1. In the concomitant

treatment, however, GI and EMI were 4.00 and 3.50, respectively.

A similar trend in reduction of GI and EMI occurred in interactions of *M. javanica* with *M. incognita* races 2, 3, and 4 (Table 1). The reductions were consistent with the interaction of *M. javanica* with any race of *M. incognita*.

Population of females, total population, and Rf: The number of mature females and total population density of each nematode species and race declined ($P = 0.05$) in concomitant inoculations, irrespective of the race of *M. incognita* with *M. javanica* (Table 2). The number of mature females per root system infected by both nematode species was reduced. In single *M. javanica* and *M. incognita* inoculations with 2,000 J2, the number of mature females per root system was 1,055 *M. javanica* and 1,001 *M. incognita* race 1, but in concomitant inoculation with Pi 1,000 J2 of each, the number of females irrespective of the species was reduced to 823. In concomitant inoculations more *M. javanica* than *M. incognita* race 1 females developed. From 823 females recovered, 483 were *M. javanica* and 340 were *M. incognita* race 1. When these numbers were compared with numbers of females recovered from single inoculation Pi 1,000 J2 of each species, the numbers of females of both species were reduced ($P = 0.01$). The reduction in number of females of *M. incognita* race 1 (45%) was greater than *M. javanica* (30%) (Table 2).

Total nematode population densities in soil and roots in concomitant treatments were also reduced (Table 2). For example, in the *M. javanica* + *M. incognita* race 1 treatment, the total nematode population densities were 1,392 in contrast to 1,855 *M. javanica* and 1,695 *M. incognita* race 1 in single species inoculation at Pi 2,000 J2. The decrease in total population density was significant when compared with *M. incognita* race 1 ($P = 0.05$) and *M. javanica* ($P = 0.01$). The reproduction factor was also reduced ($P = 0.05$) in concomitant inoculation of the species compared with single species inoculation at the same Pi.

When *M. javanica* interacted with *M. in-*

TABLE 1. Interspecific interaction between *Meloidogyne javanica* (Mj) and *M. incognita* races 1, 2, 3, and 4 (MiR₁, MiR₂, MiR₃ and MiR₄) on tomato.

Treatment	Inoculum level (Pi)†	Shoot growth			GI‡	EMI‡
		Length (cm)	Fresh weight (g)	Dry weight (g)		
Uninoculated (control)		17.87	12.43	4.27		
Mj	1,000	16.04	11.30	3.95	3.50	3.50
	2,000	15.18	11.25	3.00	4.50	4.50
MiR ₁	1,000	16.10	11.36	3.98	3.00	3.00
	2,000	15.21	11.28	3.85	4.50	4.00
Mj + MiR ₁	1,000 + 1,000	15.25	11.35	3.90	4.00	3.50
LSD 0.05		1.72	0.65	0.28	0.21	0.25
0.01		2.82	1.62	0.75	0.45	0.52
Uninoculated (control)		19.87	14.43	5.27		
Mj	1,000	18.05	13.39	4.96	3.50	3.50
	2,000	17.18	13.21	4.82	4.50	4.50
MiR ₂	1,000	18.12	13.40	4.98	3.25	3.00
	2,000	17.22	13.25	4.88	4.50	4.25
Mj + MiR ₂	1,000 + 1,000	17.25	13.28	4.90	4.00	3.75
LSD 0.05		1.75	0.75	0.29	0.20	0.13
0.01		2.94	1.62	0.82	0.48	0.28
Uninoculated (control)		22.25	12.95	5.90		
Mj	1,000	20.35	12.20	5.05	3.50	3.50
	2,000	19.95	11.70	4.95	5.00	4.75
MiR ₃	1,000	20.80	12.40	5.15	3.50	3.00
	2,000	20.50	11.85	4.97	4.25	3.75
Mj + MiR ₃	1,000 + 1,000	20.85	11.95	5.00	4.00	3.50
LSD 0.05		1.35	0.75	0.82	0.15	0.12
0.01		2.90	1.28	1.38	0.32	0.28
Uninoculated (control)		24.25	14.95	6.95		
Mj	1,000	22.30	14.10	6.15	3.50	3.00
	2,000	21.95	13.75	5.92	5.00	4.25
MiR ₄	1,000	22.36	14.15	6.17	3.00	3.00
	2,000	22.00	13.80	5.94	4.50	4.25
Mj + MiR ₄	1,000 + 1,000	21.98	13.79	5.94	4.00	3.75
LSD 0.05		1.40	0.75	0.80	0.18	0.22
0.01		2.94	1.35	1.46	0.40	0.46

Each value is a mean of five replicates.

† Pi = initial population.

‡ Root-gall index (GI) and egg-mass index (EMI) rating 0-5 scale: 0 = 0, 1 = 1-2, 2 = 3-10, 3 = 11-30, 4 = 31-100, 5 = >100 galls or egg masses per root system.

cognita race 2, the number of females of both species declined ($P = 0.05$) (Table 2). In concomitant inoculations, the number of recovered *M. javanica* females was greater than that of *M. incognita* race 2. The percentage of reduction for *M. incognita* race 2 was greater (48%) than for *M. javanica* (22%). Reduction ($P = 0.05$) in total populations and Rf values occurred in concomitant treatments, when compared with single species inoculation at the same Pi.

When *M. javanica* interacted with *M. incognita* races 3 and 4, a similar decline ($P = 0.05$) in total number of females, total population density, and Rf occurred (Ta-

ble 2). The decline in the number of females was greater for *M. incognita* races 3 and 4 than for *M. javanica*.

Interactive effects on nematodes: The fecundity of *M. incognita* races 1, 2, 3, and 4 was adversely influenced by *M. javanica* (Table 3). However, fecundity of *M. javanica* was not affected by *M. incognita*, except race 2. In interaction of *M. javanica* and *M. incognita* race 2, the fecundity of both species was adversely affected similarly. In single inoculation with Pi 2,000 J2, the mean and range values of *M. javanica* fecundity were greater than those of *M. incognita* race 1. In concomitant treatments

TABLE 2. Interspecific interaction between *Meloidogyne javanica* (Mj) and *M. incognita* races 1, 2, 3, and 4 (MiR₁, MiR₂, MiR₃, and MiR₄) on tomato.

Treatment	Inoculum level (Pi)†	Soil population		Root population			Pf‡	Rf‡	Females (N)	
		J2	Male	J2	J3 + J4	Mature female			Mj	MiR ₁ or MiR ₂
Mj	1,000	427	28	47	37	687	1,226	1.22	687	
	2,000	629	35	61	73	1,055	1,855	0.93	1,055	
MiR ₁	1,000	357	27	41	33	617	1,075	1.08		617
	2,000	532	31	57	73	1,001	1,695	0.84		1,001
Mj + MiR ₁	1,000 + 1,000	408	32	64	64	823	1,392	0.70	483	340
LSD 0.05						130	271	0.11	46	77
	0.01					245	316	0.25	102	132
Mj	1,000	421	31	38	33	680	1,205	1.20	680	
	2,000	638	44	81	72	1,011	1,844	0.91	1,011	
MiR ₂	1,000	392	21	25	30	665	1,125	1.12		665
	2,000	616	37	90	62	955	1,759	0.88		955
Mj + MiR ₂	1,000 + 1,000	420	29	69	72	880	1,469	0.74	534	346
LSD 0.05						123	175	0.11	82	115
	0.01					275	269	0.24	182	219
Mj	1,000	420	30	40	35	675	1,200	1.20	675	
	2,000	640	45	80	75	1,000	1,840	0.92	1,000	
MiR ₃	1,000	370	18	22	25	600	1,037	1.04		600
	2,000	600	35	75	85	940	1,701	0.85		940
Mj + MiR ₃	1,000 + 1,000	418	30	70	72	885	1,490	0.74	595	290
LSD 0.05						51	209	0.08	75	81
	0.01					158	432	0.20	148	179
Mj	1,000	420	30	35	35	662	1,182	1.18	662	
	2,000	662	38	62	68	1,028	1,818	0.91	1,028	
MiR ₄	1,000	300	15	40	50	538	943	0.94		538
	2,000	680	32	65	62	880	1,619	0.89		880
Mj + MiR ₄	1,000 + 1,000	422	28	58	60	755	1,323	0.66	525	230
LSD 0.05						125	183	0.08	89	119
	0.01					280	341	0.21	148	281

Each value is a mean of five replicates.

† Pi = initial population; Pf = final population.

‡ Rf = reproduction factor: Pf/Pi.

TABLE 3. Interactive effects on fecundity of *Meloidogyne javanica* and races 1, 2, 3, and 4 of *M. incognita* on tomato.

Treatment	Eggs/egg mass (N)		Reduction (%)
	Range	Mean	
Single inoculation (2,000 J2)			
<i>M. javanica</i>	280-575	421	
<i>M. incognita</i>			
Race 1	260-425	345	
Race 2	225-440	360	
Race 3	240-418	330	
Race 4	236-432	340	
Concomitant inoculation (1,000 + 1,000 J2)			
<i>M. javanica</i> +	270-565	418	0.71
<i>M. incognita</i> race 1	200-380	293**	15.07
<i>M. javanica</i> +	265-415	360*	14.49
<i>M. incognita</i> race 2	200-398	300*	16.67
<i>M. javanica</i> +	275-555	415	1.43
<i>M. incognita</i> race 3	220-380	280**	15.15
<i>M. javanica</i> +	265-558	417	0.95
<i>M. incognita</i> race 4	200-390	305*	10.29

Each value is a mean of 15 egg masses.

* and ** = values are different at $P = 0.05$ and $P = 0.01$, respectively, according to Student's *t*-test over single inoculation.

the mean and range values of fecundity of both species declined. When compared with single inoculations with Pi 2,000 J2, fecundity of *M. incognita* race 1 was reduced ($P = 0.05$) in the presence of *M. javanica*. The percentage of reduction in fecundity was greater for *M. incognita* race 1 than for *M. javanica*.

In the interaction between *M. javanica* and *M. incognita* race 2, fecundity was reduced ($P = 0.05$) by 17% and 14%, respectively.

The interaction between *M. javanica* and *M. incognita* race 3 decreased the fecundity of *M. incognita* race 3 alone. Similarly *M. javanica* affected the fecundity of *M. incognita* race 4 only. The reductions were 15% and 10% for *M. incognita* races 3 and 4, respectively, compared with 1% for *M. javanica*.

The morphometrics of *M. javanica* and all races of *M. incognita* were not affected by concomitant inoculations.

DISCUSSION

Interaction between two nematodes may be harmful to one or both species (antag-

onistic), have no effect (neutral), or be beneficial to one or both species (mutualistic). The effects of the nematode populations on each other are generally related to the nature of parasitism; competition is more severe between species with similar feeding habits (2,3). The interactions between sedentary endoparasites are generally mutually suppressive because they compete for the available feeding sites and cause similar histopathological and physiological alterations in the host.

Investigations on interspecific interactions between *M. javanica* and *M. incognita*, regardless of race, showed that *M. javanica* was more competitive than *M. incognita*. Variations in interaction occurred among the races of *M. incognita*. Interaction between *M. javanica* and *M. incognita* race 1 was mutually suppressive, affecting root galls, egg mass production, total number of females, total population, and the reproduction factor. These mutually suppressive effects did not reflect in the growth of the host.

In general, the host plant derives benefit from mutually inhibitory interactive effects on nematode species (2,3,10,11,19). This effect was not observed in our experiments because the host was very efficient for both nematode species, which have the same modes of parasitism and feeding sites. Although Pi 1,000 J2 of each species in the concomitant treatments produced lower population densities than Pi 2,000 J2 of either species alone, it was sufficient to cause the damage observed. Even in single inoculations of both nematode species alone, plant growth with 1,000 and 2,000 Pi did not vary ($P = 0.05$). However, reproduction of each species was affected by the presence of the other species in the same root system. Reductions in the reproductive capacity of the nematodes may have little or no effect on plant growth during a single growing season. However, the reduction in inoculum potential may be beneficial under field conditions for subsequent crops.

The interactive effects of *M. javanica* were more inhibitory than *M. incognita* race

1 in their antagonistic relationship. *Meloidogyne javanica* produced more females than *M. incognita* race 1 at the same Pi in concomitant mixtures. A mutual inhibitory effect occurred in the interactions between *M. javanica* and *M. incognita* races 2, 3, and 4. The lack of interaction effects between *M. javanica* and *M. incognita* races 1, 2, 3, and 4 on plant growth was consistent with the effects on root galling, egg mass production, number of females produced, total nematode population, and reproduction factor. These results indicated the existence of mutually inhibitory effects of each nematode. In these antagonistic relationships with either races of *M. incognita*, *M. javanica* suffered less and developed more females than the races of *M. incognita*. The suppressive effect of *M. javanica* varied among races of *M. incognita* in relation to production of females. The suppressive effect of *M. javanica* was greater on races 3 and 4 of *M. incognita* than on races 1 and 2. Races 3 and 4 caused less inhibition of female production of *M. javanica* than did races 1 and 2. A similar inhibition was suggested by the results of the concurrent fecundity study. The fecundity of *M. javanica* was affected less than the races of *M. incognita*. The fecundity of *M. incognita* race 2 and *M. javanica* was similar. *Meloidogyne incognita* races 1 and 4 were intermediate and race 3 was the least suppressive. Therefore, in a mixed community, *M. javanica* can survive, adapt, and compete more effectively than *M. incognita*. Among *M. incognita*, races 1 and 2 can compete more aggressively than races 3 and 4.

In interactions between the species of *Meloidogyne*, dominance of *M. javanica* over *M. hapla* has been reported (13). Inhibition of reproduction and population development of *M. hapla* by *M. incognita* on tobacco cultivars has been demonstrated (6). The interactions between *M. incognita* and *M. hapla* were greatly influenced by temperature (6). Similar dominance of *M. incognita* over *M. javanica* and *M. hapla* at high temperatures and of *M. javanica* over *M. incognita* and *M. hapla* at low temperatures occurred (14).

The interspecific interactions between *M. javanica* and *M. incognita* corroborate generalization that the species of nematodes can cohabit in close proximity, influencing each other directly or indirectly (15), and one population may not exclude the other as required by the Gause principle. It also supports the statement that competition among the species of *Meloidogyne*, particularly between *M. javanica* and *M. incognita*, is weak (2). Although the antagonistic interactions between *M. javanica* and *M. incognita* were not intense, such interactions may occur in nature, influencing reproductive efficiency and population growth. Nevertheless the species coexist in a common pathosystem. Intraspecific interaction in the *Meloidogyne* species and races studied by Haider (5) was intense. Therefore, the two nematode species can cohabit when the competition among the individuals in a species is greater than the competition between the species (1). Notwithstanding the influence of other factors, it is possible that this pattern of interspecific and intraspecific interactions may occur in *M. incognita* and *M. javanica* populations in nature, thus providing opportunities for their coexistence in common pathosystems.

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