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Host–Parasite Relationships of *Meloidogyne arenaria* and *M. incognita* on Susceptible Soybean[1]

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Abstract: Pathogenicity and reproduction of single and combined populations of *Meloidogyne arenaria* and *M. incognita* on a susceptible soybean (*Glycine max* cv. Davis) were investigated. Significant galling and egg mass production were observed on roots of greenhouse-grown soybean inoculated with *M. arenaria* and *M. incognita*, in combination and individually. *M. arenaria* produced more galls and egg masses than *M. incognita*, whereas in combined inoculation with both nematode species, gall and egg production was intermediate. In growth chamber tests, inoculations with *M. arenaria* and *M. incognita*, singly or in combination, produced more galls and egg masses at 30 C than at 25 C. At 25 C, *M. arenaria* alone produced significantly more galls and egg masses than the combined *M. arenaria* plus *M. incognita*, while *M. incognita* produced the fewest. At 30 C, numbers of egg masses produced by *M. arenaria* did not differ significantly from combined *M. arenaria* and *M. incognita*. In temperature tank tests, *M. incognita* produced more galls and egg masses at 28 C than at 24 C soil temperature. In contrast, numbers of galls, egg masses, and eggs of *M. arenaria* were slightly higher at 24 C than at 28 C. Combined inoculum of both nematode species produced greater numbers of galls at 24 C than at 28 C.
Key words: *Glycine max,* interaction, concomitant, root-knot nematode, soil temperature, inoculum density, ecology.

Root-knot nematodes (*Meloidogyne* spp.), widely distributed in the southern and southeastern United States, can cause economic loss to soybean when fields are heavily infested (1,8,10,11). *M. arenaria, M. incognita,* and *M. javanica* are among the most important plant-parasitic nematodes in South Carolina soybean fields (unpubl.). Mixed populations of *M. incognita* and *M. arenaria* are increasingly found in the same soil and root samples. Although *M. incognita* is more widely distributed than *M. arenaria* or *M. javanica* on soybeans in South Carolina, all three species can infect, reproduce, and damage many commercial soybean cultivars causing yield reductions (8).

Temperature influences the pathogenicity and reproduction of *Meloidogyne* spp. (3,4,10,12,13). The dramatic increase in the incidence of fields affected by *M. arenaria* in 1982 was thought to be environmentally correlated (6). As a result of this epiphytotic, experiments were initiated to determine the comparative effect temperature has on nematode reproduction and plant growth and to compare inherent virulence of *M. arenaria* and *M. incognita* on susceptible soybean.

MATERIALS AND METHODS

Meloidogyne arenaria (Ma) and *M. incognita* (Mi) were isolated from infected soybean roots from Barnwell County, South Carolina, and increased on tomato (*Lycopersicon esculentum* Mill. cv. Rutgers) for 60–90 days in the greenhouse. Nematode eggs for inocula were extracted from tomato roots by the NaOCl method (7).

Greenhouse experiment: Ten-day-old soybean (*Glycine max* Merr. cv. Davis) seedlings were transplanted into steam-sterilized 1:1 by volume sand:Varina sandy loam in 15-cm-d plastic pots (one plant per pot) and inoculated with nematode eggs suspended

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TABLE 1. Production of galls and egg masses by *Meloidogyne arenaria* (Ma) and *M. incognita* (Mi) singly and in combination on Davis soybean in the greenhouse. Replicated six times.

Treatment	Pi* (eggs)	Root gall index†	Egg mass index
Ma	6,000	4.50 a	5.00 a
Mi	6,000	3.50 b	3.25 c
Ma + Mi	3,000 + 3,000	4.00 ab	4.25 b
Control	0	0 c	0 d

Means in a column followed by same letter are not significantly different ($P = 0.05$) according to Duncan's multiple-range test.

* Pi = initial infestation level per 1.5 liters soil.

† 0–5 scale: 0 = 0, 1 = 1–2, 2 = 3–10, 3 = 11–30, 4 = 31–100, 5 = > 100 galls or egg masses.

in 10 ml water. Inoculum levels were 6,000 Ma eggs, 6,000 Mi eggs, or a mixture of 3,000 Ma plus 3,000 Mi eggs per pot. Noninoculated plants served as controls. Pots were arranged in a randomized complete block design with six replications in a greenhouse at 20–26 C.

The experiment was terminated 7 weeks after inoculation. Roots were washed free of soil and stained in aqueous phloxine B. Galls and egg masses were rated on a 0–5 scale (0 = 0, 1 = 1–2, 2 = 3–10, 3 = 10–30, 4 = 31–100, and 5 = > 100 galls and egg masses).

Growth chamber experiment: Seven-day-old soybean seedlings were transplanted, one per pot, into steam-sterilized 1:1 by volume sand:Varina sandy loam soil in 15-cm-d plastic pots. Three days after transplanting, plants were inoculated with 6,000 Ma eggs, 6,000 Mi eggs, or a mixture of 3,000 Ma eggs plus 3,000 Mi eggs per pot. Noninoculated plants served as controls. Pots were arranged in a randomized complete block design with eight replications in growth chambers at 25 and 30 C.

The experiment was terminated 7 weeks after inoculation. Roots were washed free of soil and stained in aqueous phloxine B. Gall and egg mass numbers and root and shoot dry weights were determined.

Temperature-tank experiments: Seven-day-old soybean seedlings were transplanted into steam-sterilized sandy clay soil in 1.9-liter plastic containers. Seven days after transplanting, plants were inoculated with 2,500, 5,000, or 10,000 Ma or Mi eggs per plant. Noninoculated plants served as controls. Plants were arranged in a randomized complete block design with five replications in each of two water baths at 24 C or two water baths at 28 C in the greenhouse.

The experiment was terminated 7 weeks after inoculation. Plant roots were washed free of soil and stained with phloxine B. Numbers of galls and egg masses and fresh weights of roots and shoots were determined.

Fourteen-day-old soybean seedlings were inoculated with different combined inoculum levels (250 + 250, 500 + 500, 1,000 + 1,000, 2,500 + 2,500, 5,000 + 5,000, and 7,500 + 7,500 eggs) of Ma and Mi. Treatments were replicated five times in two greenhouse water baths at each of two temperatures, either 24 or 28 C. Seven weeks after nematode inoculation, gall and egg mass numbers and root and shoot dry weights were determined.

RESULTS

Greenhouse experiment: Ma produced more galls and egg masses than Mi, and the combined inoculation with both nematode species produced intermediate numbers of galls and egg masses (Table 1).

Growth chamber experiment: At 25 C, Ma produced significantly more galling and egg masses ($P = 0.05$) than did the combined Ma + Mi, and Mi produced the fewest galls and egg masses (Table 2). Root dry weights were suppressed ($P = 0.05$) by Ma and combined Ma + Mi but not by Mi. Shoot dry weights of nematode infected plants did not differ significantly from the controls.

At 30 C, numbers of egg masses produced by Ma did not differ significantly from those produced by Ma + Mi, although more galls were produced in the combination treatment (Table 2). Mi produced fewer galls and egg masses than the other nematode treatments. More galls and egg masses were observed at 30 C than at 25 C. Root dry weights were suppressed ($P = 0.05$) by the combined Ma + Mi treatment but not by Ma or Mi. Shoot dry weights were suppressed by Ma and combined Ma + Mi treatments but not by Mi.

Effect of inoculum levels of Ma and Mi in temperature tanks: Ma produced more galls and egg masses than Mi at 24 C (Table 3). Ma at an initial inoculum level (Pi) of 10,000

TABLE 2. Effect of *Meloidogyne arenaria* (Ma) or *M. incognita* (Mi) or combined Ma + Mi on number of galls and egg masses and dry weights in grams of roots and shoots of Davis soybean at 25 and 30 C in the growth chamber. Replicated eight times.

		25 C				30 C			
Treatment	Pi* (eggs)	Galls	Egg masses	Root wt	Shoot wt	Galls	Egg masses	Root wt	Shoot wt
Ma	6,000	80.0 a	70.0 a	1.58 b	3.22 a	120.9 b	80.9 a	1.55 ab	4.00 b
Mi	6,000	28.5 c	24.3 c	1.74 ab	3.41 a	40.1 c	39.3 b	1.70 ab	4.92 a
Ma + Mi	3,000 + 3,000	50.0 b	48.8 b	1.65 b	3.19 a	140.9 a	78.3 a	1.50 b	4.29 b
Control	0	0 d	0 d	1.97 a	3.34 a	0 d	0 c	1.75 a	5.01 a

Data followed by the same letter in columns are not significantly different ($P = 0.05$) according to Duncan's multiple-range test.
* Pi = initial infestation level per 1.5 liters soil.

eggs induced significantly more galls and egg masses ($P = 0.05$) than at Pi 2,500 but not at Pi 5,000. There were no significant differences in numbers of galls and egg masses produced by different inoculum levels of Mi.

Root and shoot fresh weights were greater with Mi at Pi 2,500 than at higher inoculum levels or in the control. Other Ma and Mi Pi did not differ in root fresh weights from the control. Shoot fresh weights were significantly decreased with Ma at Pi 5,000 and 10,000 and Mi at 10,000.

At 28 C, Ma at the higher inoculum levels (Pi 5,000 and 10,000) produced significantly more galls and egg masses than the other Ma and Mi inoculum levels. Different Mi inoculum levels resulted in no differences in the numbers of galls and egg masses. Galling and egg mass production by Mi were greater at 28 C than at 24 C.

Root fresh weights were not significantly affected by the nematode treatments, whereas shoot fresh weights were suppressed by Ma.

Combined inoculum levels of Ma and Mi in temperature tanks: At 24 C, numbers of galls and egg masses increased with increments of Pi of combined Ma + Mi (Table 4). Numbers of galls and egg masses among the nematode treatments differed ($P = 0.05$), with the exception of the two lowest Pi.

Root galling was severe and accounted for much of the root biomass. Root fresh weights were different only at Pi 1,000 + 1,000, whereas shoot fresh weights were suppressed at all nematode Pi. The degree of galling was inversely related to shoot fresh weight.

At 28 C, gall and egg mass production was lower than at 24 C but followed the same pattern (Table 4).

TABLE 3. Effect of initial inoculum levels of *Meloidogyne arenaria* or *M. incognita* on numbers of galls and egg masses, and fresh weights in grams of roots and shoots of Davis soybean at 24 and 28 C soil temperature. Replicated five times.

	24 C				28 C			
Eggs/1.5 liters soil	Galls	Egg masses	Root wt	Shoot wt	Galls	Egg masses	Root wt	Shoot wt
M. arenaria								
2,500	326.8 b	315.4 b	2.88 ab	2.35 bc	235.4 c	217.6 c	2.34 a	0.94 b
5,000	458.4 ab	443.8 ab	2.47 b	1.48 d	436.0 b	416.2 b	2.09 a	0.77 b
10,000	536.8 a	518.0 a	2.61 b	1.16 d	530.6 a	510.4 a	1.48 a	0.39 b
M. incognita								
2,500	29.4 c	27.4 c	3.85 a	3.53 a	113.2 d	107.0 d	2.59 a	4.00 a
5,000	62.4 c	57.6 c	3.05 ab	2.56 b	128.0 d	122.6 c	2.44 a	3.20 a
10,000	56.8 c	51.6 c	1.33 c	1.58 cd	201.4 cd	193.4 cd	1.74 a	3.02 a
Control	0 d	0 d	1.94 bc	2.67 b	0 e	0 e	2.47 a	4.52 a

Data followed by the same letter in columns are not significantly different ($P = 0.05$) according to Duncan's multiple-range test.

TABLE 4. Effect of different combined inoculum levels of *Meloidogyne arenaria* plus *M. incognita* on numbers of galls and egg masses and fresh weights in grams of roots and shoots of Davis soybean at 24 and 28 C soil temperature. Replicated five times.

Eggs/1.5 liters soil	24 C				28 C			
	Galls	Egg masses	Root fresh wt	Shoot fresh wt	Galls	Egg masses	Root fresh wt	Shoot fresh wt
250 + 250	88.6 e	60.2 e	2.27 ab	2.62 b	81.6 c	74.4 c	2.41 ab	1.89 b
500 + 500	118.6 e	87.4 e	2.14 ab	2.30 bc	115.6 c	109.6 a	2.46 ab	1.81 b
1,000 + 1,000	231.4 d	210.4 d	1.87 b	1.55 cd	204.6 b	199.4 b	2.03 ab	1.47 bc
2,500 + 2,500	388.6 c	364.6 c	2.15 ab	1.53 cd	219.2 b	212.2 b	1.72 ab	0.89 cd
5,000 + 5,000	547.0 b	515.6 b	2.82 ab	1.09 d	322.6 a	316.2 a	1.81 ab	0.49 d
7,500 + 7,500	646.6 a	620.8 a	2.41 ab	1.12 d	309.0 a	292.6 a	1.34 b	0.40 d
Control	0 f	0 f	2.93 a	3.55 a	0 d	0 d	2.49 a	3.12 a

Data followed by the same letter within a column do not differ significantly from each other ($P = 0.05$) according to Duncan's multiple-range test.

DISCUSSION

This study confirms that Davis soybean is a susceptible and favorable host to Ma and Mi as shown by others (9,11). However, our comparative tests showed that Ma produces more galls and egg masses and is more virulent than Mi on susceptible soybean.

Temperature affects movement, rate of reproduction, and expression of nematode damage to host plants (14). Each nematode species has its own temperature requirements (12) which may be affected by plant cultivar (4). Plant growth is also affected by temperature, and this may influence the relationship between initial nematode level and plant growth (10). The temperatures chosen for our study fall within a broad optimal temperature range for rate of reproduction of root-knot nematodes (12); nevertheless, 28–30 C soil temperature was favored by Mi, whereas the reproductive rate for Ma was excellent, and greater than Mi, at both regimes.

The dramatic increase in incidence of Ma on flue-cured tobacco in 1982 (6) and soybean (unpubl.) was correlated with air temperatures 6 C higher than the 18-year average for the month of April (J. P. Krausz, unpubl.). The following year during this same month, air temperature was cooler than normal, soils were excessively moist, and problems with *Meloidogyne* were less numerous. However, rate of plant growth was initially very slow in 1983, and this may also relate to reduced nematode reproductive factor and equilibrium density (10). Ma is able to efficiently utilize lower temperature within the broad optimal range of 24–32 C. This characteristic may enable it to dominate Mi on susceptible hosts.

It is not known from these studies if the greater number of egg masses in Ma treatments, compared with Mi, is due to greater embryonic development and eclosion rates, penetration rate, or developmental success. There was no difference in number of emerging juveniles among four major *Meloidogyne* species at four temperatures between 15 and 30 C (5), but more Ma than Mi were found in roots of tobacco (2).

The increased soybean crop losses, coincident with the spread of Ma, are related to the greater population potential and growth suppression of Ma, and control efforts should be directed primarily toward Ma rather than Mi.

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