

## Crop Rotation and Nematicide Effects on the Frequency of *Meloidogyne* spp. in a Mixed Population

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### ABSTRACT

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The effects of crop rotation and nematicide 1,3-dichloropropene (1,3-D) on the relative frequency of *M. incognita* race 3 and *M. arenaria* race 2 and on tobacco yields were determined in a sandy loam soil. Cropping sequences altered the species composition and population densities of *Meloidogyne* spp. and increased tobacco yields. *M. incognita* predominated when cotton or corn preceded tobacco; *M. arenaria* predominated when soybean or peanut preceded tobacco. Fumigation of tobacco land increased the density of *M. arenaria* compared to *M. incognita*. The

effects of a previous crop on tobacco yields varied in successive years. Cotton, corn, peanut, sorghum, or rye-fallow preceding tobacco in 1985 enhanced yields compared to yields when soybean preceded tobacco. Rye-fallow preceding tobacco in 1987 resulted in greater tobacco yields than when tobacco was preceded by soybean, corn, cotton, sorghum or peanut. Application of 1,3-D increased tobacco yields, except when preceded by rye-fallow.

*Additional keywords:* nematode, rye.

Root-knot nematodes (*Meloidogyne* spp.) are commonly associated with field crops, particularly flue-cured tobacco (*Nicotiana tabacum* L.) in the southeastern United States (16,19). Approximately 88% of the tobacco acreage in South Carolina is treated annually with a nematicide, but decreases in production caused by *Meloidogyne* spp. still range from 0.5 to 1.4% of South Carolina's total tobacco crop (13,21). *Meloidogyne incognita* (Kofoid & White) Chitwood, races 1 and 3, is the most common species of *Meloidogyne* in North and South Carolina's tobacco fields; however, *M. arenaria* (Neal) Chitwood, *M. javanica* (Treub) Chitwood, and *M. incognita* races 2 and 4 are increasing in importance (1,11). This complicates traditional crop-rotation schemes because reproduction of different species of *Meloidogyne* varies by crop and cultivar (1,11,16,18). Species of *Meloidogyne* that are more aggressive than *M. incognita*, such as *M. arenaria* and *M. javanica*, appear to be increasing in frequency in most flue-cured tobacco-producing states (1,11). With changes in species composition, the likelihood of increased losses caused by root-knot nematodes is great.

Nematicides and plant resistance to *M. incognita* races 1 and 3 have been key components in the management of root-knot nematode on tobacco. During 1982, an epidemic of root-knot disease occurred on flue-cured tobacco in South Carolina (11), and cultivars resistant to *M. incognita* frequently were affected by severe root galling. *M. arenaria* and *M. incognita*, the principal species involved, were frequently found in the same field. *M. arenaria* parasitism of a cultivar resistant to *M. incognita* race 3 can change the resistance of that cultivar to *M. incognita* (8,26). *M. arenaria* is more difficult to control with nematicides than is *M. incognita* (13), and no commercial tobacco cultivars are resistant to this species (2,18). With the increasing occurrence of *M. arenaria* in South Carolina, nematode resistance in tobacco may play a diminished role in root-knot nematode control unless commercial cultivars with resistance to *M. arenaria* are developed.

Crop rotation has been used successfully to reduce nematode population densities and to increase tobacco yields (6,12,23). Because multispecies populations of root-knot nematode are in-

creasingly widespread, the effects of crop rotation must be completely characterized. Because of wide variations in aggressiveness and host compatibility among *Meloidogyne* spp., the different effects of crop rotation on *Meloidogyne* spp. may play a key role in the design of long-term control programs for root-knot nematodes. In addition, cropping history may play a role in the predominance of different *Meloidogyne* spp. We report on field tests to determine the value of selected rotation crops and nematicide 1,3-dichloropropene (1,3-D) for management of mixed populations of *M. arenaria* race 2 and *M. incognita* race 3 in a 2-yr rotation with tobacco.

### MATERIALS AND METHODS

**Inoculum and field preparation.** *M. arenaria* race 2 and *M. incognita* race 3 were isolated from tobacco in Florence County, SC, and were increased on tomato (*Lycopersicon lycopersicum* (L.) Karsten 'Rutgers') in a greenhouse. Species confirmation and race identification were based on differential host tests, perineal patterns, and body length of second-stage juveniles (J2) (25). Eggs were extracted from roots of 60-day-old tomato plants in 0.05% sodium hypochlorite and were washed in tap water (14).

The trials were located at the Pee Dee Research and Education Center, Florence, SC, using Norfolk sandy loam soil (pH 5.9, 75% sand, 17% silt, 8% clay, 0.08% organic matter). During 1983, field plots planted in soybean the previous year were fumigated with ethylene dibromide (EDB, 90% EC) applied with a gravity flowmeter and were injected 15 cm deep with a single chisel per row at 14 L/ha (1.7 ml/m). The fumigant was placed in the center of a 60-cm-wide bed. Bedding discs were used to seal the chisel opening and to form a 36-cm-high bed with fumigant placed 40 cm from the top of the bed. Three weeks after fumigation, tobacco cultivar Coker 319 seedling roots were infested with a 50:50 mixture of *M. arenaria* race 2 and *M. incognita* race 3 eggs. Roots were dipped into a water suspension of eggs (500 eggs/ml of each nematode species) to which 6 g of Terra-sorb per liter, a gelatinized starch hydrolized polyacrylonitrile copolymer, (Industrial Services International, Inc., Bradenton, FL) was added (10). Seedlings were immediately transplanted into test subplots

consisting of four rows (rows were spaced 1.2 m apart × 10.6 m long) with plants spaced 60 cm apart within the row (10). A 1.2-m border separated all plots and subplots within a block. Infestation of tobacco roots with a 50:50 mixture of *M. incognita* race 3 and *M. arenaria* race 2 resulted in uniform root galling of tobacco at the test site in 1983.

**Crop sequence, nematicide application, and *Meloidogyne* spp. populations, trial 1.** During 1984, selected crops were planted in the previously infested plots and were alternated with tobacco in a 2-yr rotation. The treatment design was factorial (six rotation crops and two nematicide treatments) (24). The rotation crops and cultivars were selected based on their level of resistance to root-knot nematodes and were classified susceptible, moderately resistant, or resistant based on the level of reproduction of *Meloidogyne* spp.: peanut was resistant to *M. incognita* and to *M. arenaria* race 2 (25); corn was susceptible to *M. incognita* with moderate resistance to *M. arenaria* (28); cotton was resistant to *M. arenaria* and was susceptible to *M. incognita* race 3 (25); soybean cv. Coker 488 was susceptible to *M. arenaria* and to *M. incognita* and cv. Coker 368 was resistant to *M. incognita* and was susceptible to *M. arenaria* (20); rye was moderately resistant to *M. arenaria* and to *M. incognita* (17); and sorghum was resistant to *M. incognita* and to *M. arenaria* (9). The selected crops and planting dates included corn (*Zea mays* L. 'Pioneer 3369A') on 5 April 1984 and 12 April 1986; soybean (*Glycine max* (L.) Merr. 'Coker 488' and 'Coker 368'), cotton (*Gossypium hirsutum* L. 'Coker 310'), sorghum (*Sorghum bicolor* (L.) Moench 'Coker 7723'), and peanut (*Arachis hypogaea* L. 'Floriant') on 17 May 1984 and 6 May 1986; and rye-fallow (*Secale cereale* L. 'Abruzzi') on 15 October 1983 and 17 November 1985. Disc harrowing and in-row subsoiling, 35 cm deep, preceded all treatments, except rye-fallow, which was disc harrowed. Seeding rates for corn, soybean, cotton, sorghum, and peanut were 6, 23, 13, 20, and 13 seeds/m of row, respectively. The selected crops were planted into subplots consisting of four rows (rows were spaced 1 m wide × 10.6 m long) centered in the previously infested plots. Rye seeds were broadcast. All crops were maintained by standard agronomic practices; no supplemental irrigation was supplied. Rye plots were mowed at maturity and disc harrowed, as needed, to suppress weeds.

Tobacco seedlings, Coker 319, were transplanted on 30 April 1985 and 18 May 1987 into plots previously planted to the rotation crops during 1984 and 1986. Plots were arranged in a randomized complete-block design with the previous crop as whole-plot treatments and nematicide application as subplot treatments (24). Disc harrowing and in-row subsoiling, 35 cm deep, preceded all

treatments. A 1.2-m border separated all whole plots and subplots within a block, and a 4.6-m border separated each block. Cultivation for bed preparation, fertilizer applications, and weed control was conducted parallel to the rows from block to adjacent block. The direction of cultivation provided a 4.6-m border between cultivated plots to minimize plot-to-plot contamination. All crop and nematicide treatments were replicated four times. Fumigant nematicide 1,3-D (94%), 56 L/ha (6.7 ml/m), was applied to a four-row subplot within each eight-row whole plot on 10 April 1985 and 10 April 1987, as previously described. Soil samples consisting of a composite of 20 cores per plot, each 2 cm in diameter × 20 cm deep, were removed from each subplot at bimonthly intervals. A 500-g soil sample from each subplot was assayed for nematodes after extraction by a semiautomatic elutriator and by the sugar centrifugal-flotation method (4,15). Mature tobacco leaves were harvested three times from the center two rows in each plot during 1985 and 1987. Yield was based on fresh leaf weight, assuming that leaf weight was 20% of fresh weight. At the last harvest, roots of 10 plants from the center two rows in each plot were excavated at random and were rated for galling on a 0–10 scale, for which 0 = no galling and 10 = 100% of the root-surface galled (3).

After the last tobacco harvest (1987), soil samples consisting of a composite of 40 cores per plot were removed from the root zone of plants in the center two rows in each subplot. A 1,000-g soil sample from each subplot was bioassayed for *Meloidogyne* spp. by transplanting a Rutgers tomato seedling into a pot containing the soil and by maintaining the plants in a greenhouse for 50 days. Plant roots were removed from the pots and were washed free of soil. Second-stage juveniles (J2) were extracted from roots in a fine water mist for 5 days (3), were heat relaxed, and were preserved in 2% formaldehyde solution. Roots from the mist chamber were then stained by the sodium hypochlorite acid fuchsin method (5) and were stored in glycerin for later inspection of the perineal patterns of excised females. The length of J2s was measured with a Leitz Dialux 20 microscope fitted with a Leitz Wetzlar tracing device (Ernst Leitz Inc., GMBH D 6330, Wetzlar, Germany). With a Zeiss interactive digital analysis system (Carl Zeiss, Inc., Thornwood, NY), 100 J2s of each *M. arenaria* and *M. incognita* isolate used to inoculate the field were measured, and confidence limits were set. Lengths of J2s from the *M. incognita* race 3 population used in this study ranged from 363 to 410 μm. Lengths of J2s from the *M. arenaria* population used in this study ranged from 437 to 486 μm. Body lengths of both nematode species were within the range of published values (25). The ratio of the two species in each subplot was

TABLE 1. Effect of previous crop and nematicide application on percentages of *Meloidogyne* spp. within a mixed population of *M. arenaria* race 2 and *M. incognita* race 3

Crop sequence <sup>w</sup>					Alternate crop resistance ratings <sup>x</sup>		Tomato bioassay of soil (1987) <sup>y</sup>				
	1984	1985	1986	1987	MI	MA	J2 (× 1,000)/root system		<i>M. arenaria</i> (%)		
							Nematicide		Nematicide		
Corn	tobacco	corn	tobacco	S	MR	(-)	(+)	(-)	(+)		
Soybean (s)	tobacco	soybean (s)	tobacco	S	S	28.4 a	26.8 a	22 c	56 b		
Soybean (r)	tobacco	soybean (r)	tobacco	R	S	17.5 a	10.3 a	97 a	87 a		
Cotton	tobacco	cotton	tobacco	R	R	20.3 a	17.1 a	95 a	80 a		
Sorghum	tobacco	sorghum	tobacco	S	R	31.2 a	23.1 a	16 c	75 ab		
Peanut	tobacco	peanut	tobacco	R	R	22.1 a	21.2 a	65 b	70 ab		
Rye-fallow	tobacco	rye-fallow	tobacco	R	R	31.2 a	23.1 a	85 ab	90 a		
LSD ( <i>P</i> = 0.05)						19.0 a	20.0 a	80 ab	82 a		
						NS <sup>z</sup>		18.6			

<sup>w</sup>(s) = *M. incognita* susceptible cv. Coker 488; (r) = *M. incognita* resistant cv. Coker 368.

<sup>x</sup>MI = *M. incognita*; MA = *M. arenaria*; S = susceptible; MR = moderate resistance; R = resistant.

<sup>y</sup>Data are the means of four replications. Means within a column with the same letter are not different (*P* = 0.05) according to LSD. LSD values for J2 numbers and percent *M. arenaria* are for comparison of nematicide effects within a specific crop treatment. (+) = 1,3-D (56 L/ha) applied to tobacco in 1985 and 1987; (-) = no treatment. J2 = second-stage juvenile population densities of *Meloidogyne* spp. extracted from tomato roots 50 days after planting in soil collected from each plot.

<sup>z</sup>NS = not significant.

based on 50 J2s that were within the specified values. *M. arenaria* is the only root-knot nematode in South Carolina with larvae within the specified range; however, there are other species of root-knot nematode with shorter larvae similar to *M. incognita*. When 50% of the larvae in a sample were classified as *M. incognita*, we examined 10 perineal patterns from the sample to ascertain if another species was present (25). No other species of root-knot nematode was observed within the sampled plots.

**Crop sequence and *Meloidogyne* spp. populations, trial 2.** After the completion of trial 1, the test site was tilled with a moldboard plow and was disc harrowed twice in opposite directions. The test site contained varying mixtures of *M. arenaria* and *M. incognita*. Plot designations were rerandomized, and selected rotation crops were planted as before in individual plots consisting of 16 rows (rows were 1 m wide  $\times$  10.6 m long) arranged in a randomized complete-block design (24). The selected crops and planting dates included: rye-fallow, 10 November 1987; corn, 28 April 1988; cotton, 18 May 1988; and sorghum, 18 May 1988. All plots were maintained as previously described. Rye plots were mowed at maturity and were disc harrowed, as needed, to retard weed growth. Soil samples, consisting of a composite of 80 cores, were removed from each plot on 31 March 1989. A 1,000-g soil subsample from each plot was bioassayed for *Meloidogyne* spp., and the species ratios were determined as previously described. Bioassay plants were maintained in a greenhouse for 50 days and were evaluated for nematode development. Each root system, washed free of soil, was stained in Phloxine B (150 mg/L) for 15 min, and egg masses were counted (7).

Data from experiments were subjected to ANOVA with the MSTAT computer software package (Michigan State University, East Lansing, MI). Treatment means were compared using LSD or Duncan's multiple range tests.

## RESULTS

**Previous crop-affected nematode populations, trial 1.** In non-fumigated soils, cotton or corn preceding tobacco resulted in a lower *M. arenaria*/*M. incognita* ratio ( $P < 0.05$ ) in soil after the last tobacco harvest than was present when tobacco was preceded by soybean, sorghum, peanut, or rye-fallow (Tables 1 and 2). In nonfumigated soil, sorghum in rotation with tobacco resulted in a lower *M. arenaria*/*M. incognita* ratio than that for tobacco preceded by soybean, but the *M. arenaria*/*M. incognita* ratio was greater ( $P < 0.05$ ) than that for tobacco preceded by corn or cotton (Table 1 and 2). Analysis of variance revealed a significant crop  $\times$  nematicide interaction (Table 2). The *M. arenaria*/*M. incognita* ratio was increased ( $P < 0.05$ ) when tobacco preceded by cotton or corn was fumigated. Tobacco preceded by soybean, sorghum, peanut, or rye-fallow had a similar *M. arenaria*/*M. incognita* ratio in fumigated and nonfumigated tobacco plots. (Tables 1 and 2).

Population densities of *Meloidogyne* spp. varied among rotation crops (Fig. 1). Soybean supported the greatest populations during 1984 and 1986, and peanut, corn, sorghum, and rye

TABLE 2. Analysis of variance for population density and interspecific percentages of *Meloidogyne* spp. within concomitant populations of *M. arenaria* race 2 and *M. incognita* race 3, as affected by previous crop and nematicide application.

Source	df	Mean squares <sup>y</sup>	
		J2 ( $\times$ 1,000)/ rot <sup>z</sup>	<i>M. arenaria</i> (%)
Replicates	3		
Crop (C)	6	204,735,671	3,655*
Error <sub>a</sub>	18	131,030,169	269
Nematicide (N)	1	239,557,125	1,921*
C $\times$ N	6	30,702,993	1,372*
Error <sub>b</sub>	21	124,010,250	160

<sup>y</sup>  $P = 0.01$  (\*).

<sup>z</sup> J2 = second-stage juveniles of *Meloidogyne* spp. extracted from tomato roots 50 days after planting in rhizosphere soil.

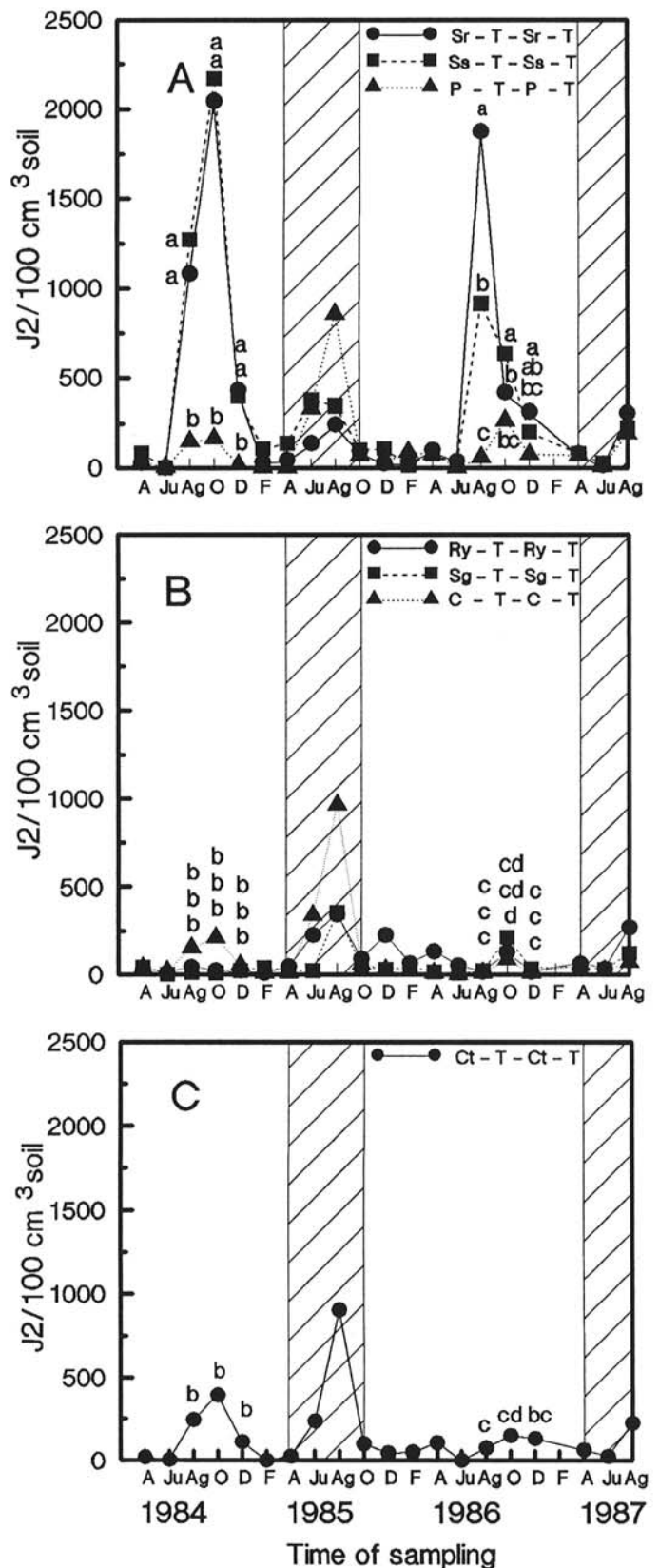


Fig. 1. Populations of *Meloidogyne* spp., second-stage juveniles (J2; J2 per 100 cm<sup>3</sup> of soil) extracted from the root zone of A, soybean (Sr = cv. Coker 368 and Ss = cv. Coker 488) and peanut (P = cv. Florigiant), B, rye-fallow (Ry = cv. Abruzzi plus clear cultivation after crop maturity), sorghum (Sg = cv. Coker 7723), and corn (C = cv. Pioneer 3369A), and C, cotton (Ct = cv. Coker 310). All were grown in a 1-yr rotation with tobacco (T = cv. Coker 319). Values within a sample period followed by the same letter are not different according to LSD ( $P = 0.05$ ). Shaded areas represent time period in which tobacco was present.

TABLE 3. Yield of Coker 319 tobacco, root-galling index, and final population density of *Meloidogyne* spp., second-stage juveniles (J2) as affected by previous crop with (+) and without (-) 1,3-D nematicide application

Crop sequence <sup>y</sup>				Yield (kg/ha) <sup>w</sup>				Root galling <sup>x</sup>				J2/100 cm <sup>3</sup> soil (PF) <sup>y</sup>			
				1985		1987		1985		1987		1985		1987	
1984	1985	1986	1987	-	+	-	+	-	+	-	+	-	+		
Corn	tobacco	corn	tobacco	2,374 a	3,616 a	2,108 b	3,368 a	5.6 bc	2.2 a	5.9 a	5.8 a	963 a	337 a	69 a	106 a
Soybean (s)	tobacco	soybean (s)	tobacco	937 b	3,332 a	1,816 b-d	2,799 a	8.5 a	0.7 a	8.0 a	6.3 a	344 a	306 a	225 a	69 a
Soybean (r)	tobacco	soybean (r)	tobacco	566 b	3,333 a	1,375 cd	2,798 a	8.6 a	1.9 a	7.2 a	6.1 a	244 a	319 a	306 a	238 a
Cotton	tobacco	cotton	tobacco	2,265 a	3,093 a	1,639 b-d	3,225 a	5.1 bc	1.2 a	7.5 a	5.7 a	900 a	125 a	225 a	175 a
Sorghum	tobacco	sorghum	tobacco	2,048 a	2,962 a	1,198 d	2,760 a	2.9 d	1.5 a	6.6 a	4.7 a	356 a	350 a	119 a	50 a
Peanut	tobacco	peanut	tobacco	2,309 a	3,245 a	2,214 b	3,187 a	4.2 cd	1.1 a	7.2 a	5.6 a	856 a	138 a	194 a	219 a
Rye-fallow	tobacco	rye-fallow	tobacco	2,788 a	3,398 a	3,081 a	2,909 a	6.3 b	1.2 a	7.7 a	5.5 a	344 a	324 a	269 a	94 a
LSD ( <i>P</i> = 0.05)				804		809		1.6		2.8		739		NS <sup>z</sup>	

<sup>y</sup> (s) = *M. incognita* susceptible cv. Coker 488; (r) = *M. incognita* resistant cv. Coker 368.

<sup>w</sup>Data are the means of four replications. Means within a column with the same letter are not different (*P* = 0.05) according to LSD. LSD values are for yield, root galling, and *Meloidogyne* spp. J2s compare nematicide effects within a specific crop treatment. (+) = 1,3-D (56 L/ha), (-) = no treatment.

<sup>x</sup> Root-gall index based on a 0-10 scale: 0 = no root galling and 10 = 100% of the root surface galled.

<sup>y</sup> J2 = second-stage juvenile. PF = final population densities of *Meloidogyne* spp. extracted from 100 cm<sup>3</sup> soil 130 days after planting.

<sup>z</sup> NS = not significant.

TABLE 4. Analysis of variance for tobacco yield, root-gall index, and second-stage juveniles (J2) of *Meloidogyne* spp. after rotation with soybean, cotton, sorghum, peanut, or rye-fallow with or without 1,3-D

Source	df	Mean squares					
		Yield (kg/ha)		Root galling		J2/100 cm <sup>3</sup> soil (PF) <sup>x</sup>	
		1985	1987	1985	1987	1985	1987
Replicates	3						
Crop (C)	6	1,446,290***	1,087,818**	9**	2 NS <sup>z</sup>	143,346 NS	36,495 NS
Error <sub>a</sub>	18	395,573	229,506	2	2	361,615	25,612
Nematicide (N)	1	26,835,763**	16,562,625**	283**	31**	1,268,715*	59,475 NS
C × N	6	1,427,844**	742,488*	10**	1 NS	293,651 NS	13,095 NS
Error <sub>b</sub>	21	298,419	302,144	1	4	252,058	19,988

<sup>x</sup> PF = final nematode population density at tobacco harvest.

<sup>y</sup> *P* = 0.05 (\*); *P* = 0.01 (\*\*).

<sup>z</sup> NS = not significant.

supported minimal reproduction of *Meloidogyne* spp. (Fig. 1A and 1B). Reproduction of *Meloidogyne* spp. was moderate on cotton during 1984 and was low during 1986 (Fig. 1C). The final nematode population density at tobacco harvest (PF) during 1985 and 1987 was not affected significantly by the previous crop (Tables 3 and 4).

Differences (*P* = 0.05) in tobacco yields and root galling were observed (Tables 3 and 4). In nonfumigated plots (1985), cotton, corn, peanut, sorghum, or rye-fallow preceding tobacco enhanced tobacco yields compared to soybean preceding tobacco. In nonfumigated plots (1987), rye-fallow preceding tobacco enhanced tobacco yields compared to soybean, corn, cotton, sorghum, or peanut. Analysis of variance revealed a significant crop × nematicide interaction (Table 4). Fumigation of plots increased tobacco yields when the tobacco crop was preceded by peanut, sorghum, cotton, soybean, or corn (Table 3 and 4). Fumigation of plots did not increase tobacco yields significantly when tobacco was preceded by rye-fallow.

In nonfumigated plots (1985), there was less root galling on tobacco preceded by sorghum than on tobacco preceded by cotton, soybean, corn, or rye-fallow. However, tobacco in nonfumigated plots preceded by corn, cotton, sorghum, peanut, or rye-fallow had a lower root-galling index than did tobacco preceded by soybean (Table 3). Analysis of variance revealed a significant crop × nematicide interaction for root galling during 1985 (Table 4). Fumigation of tobacco preceded by corn, soybean, cotton, peanut, or rye-fallow suppressed root galling; however, fumigation did not suppress galling significantly in tobacco preceded by sorghum (Table 3). In 1987, root-galling of tobacco was not affected significantly by the previous crop, and fumigation with 1,3-D reduced (*P* < 0.05) root galling (Table 3 and 4).

TABLE 5. Population density and percentages of different *Meloidogyne* spp. within mixed populations of *M. arenaria* race 2 and *M. incognita* race 3, as affected by previous crop<sup>y</sup>

Previous crop <sup>x</sup>	Tomato bioassay of soil (1989)	
	Egg masses/ root system	<i>M. arenaria</i> (%)
Sorghum	25 b	...
Corn	139 b	16 bc
Cotton	160 b	6 c
Rye-fallow	146 b	43 ab
Tobacco (s)	795 a	47 ab
Tobacco (r)	660 a	63 a

<sup>y</sup> Data are the means of four replications. Means within a column with the same letter are not different (*P* = 0.05) according to Duncan's multiple range test.

<sup>z</sup> (s) = *M. incognita* susceptible cv. Coker 319; (r) = *M. incognita* resistant cv. Coker 176.

**Previous crop-affected nematode populations, trial 2.** Population densities of *Meloidogyne* spp. in soil as determined by bioassay were affected by the previous crop (*P* = 0.05) (Table 5). Tomato roots planted in soil from plots previously planted to sorghum, corn, cotton, or rye-fallow contained fewer (*P* = 0.05) egg masses than did plots previously planted to tobacco. The *M. arenaria*/*M. incognita* ratio varied in plots with different cropping histories. Plots previously planted to cotton contained a lower *M. arenaria*/*M. incognita* ratio than did plots previously planted to tobacco or rye-fallow. The *M. arenaria*/*M. incognita* ratio did not differ significantly between plots previously planted

to corn versus cotton ( $P=0.05$ ) (Table 5). Plots previously planted to sorghum supported minimal reproduction in the tomato bioassay; as a result, the *M. arenaria*/*M. incognita* ratio could not be determined.

## DISCUSSION

Crop rotation can be used to manage *Meloidogyne* spp. on tobacco. The success of this tactic relies on the proper identification of the species of root-knot nematode present within a field and on an understanding of the effects of rotation crops on the species, races, and populations of *Meloidogyne* present.

Crop sequence had a profound effect on the relative frequencies of *Meloidogyne* spp. Selection of rotation crops apparently can shift root-knot nematode populations from more-aggressive to less-aggressive species or vice versa. Shifting of root-knot nematode populations can be a valuable strategy in the design of long-term integrated control programs in which host-plant resistance plays a pivotal role. In addition, rotation crops that have a high level of resistance to *M. arenaria* race 2 and *M. incognita* race 3, such as peanut and sorghum, did not behave uniformly with respect to their individual impacts on species shifts. Root-knot nematodes can reproduce at a rapid rate, so the predominance of a particular species of *Meloidogyne* in a multispecies population after the harvesting of a rotation crop and then tobacco could critically impact yields.

Corn and cotton are used frequently in South Carolina in rotations with tobacco and are better hosts for *M. incognita* than for *M. arenaria* (22,25,28). This difference in host suitability provided selection pressure in a field setting. Corn and cotton reduced the *M. arenaria*/*M. incognita* ratio and may be a valuable tool for managing the more aggressive species, *M. arenaria*. In contrast, root-knot nematode reproduction was abundant on soybean. Soybean cultivar Coker 488, which is susceptible to *M. incognita*, apparently did not affect the frequency of *Meloidogyne* spp. relative to the frequency associated with Coker 368, which is resistant to *M. incognita*. At the completion of the study, the predominant species after a soybean rotation was *M. arenaria*. The decline in cotton acreage during the preceding decade in the southeastern United States along with simultaneous increases in soybean acreage may have played a key role in the increased occurrence of *M. arenaria* in South Carolina.

Nematicide application reduced the population densities of both *Meloidogyne* spp., but the *M. arenaria*/*M. incognita* ratio increased in some cases. This negated the positive effects of rotation related to species composition. Widespread use of nematicides may shift populations of *Meloidogyne* spp. within multispecies root-knot nematode communities. The increases in *M. arenaria* may be caused in part by widespread use of nematicides in South Carolina and may play a significant role in long-term losses caused by root-knot nematode.

Root-knot nematode populations and tobacco yields varied when tobacco was preceded by different rotation crops. However, a 1-yr rotation to any crop was insufficient to suppress root-knot nematode population densities acceptably. Only rye-fallow failed to show a yield increase after fumigation with 1,3-D. The observed increases in tobacco yields after 1,3-D application suggest sufficient populations of *Meloidogyne* spp. were present to reduce yields after a 1-yr rotation. Abundant root galling was observed in all plots that did not receive fumigant nematicide during 1985 and 1987. Rye-fallow provided the greatest yields in the absence of a nematicide, but constant weed regrowth required frequent tillage to suppress weeds, and extensive root galling was observed in the rye-fallow-tobacco plots at the end of the tobacco crop. Many weeds are excellent hosts for *Meloidogyne* spp. and can provide a source of inoculum for the following year (27). Root-knot nematode populations were low after sorghum in 1986; however, we noted a substantial yield increase in tobacco after sorghum (1987) with the application of 1,3-D. Control of other nematode species, such as lesion nematode, may have contributed to the yield response after 1,3-D application. Tobacco is a poor host for lesion nematode, but the nematode

will migrate into tobacco roots and cause severe root damage and brown root rot disease (19). Lesion nematode populations decline after tobacco and may not be detected with a soil nematode assay (19).

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