Journal of Nematology 27(2):178–188. 1995.

Effects of Peanut-Tobacco Rotations on Population Dynamics of *Meloidogyne arenaria* in Mixed Race Populations[1]

ANAN HIRUNSALEE, K. R. BARKER, and M. K. BEUTE[2]

Abstract: A 3-year microplot study was initiated to characterize the population dynamics, reproduction potential, and survivorship of single or mixed populations of *Meloidogyne arenaria* race 1 (Ma1) and race 2 (Ma2), as affected by crop rotations of peanut 'Florigiant' and *M. incognita* races 1 and 3-resistant 'McNair 373' and susceptible 'Coker 371-Gold' tobacco. Infection, reproduction, and root damage by Ma2 on peanut and by Ma1 on resistant tobacco were limited in the first year. Infection, reproduction, and root-damage potentials on susceptible tobacco were similar for Ma1 and Ma2. In the mixed (1:1) population, Ma1 was dominant on peanut and Ma2 was dominant on both tobacco cultivars. Crop rotation affected the population dynamics of different nematode races. For years 2 and 3, the low numbers of Ma1 and Ma2 from a previous-year poor host increased rapidly on suitable hosts. Ma1 had greater reproduction factors ([RF] = population density at harvest/population density at preplanting) than did Ma2 and Ma1 + Ma2 in second-year peanut plots following first-year resistant tobacco, and in third-year peanut plots following second-year tobacco. In mixed infestations, Ma1 predominated over Ma2 in previous-year peanut plots, whereas Ma2 predominated over Ma1 in previous-year tobacco plots. Moderate damage on resistant tobacco was induced by Ma1 in the second year. In the third year, moderate damage on peanut was associated with 'Ma2' from previous-year peanut plots. The resistant tobacco supported sufficient reproduction of Ma1 over 2 years to effect moderate damage and yield suppression to peanut in year 3.

Key words: Arachis hypogaea, interaction, *Meloidogyne arenaria, Nicotiana tabacum,* parasitic fitness, peanut, population dynamics, reproduction potential, root-knot, rotation, tobacco.

Peanut (*Arachis hypogaea* L.) and tobacco (*Nicotianum tabacum* L.) are damaged by many nematode species (15,27). In the United States, the most serious species for both crops are root-knot nematodes (*Meloidogyne* spp.). On peanut, the most common species are *M. arenaria* (Neal) Chitwood race 1 and *M. hapla* Chitwood. Tobacco is parasitized by *M. arenaria, M. incognita* (Kofoid & White) Chitwood, *M. javanica* (Treub) Chitwood, and *M. hapla. Meloidogyne hapla* is considered to be the prevalent species in most peanut-producing areas of North Carolina (15). *Meloidogyne arenaria* has become increasingly important on peanut because of its high reproductive potential and damage potential for this crop (13). Still, *Meloidogyne incognita* is the most severe nematode on tobacco in North Carolina, but in recent years, this species has been declining in prevalence, with *M. arenaria* and *M. javanica* increasing (1,11,25). Race 1 of *M. arenaria* causes slight damage on *M. incognita*-resistant tobacco, whereas race 2 severely damages resistant as well as susceptible tobacco (1). Peanut is resistant to race 2 of *M. arenaria* (23). Concomitant infestations of both races of this species are common in fields rotated with both peanut and tobacco (25). Management of root-knot nematodes on both peanut and flue-cured tobacco in the southeastern United States has been based heavily on nematicides (11,22). Resistant cultivars of tobacco are effective only for races 1 and 3 of *M. incognita* (11); no peanut cultivars resistant to *M. arenaria* race 1 are currently available (16).

Crop rotation is one of the oldest and most important approaches to control nematodes parasitizing annual crops (18,24). Because effective chemical control methods are relatively expensive and sub-

Received for publication 27 April 1994.

[1] The research reported in this publication was funded, in part, by the North Carolina Agriculture and Life Sciences Experiment Station, The Rotary Foundation of Rotary International, the government of Thailand, USAID Peanut CRSP (DAN-40480G-SS-2065-00), USAID/OICD (58-319R-1-008), and Khon Kaen University.

[2] Former Graduate Student and Professors, Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695-7616. Present address of first author: Department of Plant Pathology, Faculty of Agriculture, Khon Kaen University, Khon Kaen, 40002, Thailand.

The authors thank Charles Echerd, Dewitt Byrd, Joe Phillips, Joyce Hollowell, Ginger Driver, Christy Jeffries, Julia Schmitt, Alan Walters, M. L. Gumpertz, B. B. Shew, S. R. Koenning and Katherine Kershaw.

ject to environmental constraints, and the numbers of resistant crop cultivars are limited, crop rotation is still widely recommended. In an optimum rotation, the preceding crop suppresses population levels of the target nematode and prevents damage to the next crop (10). Generally, the degree of control is based on the level of susceptibility and resistance of the crops involved and the sequences of cropping (29). Choice of alternate crops, however, becomes limited when the target is root-knot nematodes, which have a very wide host range (18,29). Cropping practices impact both the population density and composition of the nematode community. For example, continuous monoculture tends to narrow the spectrum of communities to those species favoring a single host (17). In contrast, multiculture induces wide fluctuation in nematode population structure (6,17). An increase in *M. arenaria* and *M. javanica* and a decrease in *M. incognita* have frequently been observed in U.S. production areas where *M. incognita*-resistant tobacco cultivars have been used extensively (1,21). Similar practices also resulted in race shifting of *Heterodera glycines* on soybean in North Carolina (24). For nematode populations with high genetic variability, a narrow cropping pattern can exert selection pressure upon the nematode population to such an extent that resistance-breaking "pathotypes" can emerge and gradually build up after a period of years (18). Nematode population density and community diversity are also affected indirectly by crop rotation. Proper rotation preserves competitive, antagonistic, and predaceous nematodes and other organisms, resulting in buffering against increases in parasitic species (18).

Although multi-species infestations of root-knot nematodes are widespread, studies on interactions among these species in crop rotations are limited (6,10,11). Development of a successful rotation system in a complex infestation with mixed nematode populations depends on the characterization of the interactions and population dynamics of each species.

The objectives of this study were to i) characterize the population dynamics and subsequent crop damage by the two host races of *M. arenaria* in mixed populations in peanut- tobacco rotations, and ii) determine the reproduction potential and parasitic fitness of each race in a mixed infestation as affected by the crop rotations.

Materials and Methods

Nematode infestation and plant culture: This rotation study was done in field microplots (2) for 3 successive years. The experimental design was a split-plot consisting of the nematode treatment as the main-plot and the crop rotation as a subplot with six replications. Three nematode treatments included two single populations of *Meloidogyne arenaria* race 1 (Ma1) and race 2 (Ma2), and a mixture of the two populations. The crop cultivars used in the rotation system were peanut (P) 'Florigiant', *M. incognita* (Mi) races 1 and 3-resistant tobacco (TR) 'McNair 373', and susceptible tobacco (TS) 'Coker 371-Gold'. The crop-rotation patterns for 3 years were P-P-P, P-TR-P, P-TS-P, TR-P-P, TR-TR-P, TR-TS-P, TS-P-P, TS-TR-P, and TS-TS-P. In the first year, each crop cultivar was planted in three plots per nematode treatment. During successive years, planting followed the nine cropping patterns designated for each nematode treatment.

Nematode populations of Ma1, originally from a peanut field in North Carolina, and Ma2, originally from an MI-resistant tobacco field in North Carolina, were increased separately on tomato (*Lycopersicon esculentum* Mill. 'Rutgers') in a greenhouse. Eggs of nematodes were extracted from roots using NaOCl (8). The initial inoculum concentrations were 500 eggs/500-cm^3 soil of each single nematode population or a total of 1,000 eggs for the mixed inoculum.

Field microplots (circular, 76-cm di) established in Fuquay sand (94% sand, 5.5% silt, and 0.5% clay) at Central Crop Research Station, Clayton, North Carolina, were fumigated with ca. 98 g a.i. methyl bromide + 2 g a.i. chloropicrin per square

meter in the fall, before initiation of the experiments. Commercial preparation of *Bradyrhizobium* (cowpea type, Nitragin Co., Milwaukee, WI) was added to peanut microplots (5.6 kg/ha) at planting in 1990. Nematode eggs were introduced into appropriate plots in 1,000 ml of water and incorporated thoroughly 15 cm deep.

Twelve seeds of peanut or two seedlings of tobacco were planted in respective microplots. Peanut seedlings were thinned to six plants after emergence. Irrigation was provided as needed. Normal insect and weed control practices for each crop were followed. At flowering, each peanut plot received one application of land plaster (300 kg/ha) as a calcium source.

In the second and third years, carryover nematodes served as the inocula. Before planting, all microplots received basic fertilizer treatments based on North Carolina Department of Agriculture soil tests. Plots newly planted to peanut also received *Bradyrhizobium* inoculation. Planting and cultural practices were done as described for the first year.

Nematode and crop assays: Plots were sampled at midseason and harvest of each year to determine nematode population densities in soil. Each soil sample consisted of 12 cores (2.5-cm-d × 20-cm deep), except at midseason of the first year when six soil cores of 5 × 20 cm from the root zone were used to collect both soil and root samples. Roots were separated before soil processing. Nematode population densities were assayed from 500-cm^3 soil samples elutriated and centrifuged to extract juveniles (2). Eggs were extracted from root fragments collected from the elutriator (2). Reproduction factors (19) were calculated from nematode population density in soil (juveniles + eggs) at harvest (Pf)/initial inoculum or population density at preplanting (Pi). Winter survivorship ratios of nematodes were computed from Pi/Pf of the immediate preceding year. Subsamples of 250 cm^3 soil from tobacco plots at midseason and harvest samplings were used for bioassay on peanut 'Florigiant' (resistant to Ma2) in a greenhouse (7) to characterize nematode interaction in the mixed populations on tobacco.

Roots were separated from soil samples and washed at midseason of the first year to determine the nematode population density and reproduction in roots. Root sub-samples (1-g) were used to quantify numbers of galls and egg masses; eggs were extracted with NaOCl (2). Another 1-g root sample was used for extraction of juvenile and adult nematodes with pectinase (30). Only swollen juveniles and adult nematodes were counted. Remaining roots of each sample from mixed population plots were used to collect 20 egg masses for bioassay by single-egg-mass inoculation on peanut in a greenhouse to determine the proportion of each race in the mixture (7).

At midseason, crop growth was subjectively rated using a 0–10 scale, based on both plant vigor and leaf color (0 = dead, 10 = normal growth). Tobacco leaves for yield determination were harvested twice in the first year only. In the second year most plants died before harvest.

At the end of the season, plants in each plot were uprooted, and root systems and peanut pods were rated from all plants for gall and necrosis indices (0–100% area galled, or necrotic, per root system or plant) (13). Peanut root-nodule indices (1 = no nodules, 10 = heavily nodulated) also were made for root systems. Peanut pods were collected, and pod yield was determined by dry weight.

Statistical analysis: To equalize variances, nematode data were transformed to $\log_{10}(X + 1)$, and root galling data from soil-bioassays were transformed to arcsin (square root [X/100]) before analysis. Analysis of variance (ANOVA) was performed for nematode-counts, soil bioassay, and first-year-crop-damage data. Tukey's HSD was used for multiple mean comparisons. Crop-damage data of the third year were regressed against preplant and midseason soil-nematode numbers.

Results

First Year: At midseason, juvenile (J2) population densities in soil of Ma2 on pea-

nut and Ma1 on resistant tobacco were low (Table 1). All nematode population densities were greater at harvest than at midseason (Tables 1,2). Numbers of J2 and eggs of Ma2 on peanut and Ma1 on resistant tobacco were much lower than those of the other infestations. All infestations in susceptible tobacco plots had similar J2 and egg population densities. The aggressive populations on peanut (Ma1 and the mixture) had much higher population densities than those on tobacco (Ma2 and the mixture) (Table 2).

Low gall ratings in a peanut bioassay in a greenhouse showed that Ma2 predominated over Ma1 in the mixed population on tobacco at both midseason and harvest (Table 3). The degree of dominance of Ma2 over Ma1 on susceptible tobacco was less than on the resistant cultivar.

Root infection (swollen juveniles + adults per g-root) and egg production (egg masses and eggs per g-root) at midseason of Ma1 on resistant tobacco and Ma2 on peanut were restricted (Table 1). On susceptible tobacco, Ma1 had greater infection incidence than did Ma2, but both nematodes had similar reproduction potentials. The mixture of the two races had infection and reproduction capacities similar to those of Ma1 on peanut and Ma2 on resistant tobacco. On the susceptible tobacco, however, egg masses (representing numbers of egg-laying females) of the mixed population were fewer than those for Ma2 alone. Based on single egg-mass bioassays, the majority of egg-laying females in mixed infection on tobacco was Ma2. Percentage of Ma2 on resistant tobacco (96.7%) was greater ($P = 0.05$) than that on the susceptible cultivar (89.4%).

Reproduction factor (RF) of the mixed population was smaller than that of Ma1 on peanut and Ma2 on resistant tobacco (Table 4). The RF of Ma1 + Ma2 on resistant tobacco was similar to that of Ma1. On susceptible tobacco, all infestations had similar RFs.

Root-gall induction (galls per g-root) at midseason by Ma2 on peanut and by Ma1 on resistant tobacco was restricted (Table 1). Mixed population induced root gall numbers similar to Ma1 on peanut and Ma2 on resistant tobacco. All nematode treatments on susceptible tobacco caused similar root galling. At harvest, Ma2 still did not cause galling on roots and pods of peanut, and induced less necrosis on roots and pods than did Ma1 or mixed population (Table 2). Root and pod damage (gall and necrosis indices) induced by mixed infections was less than that caused by Ma1. Root galling and necrosis indices on resistant tobacco infected by Ma1 were limited. Resistant tobacco plants infected by Ma2, or the mixture, had similar growth indices

TABLE 1. Reproduction and associated root galling at midseason for single or mixed populations of *Meloidogyne arenaria* race 1 (Ma1) and race 2 (Ma2) on peanut and tobacco in microplots in the first year (1990).

Crop	Nematode population†	J2 per 500-cm³ soil	Nematodes per g-root			Galls per g-root
			Swollen J2 + adults	Egg masses	Eggs	
Peanut	Ma1	3,294 a	274 a	38 a	28,203 a	172 a
	Ma2	8 b	13 b	0 b	302 b	0 b
	Ma1 + Ma2	1,372 a	207 a	25 a	19,708 a	158 a
Resistant tobacco‡	Ma1	13 b	2 b	1 b	169 b	2 c
	Ma2	3,446 a	48 a	110 a	28,004 a	147 a
	Ma1 + Ma2	2,273 a	61 a	71 a	17,716 a	92 b
Susceptible tobacco	Ma1	937 a	96 a	55 ab	16,504 a	113 a
	Ma2	2,272 a	46 b	81 a	20,557 a	142 a
	Ma1 + Ma2	2,006 a	84 ab	48 b	14,720 a	90 a

Data are means of 18 replicates. Statistical analyses of nematode-count data were based on $\log_{10}(X + 1)$ transformed data. Means within column within each crop followed by a common letter are not different, according to Tukey's HSD ($P = 0.05$).
† Initial population level was 500 eggs/500 cm³ soil for each single population, 1,000 for the mixture.
‡ Resistant to *Meloidogyne incognita* races 1 and 3, and *M. arenaria* race 1.

TABLE 2. Nematode population densities at harvest in soil and crop damage for single or mixed populations of *Meloidogyne arenaria* race 1 (Ma1) and race 2 (Ma2) on peanut and tobacco in microplots of the first year (1990).

Crop	Nematode population†	Nematodes/500-cm³ soil		Root-gall indices (0–100)‡	Root-necrosis indices (0–100)‡	Growth indices (0–10)§
		J2	Eggs			
Peanut	Ma1	9,697 a	79,232 a	79 a	37 a	—
	Ma2	461 b	741 b	0 c	9 b	—
	Ma1 + Ma2	8,750 a	65,862 a	65 b	31 a	—
Resistant tobacco¶	Ma1	2,483 b	1,912 a	5 b	1 b	9.5 a
	Ma2	7,591 a	4,074 a	89 a	96 a	0.8 b
	Ma1 + Ma2	8,065 a	2,750 a	89 a	96 a	1.1 b
Susceptible tobacco	Ma1	5,482 a	1,978 ab	89 a	88 b	1.9 a
	Ma2	4,719 a	2,075 b	89 a	94 ab	0.7 a
	Ma1 + Ma2	5,786 a	4,191 a	88 a	98 a	0.6 a

Data are means of 18 replicates. Statistical analyses of nematode-count data were based on $\log_{10}(X + 1)$ transformed data. Means within column within each crop followed by a common letter are not different, according to Tukey's HSD ($P = 0.05$).
† Initial population level was 500 eggs/500 cm³ of soil for each single population, 1,000 for mixtures.
‡ 0 = no gall or necrosis; 100 = 100% of root- or pod-surface galled or necrotic per root system or plant.
§ 0 = dead; 10 = maximum growth; low numbers of nematodes used in 1990 did not affect plant growth.
¶ Resistant to *Meloidogyne incognita* races 1 and 3, and *M. arenaria* race 1.

and root damage. Susceptible tobacco was severely galled by all nematode populations; however, tobacco yields were not affected by the initially low-level nematode treatments.

Second Year: With similar survivorship of most nematode populations (Table 4), residual inoculum densities of all infestations at preplanting of the second year were proportional to the previous harvest population densities. Total nematodes (J2 + eggs) of Ma2 in soil following first-year peanut plots and Ma1 following first-year resistant tobacco plots were low (Fig. 1A). Populations of the mixed infestations were similar to those of Ma1 following first-year peanut plots and Ma2 following first-year resistant tobacco plots. Population densities following susceptible tobacco did not differ.

TABLE 3. Reaction (root galling) of peanut 'Florigiant' in greenhouse to single or mixed populations of *Meloidogyne arenaria* race 1 (Ma1) and race 2 (Ma2) in bioassay soil taken from microplots planted to tobacco in the first year (1990).

Nematode population	Root-gall indices (0–100)†	
	Resistant‡ tobacco§	Susceptible‡ tobacco
Midseason, Year 1 (1990)		
Ma1	1.8 a	81.7 a
Ma2	0.5 a	1.5 b
Ma1 + Ma2	2.3 a	8.2 b
End-of-season, Year 1 (1990)		
Ma1	11.6 a	27.7 a
Ma2	0.1 b	0.2 b
Ma1 + Ma2	0.3 b	1.8 b

Data are means of six replicates for midseason and 18 replicates for end-of-season. Analyses of data were based on arcsin (square root [X/100]) transformed data.
Means within column followed by a common letter are not different according to Tukey's HSD ($P = 0.05$).
† 0 = no gall; 100 = 100% root-surface galled.
‡ Host used in microplots (1990).
§ Resistant to *Meloidogyne incognita* races 1 and 3, and *M. arenaria* race 1.

At midseason, the low nematode populations from previous-year poor hosts increased rapidly (RF = 24 to 2,650) on susceptible suitable hosts (Ma2/P-TR, Ma2/P-TS, Ma1/TR-P, and Ma1/TR-TS) (data not included). The Ma2 population also increased rapidly on repeated (poor host) peanut (P-P). In contrast, nematodes with high population densities from previous-year suitable hosts decreased rapidly on poor hosts (Ma1 and Ma1 + Ma2/P-TR, Ma2 and Ma1 + Ma2/TR-P, and Ma2/TS-P). Populations of Ma1 on repeated suitable hosts also declined (Ma1 and Ma1 + Ma2/P-P and P-TS, Ma1/TS-TS). Multiplication of Ma1 on peanut, when following resistant tobacco (TR-P), was greater than that on peanut following susceptible tobacco (TS-P). When tobacco followed pea-

TABLE 4. Reproduction factors (RF = Pf/Pi) and survival ratio (Pi of year 2/Pf of year 1) of single or mixed populations of *Meloidogyne arenaria* race 1 (Ma1) and race (Ma2) after peanut and tobacco in microplots.

Crop	Nematode population	RF	Survival ratio
Peanut	Ma1	177.9 a	0.11 a
	Ma2	2.4 c	0.75 a
	Ma1 + Ma2	74.6 b	0.12 a
Resistant tobacco†	Ma1	8.8 b	0.12 a
	Ma2	23.3 a	0.32 a
	Ma1 + Ma2	10.8 b	0.51 a
Susceptible tobacco	Ma1	14.9 a	0.25 b
	Ma2	13.6 a	0.70 a
	Ma1 + Ma2	10.0 a	0.29 ab

Data are means of 18 replicates. Analyses were based on $\log_{10}(X + 1)$ transformed data.
Means within column followed by a common letter within each crop are not different, according to Tukey's HSD ($P = 0.05$).
† Resistant to *Meloidogyne incognita* races 1 and 3, and *M. arenaria* race 1.

nut, multiplication of Ma2 was greater on resistant tobacco than on the susceptible cultivar.

At harvest, most nematode population densities had decreased as compared to preplant levels (Fig. 1 A,B). Only Ma2 on tobacco following peanut (P-TS) had an increased population density. Ma1 had highest population density on TR-P, and Ma1 and the mixture had greater numbers than Ma2 on TS-P. On tobacco following peanut (P-TR, P-TS), Ma2 had the greatest numbers, and the mixture had numbers similar to Ma2 on P-TR and Ma1 on P-TS. On tobacco treatments following tobacco, population densities of all nematodes did not differ.

At the end of the second season, Ma2 had a greater RF than did Ma1 or Ma1 + Ma2 in plots following peanut, whereas Ma1 had greater RF in plots following resistant tobacco (Table 5). In plots following susceptible tobacco, all nematode populations had similar RFs.

Third Year: In the third year, all plots were planted to peanut. A cropping pattern × nematode interaction effect was detected for nematode Pi, crop damage, and yield.

Survivorship of nematode populations were similar, except from TS-TS plots in which survival rate of Ma2 was lower than Ma1 and the mixture (Fig. 1-C). Ma2 Pi's were greater than those of Ma1 and the mixture in P-TR and P-TS plots, but were less than those of Ma1 and the mixture in TR-P, TS-P, and TS-TS plots (Fig. 1-C). In the other plots, population densities of all infestations did not differ.

At midseason, Ma1 in most plots increased population densities (Pm) in soil (data not included). Mixed populations in previous-year peanut-related plots (P-P, P-TR, P-TS, TR-P, and TS-P) increased, whereas those in previous-year non-peanut plots (TR-TR, TR-TS, TS-TR, and TS-TS) declined or were unchanged. Ma2 Pm were either unchanged or reduced. This resulted in similar Pm of all nematodes in each previous-year peanut-related plot. In previous-year non-peanut plots, Ma1 had greater Pm than did Ma2 or the mixture.

At the end of the 1992 season, population densities of Ma2 in previous-year non-peanut plots decreased as compared to Pi (Figs. C,D). Population levels of Ma1 increased in second-year tobacco plots but declined in first-year-only tobacco plots (TR-P-P, TS-P-P).

Peanut root-galling data (at harvest) (Table 5) showed that in the mixed infestations Ma1 predominated over Ma2 in previous-year peanut-related plots, and Ma2 predominated over Ma1 in previous-year non-peanut plots. Still, Ma1 was maintained in sufficient levels on resistant and susceptible tobacco over 2 years to give significant root and pod galling on peanut.

RF values of nematodes in third-year peanut depended upon previous crop history. The RF of Ma1 was the greatest in

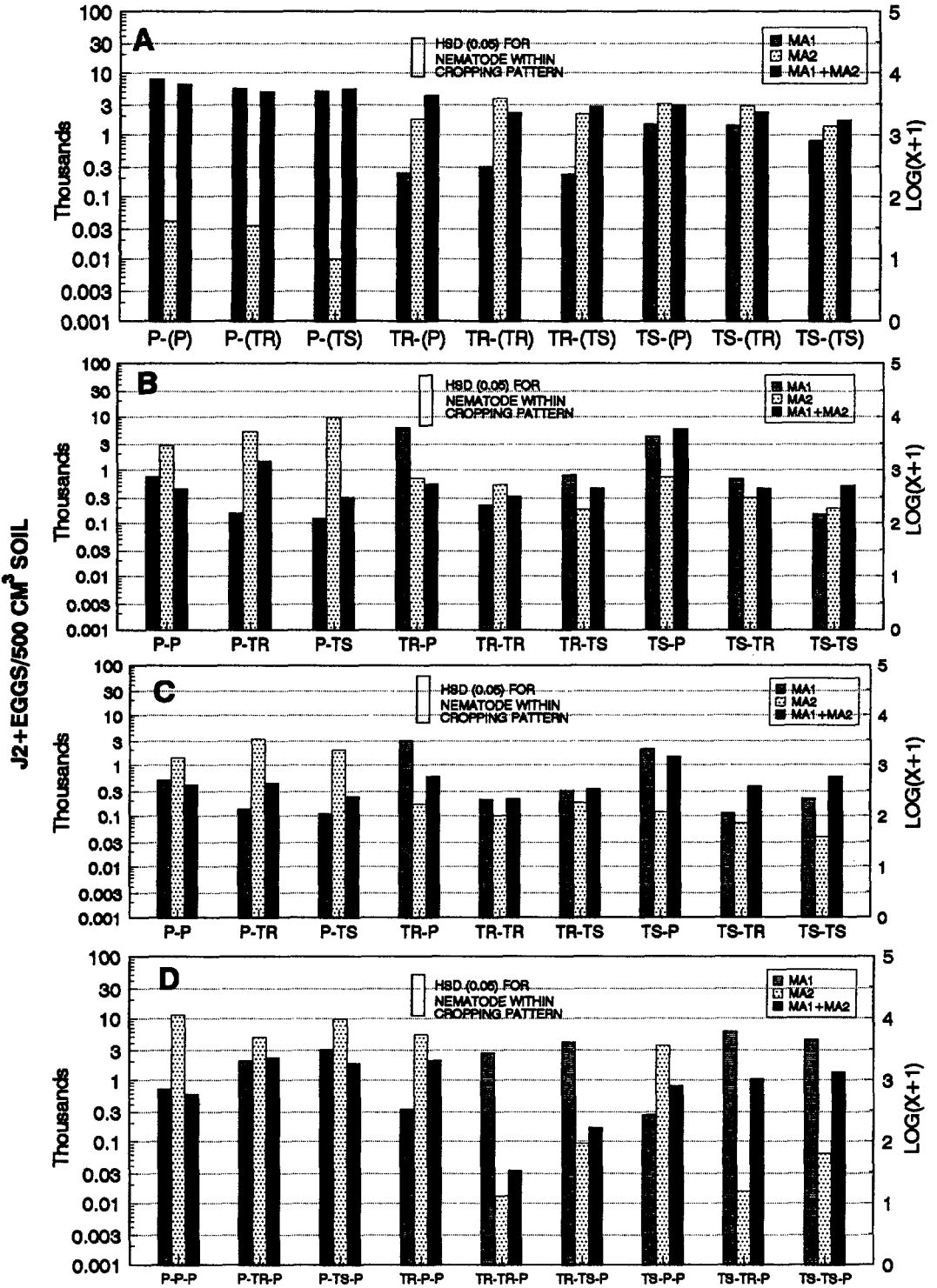

FIG. 1. Influence of rotations of peanut (P), *Meloidogyne incognita* (Ma1) races 1 and 3 and *M. arenaria* race 1 resistant tobacco (TR), and susceptible tobacco (TS) on population dynamics (preplant and end-of-season nematode numbers) of single or mixed populations of *M. arenaria* race 1 (Ma1) and race 2 (Ma2) in microplots in the second and third year. A) Second-year preplant (preplant nematode numbers are those that survived from previous year); B) Second-year end-of-season; C) Third-year preplant (nematodes that survived from previous year); and D) Third-year end-of-season.

TABLE 5. Selected nematode and crop responses in the second and third years of peanut rotations in microplots infested with single or mixed populations of *Meloidogyne arenaria* race 1 (Ma1) and race 2 (Ma2).

Cropping pattern for 3 years†	Nematode	Nematode reproduction factor (Pf/Pi)		Root diseases (0–100) 1992		Crop growth indices (0-10)/(1992)	Dry pod yield (g) (1992)
		Year 2 (1991)	Year 3 (1992)	Gall indices	Necrosis indices		
P-P-P	Ma1	0.1 b	2.2 a	86 a	93 a	1.8 b	24 b
	Ma2	1,327.4 a‡	9.6 a	41 b	30 b	4.9 a	127 a
	Ma1 + Ma2	0.1 b	2.2 a	85 a	81 a	2.3 b	23 b
P-TR-P	Ma1	<0.1 b	59.6 a	83 a	52 a	5.1 a	91 b
	Ma2	240.5 a	2.5 b	21 b	21 b	6.4 a	195 a
	Ma1 + Ma2	0.4 b	7.9 ab	78 a	45 a	5.2 a	80 b
P-TS-P	Ma1	<0.1 b	61.1 a	73 a	42 ab	6.3 a	115 a
	Ma2	2,564.4 a	8.5 a	21 b	22 b	6.0 a	171 a
	Ma1 + Ma2	0.1 b	13.0 a	74 a	44 a	5.2 a	123 a
TR-P-P	Ma1	31.7 a	0.2 b	87 a	91 a	0.6 b	1 b
	Ma2	0.5 b	46.6 a	18 b	24 c	6.1 a	163 a
	Ma1 + Ma2	0.3 b	4.4 b	78 a	47 b	5.3 a	104 a
TR-TR-P	Ma1	11.6 a	66.7 a	44 a	32 a	7.0 a	238 b
	Ma2	0.3 a	0.5 b	0 b	11 a	8.2 a	341 a
	Ma1 + Ma2	0.7 a	0.2 b	2 b	13 a	8.1 a	319 a
TR-TS-P	Ma1	107.4 a	32.2 a	57 a	30 a	6.8 a	221 b
	Ma2	0.1 b	1.2 b	1 b	10 a	8.1 a	344 a
	Ma1 + Ma2	0.2 b	1.1 b	1 b	10 a	8.3 a	324 a
TS-P-P	Ma1	6.0 a	0.2 b	80 a	98 a	1.5 b	19 b
	Ma2	0.3 a	47.9 a	25 b	20 c	5.8 a	162 a
	Ma1 + Ma2	3.9 a	2.1 b	85 a	62 b	2.1 b	29 b
TS-TR-P	Ma1	0.6 a	74.5 a	70 a	35 a	7.5 a	188 b
	Ma2	0.3 a	13.4 b	0 b	12 b	8.0 a	322 a
	Ma1 + Ma2	1.2 a	4.9 b	8 b	12 b	8.0 a	320 b
TS-TS-P	Ma1	0.3 a	61.7 a	78 a	33 a	6.9 a	150 b
	Ma2	0.2 a	3.9 b	0 b	11 b	8.2 a	331 a
	Ma1 + Ma2	0.5 a	5.3 b	13 b	13 ab	7.8 a	266 a

Data are means of six replicates. Analyses were based on $\log_{10}(X + 1)$ transformed data.

Means with column of each cropping pattern followed by a common letter are not different according to Tukey's HSD ($P = 0.05$).

† P = Peanut 'Florigiant'; TR = *Meloidogyne incognita* races 1 and 3- resistant tobacco 'McNair 373'; TS = Susceptible tobacco 'Coker 371-Gold'.

‡ Some continuous peanut plots possibly became contaminated with *M. arenaria* race 1.

plots with second-year tobacco, whereas the RF of Ma2 was the largest in plots with second-year peanut (Table 5). Mixed population had low RF similar to the low RF of single populations for the same cropping pattern.

Crop-response parameters for Ma1 were related linearly to log preplant nematode density (Pi), whereas those for Ma2 and the mixture were related better to log midseason population density (Pm). However, for all nematodes, crop growth index rated at midseason had a better relationship with Pi than Pm, whereas other crop responses (root-damage, root-nodulation, and yield) assessed at harvest had better relationships with Pm (regressions and pod/nodule data not included). Ma1 and the mixture from previous-year peanut-related plots and Ma1 from first-year TS plots caused heavy galling on peanut roots (Table 5) and pods. However, only those populations from second-year peanut plots (except the mixture from TR-P) severely suppressed third-year peanut growth and yield, and induced severe necrosis on roots. Ma1 from previous-year non-peanut plots with first-year TR (TR-TR, TR-TS) plots caused significant damage on roots and pods as well as yield losses. The degree of root necrosis associated with Ma1 from second-year non-

peanut, and mixed populations from first-year-only peanut (P-TR or P-TS), was moderate. Ma2 had a slight effect on peanut growth at midseason. Ma2 from previous-year peanut-related plots (possibly contaminated with Ma1) caused slight-to-moderate root and pod galling and some suppression of growth and yield. Ma2 and the mixture from previous-year non-peanut plots induced little damage to peanut.

Discussion

The availability and quality of food, and the ability of parasites to secure and use it, are dominant factors in population growth. Fluctuation in populations of parasitic nematodes, hence, are determined by the inherent characteristic of a given species, the status of host, and the environmental influence (17,19). Host status could be determined by the performance of the parasitic nematode, based largely on the maximum rate of reproduction (a) and equilibrium density (E) (the density at which reproduction just suffices to maintain the population) (26). For a good host, both a and E are large; on a poor host, both are small. With an intermediate host, either of the two may be fairly large and the other small, or both could be intermediate. On this basis, the first-year results indicate that peanut Florigiant is a poor host for Ma2, as is Mi-resistant tobacco McNair 373 for Ma1. The susceptible tobacco 'Coker 371-Gold' is a suitable host for both Ma1 and Ma2.

Based on both host suitability and crop damage, peanut is generally resistant to Ma2 (23). Fortnum and Currin (6) reported that this crop, as a rotation crop for tobacco in mixed infestations of Ma2 and *M. incognita* race 3, increases tobacco yield; peanut, however, does not behave uniformly in influencing species shifts. The present study demonstrates that the effect of peanut-tobacco rotations on species shifts in Ma1 + Ma2 infestations varied with crop history or sequences. Time in peanut production required for the shift of Ma2 to Ma1 in Ma2-dominant mixed population from tobacco was 1 year for the mixed population from susceptible tobacco, and 2 years for the mixed population from resistant tobacco. For the shift of Ma1 to Ma2 in Ma1-dominant mixed population from peanut, 1-year cropping of resistant tobacco was not sufficient.

Meloidogyne arenaria race 2 has little or no reproduction and produces almost no galls on peanut. However, monoculture of peanut for 2 or 3 years failed to restrict Ma2 populations to the low levels observed after first-year peanut. These Ma2 population levels may have induced some damage (foliar growth, roots, and pods) to peanut in the third year, but poor performance typically occurs anyway with continuous peanut production in North Carolina. In contrast, Ma2 from previous-year non-peanut did not cause apparent damage to this crop. This population shift may indicate changes in parasitic adaptation of Ma2 on peanut, as observed for other nematode-crop relationships in crop rotation practices (17), or contamination of plots with Ma1. In a follow-up greenhouse test involving repeated cycles of peanut and the resistant and susceptible tobacco cultivars used herein, peanut failed to support any population of Ma2. This suggested the microplot results with Ma2 on peanut were possibly due to contamination with Ma1.

Low population density of Ma1, affected by first-year resistant tobacco, was sufficient to damage peanut at late season as well as susceptible tobacco at midseason. This population level also moderately damaged subsequent resistant tobacco at midseason, as did high levels of Ma1 from first-year peanut. Two years of monoculture of resistant tobacco resulted in a population density similar to that observed after the first year. This density level caused moderate damage to peanut.

In the second year, tobacco was more sensitive to growth depression by Ma1 at low density levels than was peanut. A high population density of Ma1 caused severe growth suppression of resistant tobacco,

whereas peanut suffered moderately (stunted) from a high density level of Ma2. These results were not observed in the first year, indicating that growth restriction by the less-aggressive nematodes might also be associated with other synergistic organisms in soil (20) as well as by nematode infection (3,14,28), or occur only with high population levels.

In a related interaction study in the greenhouse (7), Ma2 suppressed root infection, reproduction, and root galling by Ma1 on peanut, whereas Ma1 limited infection, reproduction, and root galling by Ma2 on resistant tobacco, at both 2 and 6 weeks. Such inhibitory effects were not apparent in microplots at midseason, but were found at harvest for root and pod damage on peanut. The interaction among nematode populations in microplots or fields appears to be influenced by other external factors affecting infection and reproduction of each nematode (4,9,12).

In the second and third years, except for highly parasitically fit nematode populations on their respective crops, the relationships between crop-response parameters and preplant population density (Pi) were not apparent because of crop rotation effects. For example, in the second year, high Pi of Ma1 (from peanut) caused limited damage to resistant tobacco, whereas low Pi of Ma2 (from peanut) induced significant damage to both tobacco cultivars. At midseason of the second year, most susceptible plants died early, and the aggressive nematode population declined before midseason sampling. Thus, the midseason population density (Pm) was not appropriate to relate to crop response data in this year. In the third year, most of the aggressive populations did not decline at midseason, and crop rotation effects on population density of incompatible nematodes had occurred before midseason; hence, this Pm may be useful to relate to crop response parameters as suggested by Ferris (5).

The complexity of mixed infestations of nematode species or host races with overlapping of host ranges complicates the selection of crop genotypes for rotation (6). The present microplot study of peanut-tobacco rotations-Ma1 + Ma2 demonstrates such complications and how increased knowledge of these systems can be used to improve management strategies. In this study, crop genotype and crop sequence influenced species and (or) race shifting and possibly parasitic adaptation among nematode populations in the mixture. To effectively prevent damage by *Meloidogyne* species, crop rotation should be practiced in conjunction with race and species determinations, other cultural means such as destruction of roots of host crops after season, weed control, and(or) early planting (15,27).

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