Interrelationships of Meloidogyne Species with Flue-cured Tobacco[1]

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Abstract: Microplot and field experiments were conducted to determine relationships of population densities of *Meloidogyne* spp. to performance of flue-cured tobacco. A 3-yr microplot study of these interactions involved varying initial nematode numbers (P_i) and use of ethoprop to reestablish ranges of nematode densities. Field experiments included various nematicides at different locations. Regression analyses of microplot data from a loamy sand showed that cured-leaf yield losses on 'Coker 319' for each 10-fold increase in P_i were as follows: *M. javanica* and *M. arenaria*—13–19%; *M. incognita*—5–10%; *M. hapla*—3.4–5%; and 3% for *M. incognita* on resistant 'Speight G-28' tobacco. A P_i of 750 eggs and larvae/500 cm^3 of soil of all species except *M. hapla* caused a significant yield loss; only large numbers of *M. hapla* effected a loss. *M. arenaria* was the most tolerant species to ethoprop. Root-gall indices for microplot and most field-nematicide tests also were correlated negatively with yield. Relationships of P_i(s) and necrosis indices to yield were best characterized by linear regression models, whereas midseason numbers of eggs plus larvae (P_m) and sometimes gall indices vs. yield were better characterized by quadratic models. The relation of field P_m and yield was also adequately described by the Seinhorst model. Degrees of root galling, root necrosis, yield losses, and basic rates of reproduction on tobacco generally increased from *M. hapla* to *M. incognita* to *M. arenaria* to *M. javanica*. *Key words:* population dynamics, resistance, *Nicotiana tabacum*.

Root-knot nematodes, *Meloidogyne* spp., have caused severe losses of tobacco for many years (5,17). As early as the 1940s, root knot was described as being so easily recognized that a detailed description was not necessary (5). Clayton et al. (5) indicated that plants were so weak in late season from decay of galled roots that they often supported little growth of suckers. Yield losses to this pest in the early 1950s were estimated to be about 10% annually (21). Largely as a result of extensive integrated control programs, these losses have been reduced and were recently estimated to be about 0.7% in North Carolina (28).

Root knot is probably the major disease of tobacco throughout the world (17,18). Nevertheless, few efforts have been made to quantify yield losses caused by the common species of *Meloidogyne* on this crop (2,9,11, 12). Evidence indicating major yield losses to these nematodes often was obtained through fumigation of infested fields (4, 6, 9, 13, 14, 16, 20, 22, 26, 27, 29). Some of these treatments also controlled disease complexes of tobacco in which root-knot nematodes were the primary pathogen (22). Such treatments often also affected soil microflora and nitrogen levels (7,8). Following various chemical soil treatments, midseason and postharvest population densities of *Meloidogyne* spp. were correlated with tobacco yields, although some correlations were not strong (9). Recently developed nonfumigant nematicides control low to moderate populations of certain species, such as *M. incognita,* but fail to give adequate control of *M. arenaria* in North Carolina (Todd, unpublished). Root-gall indices also appear to be closely related to the yield of this crop, but different investigators have had varied results (4,6,13,14). Land management practices such as multiple cropping and rotation may increase organic matter in the soil, cycling of nutrients, and improved soil structure which may decrease population densities of nematodes (21). These practices may have both direct and indirect effects on nematode-host relationships. Crop rotation systems may be very effective for nematode control, but they must be adapted for different species of nematodes (19,21).

Epidemiological investigations of nematode diseases pose many difficulties. Still, the concepts and approaches developed by Oostenbrink (23, Seinhorst (25), Jones (15), and Ferris (10) offer promise for characterizing relationships between nematode population numbers and crop performance.

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These investigators have used various types of experiments as well as models for relating numbers of nematodes to crop yields. The objectives of the present studies were to (i) determine the relationships of initial densities (P_i) of the major species of *Meloidogyne* to tobacco yields, (ii) quantify possible relationships of densities of *M. incognita* to yield of a resistant cultivar, (iii) determine possible relationships of root galling and root necrosis with tobacco yields, (iv) secure information on reproduction of various *Meloidogyne* spp. on tobacco, and (v) obtain information on any differences among *Meloidogyne* spp. in sensitivity to the nematicide, ethoprop.

MATERIALS AND METHODS

Two types of experiments were used in these studies. The first involved 3 yr of microplot tests with varying numbers of a given species of *Meloidogyne* with chemical soil treatments superimposed in some instances. The second was a series of field nematicide tests described by Todd (27) and Ferris (9).

Microplots: Four *Meloidogyne* spp. (*M. arenaria, M. incognita, M. hapla,* and *M. javanica*) were increased separately on tomato, *Lycopersicon esculentum* Mill. 'Floradel,' in the greenhouse. Infected and uninfected plants were grown separately for 10–12 wk in a 1:1 mixture of loamy and silica sand in 15-cm-deep flats. All inocula were prepared as previously described (3). Two to six weeks prior to infestation of microplots (80 × 100 cm or 78-cm diam), the loamy sand (91% sand, 3.3% clay, 5.7% silt, and 0.8% OM) was treated with methyl bromide (0.17–0.22 kg/m²). A mixed suspension of about 1,000 spores of the endomycorrhizal fungi *Glomus mycrocarpus* var. *geosporus* and *Gigaspora giganta* were added to each plot at transplanting. Diazinon was added to transplant water (42 g WP/189 L) for wireworm control. Three 8–12-wk-old tobacco seedlings were transplanted to each rectangular plot but only two plants were placed in the smaller circular plots. Basic fertilizers, insecticides, and supplemental irrigation were provided as needed. Independent experiments were established for each nematode species. Unless otherwise stated, a randomized complete block design was used.

Nematode populations were determined at the initiation of the experiments, at midseason (10–12 wk after transplanting) and at final harvest. Nematode populations were assayed by collecting 10 cores with a 2.5-cm soil probe per plot. Nematode eggs and larvae were extracted from 500-cm³ aliquants of soil samples by elutriation-centrifugation (1).

Four types of crop response data were obtained from microplot experiments. Growth ratings on a scale of 0–10 (10 = maximum growth) were obtained approximately 6 and 10 wk after transplanting. Disease indices (0–100) were based on relative proportions of galled or necrotic roots (1) shortly after final leaf harvest. Curing, weighing, and pricing of the final tobacco products followed standard industry procedures.

Plant and nematode data were subjected to analysis of variance. Nematode population data were transformed to $\log_{10}(X + 1)$ for all statistical analyses. Regression analyses were used to relate yields to nematode numbers, root-gall, and necrosis indices. The regressions for yield vs. necrosis and root-gall indices were done per nematode species and for all four species combined.

Varying initial numbers of Meloidogyne spp.: To investigate the relationships between *Meloidogyne* spp. and tobacco response, microplots were infested in 1976 with four initial inoculum densities (P_i) (0, 750, 1,500, or 3,000 eggs and larvae/500 cm³ of soil) for each nematode species: *M. arenaria M. incognita, M. hapla,* and *M. javanica.* Varying volumes of infested and uninfested soil were incorporated to give the desired level of nematodes. Susceptible *Nicotiana tabacum* L. 'Coker 319' seedlings were transplanted in late April to each of eight replicate plots per inoculum level for each nematode species. The *M. javanica* treatments and four replicates of the *M. hapla* test were placed in the small circular plots; all other treatments were placed in the rectangular plots. A similar test with *M. incognita* was established using resistant 'Speight G-28' seedlings. The experiment with *M. incognita* on 'Coker 319' was repeated in 1978 with eight P_is. One-half of

the eight replicates in 1978 had 2,700 cm^3 peat moss per plot added 3 yr earlier.

Meloidogyne spp. response to ethoprop: The P_is of nematodes in 1977 varied, depending on overwintering survival. Half of the eight replicates of the control plots and those initially having intermediate P_is in 1976) were treated by incorporating 3.1 g (10 G) ethoprop per plot. Four replicates of the initially low-inoculum level plots received 6.2 g of ethoprop per plot. (Tobacco root systems had been removed from these replicates after final harvest of the previous experiment). Because the initial nematode counts in these experiments did not measure the effects of ethoprop, midseason numbers of eggs and larvae were utilized in the statistical analyses.

Field experiments: Data from 12 yr of field experiments that included various nematicides were analyzed to detect possible correlations of tobacco yield losses with root galling and with midseason numbers of eggs and larvae. The species of nematodes in most of these field experiments was *M. incognita*. Several nematicides were used as row treatments which provided a range of population densities between treated and untreated plots. Applications were made before or at the time of planting. Detailed procedures of actual treatments have been described previously (9,27). Because correlations of tobacco yield, value, and root-knot indices with early to midseason and postharvest *Meloidogyne* population densities have been published previously (9), only representative regressions from these experiments are included herein. The suitability of the Seinhorst model (25) and regression models for characterizing midseason numbers of eggs and larvae vs. yield was evaluated.

RESULTS

Microplots: The effects of four species of *Meloidogyne* on yield of tobacco varied greatly (Table 1). *M. arenaria* and *M. javanica* caused the greatest yield suppressions of 'Coker 319' tobacco. In addition to inducing much greater stunting and yield losses, these nematode species caused much more severe root galling and root necrosis than did *M. incognita* or *M. hapla* (Tables 1, 2).

Although *M. incognita* did not reproduce on resistant 'Speight G-28,' a P_i of 1,500 eggs and larvae/500 cm^3 of soil caused a slight yield suppression (Table 1). Except for *M. hapla,* a P_i of 750 eggs and larvae of all species suppressed yields of 'Coker 319.'

Use of linear regression models (Table 3) show that yield losses for each 10-fold increase in P_i per species in 1976 were as follows: *M. javanica*—19.0%; *M. arenaria*—16.5%; *M. incognita*—8.9%; *M. hapla*—3.4%; and 3% for *M. incognita* on resistant 'Speight G-28.' Similar yield losses were obtained in the 1977 experiments, except for *M. javanica* which caused considerably less damage in the second year. In 1978 the lowest P_i for *M. incognita* caused an important economic loss, but a P_i of 800 eggs and larvae/500 cm^3 were necessary for this effect to be statistically significant (Table 4).

The respective reproductive factors (RM for midseason, Table 1) closely parallel the potential of the four species of *Meloidogyne* in causing yield losses in tobacco. In the first set of experiments the midseason low-P_i reproductive factor was near 1,000 for *M. javanica,* more than 600 for *M. arenaria,* about 500 for *M. incognita,* and only 27 for *M. hapla.* The reproductive factor for all four nematode species decreased as the initial densities increased. By harvest time densities of all species had declined sharply as reflected by the reproductive factors (RF for final harvest).

Tobacco growth indices, yield, and value per plot generally were correlated negatively with P_i, P_m, P_f, and root-gall and root-necrosis indices for each of the nematode species (Table 5). These correlation coefficients were very similar in the experiments in which varying numbers of nematodes were added initially and in the ethoprop experiment. With the nematicide test the greatest correlations among these parameters were obtained with the midseason nematode data. Root-gall and root-necrosis indices were correlated negatively with yield, growth indices, and value per plot, but root-necrosis indices had no significant relationship to the yield of tobacco infected by *M. hapla.* Regression analysis of data from all plots—whether infested with *M. incognita, M. hapla, M. arenaria,* or *M.*

Table 1. Interactions of *Meloidogyne* spp. and tobacco in microplots (1976).

Nematode species	Mean initial nematode level (P_i)[a]	Growth indices (0-10)	Yield (g/plot)	Dollar value per plot	Gall indices (0-100)	Necrosis indices (0-100)	RM[b]	RF[b]
M. hapla								
	0	8.8	475	1.17	0	0		
	750	8.8	438	1.10	18	5	27	3
	1,500	8.3	434	1.08	24	5	8	4
	3,000	8.3	405	1.02	29	5	5	4
	LSD: $P = 0.05$	NS	NS	NS	8	NS	NS	NS
	$P = 0.01$				12	NS	NS	NS
	CV(%)	7.8	7.3	7.7	12.2		9.2	29.2
M. incognita—susceptible 'Coker 319'								
	0	9.1	504	1.25	0	0		
	750	7.5	423	1.06	34	13	527	169
	1,500	7.5	391	0.98	46	20	342*[b]	164
	3,000	6.1	301	0.75	61	29	377*[b]	79**[b]
	LSD: $P = 0.05$	1.0	58	0.14	7	13		
	$P = 0.01$	1.3	79	0.20	9	17		
	CV(%)	12.2	13.9	13.8	11.7	39.4	23.1	19.1
M. incognita—resistant 'Speight G-28'								
	0	8.9	477	1.18	0	0		
	750	8.1	454	1.13	0	0		
	1,500	8.5	447	1.11	0	0		
	3,000	8.1	407	1.00	0	0		
	LSD: $P = 0.05$	NS	39	0.10	NS	NS		
	$P = 0.01$		53	0.13	NS	NS		
	CV(%)	9.2	8.4	8.6				
M. arenaria								
	0	8.4	463	1.15	0	0		
	750	6.4	318	0.78	64	55	610	32
	1,500	4.5	224	0.53	73	48	383*[b]	23
	3,000	2.9	146	0.32	86	70	321**[b]	9**[b]
	LSD: $P = 0.05$	0.8	41	0.11	5	9		
	$P = 0.01$	1.1	56	0.15	8	12		
	CV(%)	13.9	13.8	14.7	6.9	15.3	8.0	22.2
M. javanica								
	0	7.9	372	0.89	0	3		
	750	5.8	208	0.50	45	38	1083	4
	1,500	4.0	156	0.36	56	43	731*[b]	5
	3,000	2.9	93	0.20	73	80	418**[b]	5
	LSD: $P = 0.05$	0.7	39	0.09	6	15		
	$P = 0.01$	1.0	53	0.13	9	21		
	CV(%)	14.0	18.1	18.1	10.5	27.4	6.1	18.7

[a]All data are means of four replicates; numbers of eggs and larvae/500 cm³ soil.

[b]RM = reproductive factor at midseason (number of eggs + larvae/P_i); RF = reproductive factor at final harvest. Asterisks (*, **) indicate significant difference at $P = 0.05$ and 0.01, respectively (based on analysis of $\log_{10}$ [X + 1] transformed data).

javanica—indicated that tobacco yield decreased linearly with disease indices.

In the first year parasitism by the nematodes resulted in a 7–8% loss in yield for each 10% increment of roots galled (Fig. 1A). The relationships between yield and gall indices in both years were linear (Fig. 1A) or slightly curvilinear (Fig. 1B). Root-necrosis indices also were very closely correlated negatively with yield. In the first year there was a loss of 9.6% per 10% of the root decayed, whereas in the second year this loss was 9.9% (Fig. 1C, D).

Relative sensitivity of Meloidogyne species to ethoprop: The normal and two-fold rates of ethoprop suppressed the buildup of

Table 2. Interactions of *Meloidogyne* spp. and tobacco influenced by a chemical soil treatment (1977).

Nematode species	Mean initial nematode level (P_i)[a]	Ethoprop treatment (g/plot)[b]	Growth indices (0-10)	Yield (g/plot)	Dollar value per plot	Gall indices (0-100)	Necrosis indices (0-100)	No. eggs & lavae/500 cm³ soil (in 1,000's)	
								Mid-season[c]	Final harvest[c]
M. hapla									
	0		8.5	490	1.34	1	0	<0.1	<0.1
	0	+(3.1)	7.8	459	1.27	0	0	0	0
	17,259		6.0	390	1.07	27	3	32.4	2.2
	7,564	+(6.2)	7.3	423	1.18	10	1	1.3**	1.0*
	14,022		6.3	388	1.07	42	3	45.7	5.0
	8,123	+(3.1)	6.5	423	1.17	20	1	7.9*	1.4*
	LSD: $P = 0.05$		NS†	NS†	NS	9	NS	NS	NS
	CV(%)		17.2	12.6	14.0	18.9	21.8	37.6	32.6
M. incognita									
	0		8.5	537	1.47	1	0	0	<0.1
	0	+(3.1)	8.5	537	1.48	0	0	<0.1	<0.1
	8,665		5.5	276	0.73	74	48	75.0	39.2
	5,632	+(6.2)	8.3	507	1.41	37	6	5.9**	5.8*
	10,403		5.3	335	0.91	59	36	65.2	17.3
	8,017	+(3.1)	7.0	443	1.22	51	6	17.1**	12.2
	LSD: $P = 0.05$		NS†	126	0.35	NS†	23		
	CV(%)		16.4	16.3	17.4	27.5	49.3	33.4	17.1

Table 2. (Continued)

Nematode species	Mean initial nematode level (P_i)[a]	Ethoprop treatment (g/plot)[b]	Growth indices (0-10)	Yield (g/plot)	Dollar value per plot	Gall indices (0-100)	Necrosis indices (0-100)	No. eggs & lavae/500 cm³ soil (in 1,000's) Mid-season[c]	No. eggs & lavae/500 cm³ soil (in 1,000's) Final harvest[c]
M. arenaria									
	0		7.5	421	1.15	0	0	0	<0.1
	0	+(3.1)	8.3	519	1.44	0	0	<0.1	<0.1
	2,101		3.3	128	0.30	89	70	87.1	11.4
	2,170	+(6.2)	5.0	251	0.69	70	46	49.3	6.2
	2,627		2.0	83	0.18	89	74	66.7	9.1
	4,538	+(3.1)	4.8	221	0.58	78	56	55.7	5.0
	LSD: $P = 0.05$		NS†	NS†	NS†	NS†	NS†	NS	NS
	CV(%)		30.3	29.9	37.3	8.5	24.2	16.7	13.1
M. javanica									
	0		8.0	451	1.26	0	0	0	0
	0	+(3.1)	8.3	507	1.45	0	0	<0.1	<0.1
	2,701		3.8	166	0.39	86	69	111.0	58.0
	3,386	+(6.2)	7.0	409	1.15	49	13	0.9**	12.8*
	8,086		3.5	150	0.39	86	68	103.4	76.6
	5,890	+(3.1)	7.0	403	1.14	61	22	7.4**	49.7
	LSD: $P = 0.05$		1.4	77	0.23	9	16		
	$P = 0.01$		2.2	107	0.35	13	NS		
	CV(%)		20.7	14.3	13.4	7.9	25.6	11.9	15.8

[a]Mean number of nematodes/500 cm³ of soil prior to any chemical soil treatment.
[b]Ethoprop (10g) mixed in upper 8-10 cm soil.
[c]Asterisks (*, **) indicate significant difference at $P = 0.05$ and 0.01, respectively (based on analysis of $\log_{10}$ [X + 1] transformed data).
†No significant interaction of chemical X P_i; main chemical effect and P_i effect were significant (main-effect means not included).

Table 3. Summary of effects of *Meloidogyne* spp. on tobacco yields in microplots.

Experiment		Regressions of yield vs $\log_{10}$ nematode numbers[a]			Losses/10-fold increase in "P_i"	
Nematode species	Year	Intercept (g/plot)	Slope ($\log_{10}$P)	r	Percent	Equivalent dollar loss per ha[b]
M. hapla						
	1976	476.8	−16.34	−9.36*	3.4	238
	1977 (± nematicide)[c]	466.1	−23.3	−0.57**	4.6	322
M. incognita						
	1976					
	Susceptible 'Coker 319'	512.6	−45.37	−0.67**	8.9	633
	Resistant 'Speight G-28'	480.6	−14.43	−0.46**	3.0	210
	1977 (± nematicide)[c]	567.7	−57.4	−0.82**	10.0	700
	1978 (plots with peat moss)	518.7	−26.5	−0.89**	5.1	357
M. arenaria						
	1976	474.7	−78.5	−0.86**	16.5	1,155
	1977 (± nematicide)[c]	524.8	−82.0	−0.89**	15.6	1,092
M. javanica						
	1976	378.7	−71.98	−0.91**	19.0	1,330
	1977 (± nematicide)[c]	510.3	−66.42	−0.83	13.0	910

[a]Number eggs + larvae/500 cm³ soil (P_m for nematicide treatments, P_i for others). Asterisks (*, **) indicate significantly different from the 12,800 treatment at $P = 0.05$ and 0.01, respectively.

[b]Based on 2,500 kg/ha @ $2.80/kg or $7,000/ha.

[c]Ethoprop treatment (0.0, 3.1, or 6.2 g/plot) before planting to establish wider range of effective inoculum. Regression based on midseason nematode counts.

M. hapla, M. incognita, and *M. javanica* (Table 2). These treatments also gave greater yields in plots infested with these nematodes. The development of root necrosis and, to a lesser degree, root galling were suppressed by ethoprop with these three species. In contrast, ethoprop had only a slight effect on the buildup of *M. arenaria* and related yields, root galling, and root necrosis.

This chemical soil treatment had no effect on the initially uninfested controls for the *M. incognita* and *M. hapla* tests. Ethoprop slightly enhanced the yields of the un-

Table 4. Tobacco yields with low to high initial densities of *Meloidogyne incognita*.[a]

Initial No. nemas/500 cm³ soil	Yield (g/plot)	Dollar value per plot	Pmt (in 1,000's)[b]	Root-gall indices (0-100)	Root-necrosis indices (0-100)	Mean loss/plant (dollars)
0-check	484	1.44	0	2	0	
200	446	1.34	23**	56	11	0.05
400	439	1.30	35**	64	17	0.07
800	430	1.30	49**	69	24	0.07
1,600	414	1.26	67**	72	32	0.09
3,200	430	1.31	113*	80	38	0.07
6,400	355	1.06	199	77	38	0.19
12,800	372	1.12	250	84	47	0.16
LSD:						
$P = 0.05$	53	0.17		11	4	
$P = 0.01$	70	0.23		15	7	

[a]One-half of the eight replicates per treatment had 2,700 cm³ peat moss per plot added 3 yr previously.

[b]Midseason eggs + larvae/500 cm³ of soil. Statistical analysis based on $\log_{10}$ (X + 1) transformation. Asterisks (*, **) indicate significantly different from the 12,800 treatment at P = 0.05 and 0.01, respectively.

Table 5. Correlation coefficients for growth of tobacco and numbers of *Meloidogyne* spp. (1977).[a]

Variables/nematode species	Tobacco yield	Tobacco growth indices	Dollar value per plot	Root-gall indices (0-100)	Root-necrosis indices (0-100)
M. hapla					
Tobacco yield		0.88**	0.99**	−0.44**	
Nematode numbers[b]					
P_iT	−0.66**	−0.58**	−0.62**	0.88**	0.46*
P_mT	−0.57**	−0.63**	−0.55*	0.87**	0.39*
P_fT	−0.48*	−0.54*	−0.46*	0.90**	0.35*
M. incognita					
Tobacco yield		0.93**	1.0**	−0.83**	−0.80**
Nematode numbers					
P_iT	−0.73**	−0.68**	−0.72**	0.92**	0.62**
P_mT	−0.82**	−0.77**	−0.80**	0.97**	0.72**
P_fT	−0.67**	−0.70**	−0.71**	0.89**	0.66**
M. arenaria					
Tobacco yield		0.97**	1.0**	−0.85**	−0.89**
Nematode numbers					
P_iT	−0.79**	−0.74*	−0.78**	0.94**	0.85**
P_mT	−0.89**	−0.87**	−0.91**	0.97**	0.94**
P_fT	−0.79**	−0.82**	−0.84**	0.97**	0.89**
M. javanica					
Tobacco yield		0.96	1.0	−0.77	−0.86
Nematode numbers					
P_iT	−0.67**	−0.66**	−0.67**	0.96**	0.79**
P_mT	−0.83*	−0.79**	−0.84**	0.96**	0.93**
P_fT	−0.63*	−0.73**	−0.79**	0.98**	0.86**

[a]Asterisks (*, **) indicate significance at $P = 0.05$ and 0.01, respectively.

[b]The symbols P_iT, P_mT, and P_fT refer to total nematode egg and larval populations at planting, midseason, and at harvest, respectively.

infested control plots of *M. arenaria* and *M. javanica,* but some of these control plots had become contaminated with a few nematodes.

Field experiments: Regression analysis of treatment means of *M. incognita* larval counts at midseason exhibited a linear relationship with tobacco yields (Fig. 2A). (Level of significance with quadratic model was only silghtly greater, with correlation coefficient being 0.93). When similar analyses were done with total numbers of eggs and larvae at midseason, the relationship between yield and total nematode numbers was better described by a quadratic model or by the Seinhorst model (Fig. 2B). Root-gall indices for field-nematicide treatment means were also correlated negatively with yields. In a field near the microplots, yield loss was 6.2% for each 10% increment of root galling (Fig. 3A). Although these relationships were relatively constant in several fields in which tobacco was growing within a region, yield losses for tests in the Piedmont (heavier fine-textured soils) were much less than those for tests in the Coastal Plain (sandier soils) (Fig. 3).

DISCUSSION

Close agreement in results was obtained relating nematode numbers to tobacco yields in microplots for two growing seasons. The removal of the plant remains in the low nematode-density plots at the final harvest (1976) aided in maintaining somewhat similar nematode population ranges from one year to the next. The numbers of second-stage larvae at the beginning of the second season were generally greater than the total numbers of eggs and larvae added to the plots in 1976. Nevertheless, with the use of ethoprop in one-half of the plots, yield losses were very similar for both years for all species except *M. arenaria.*

The capacity of *M. javanica* and *M. arenaria* to cause much greater root damage

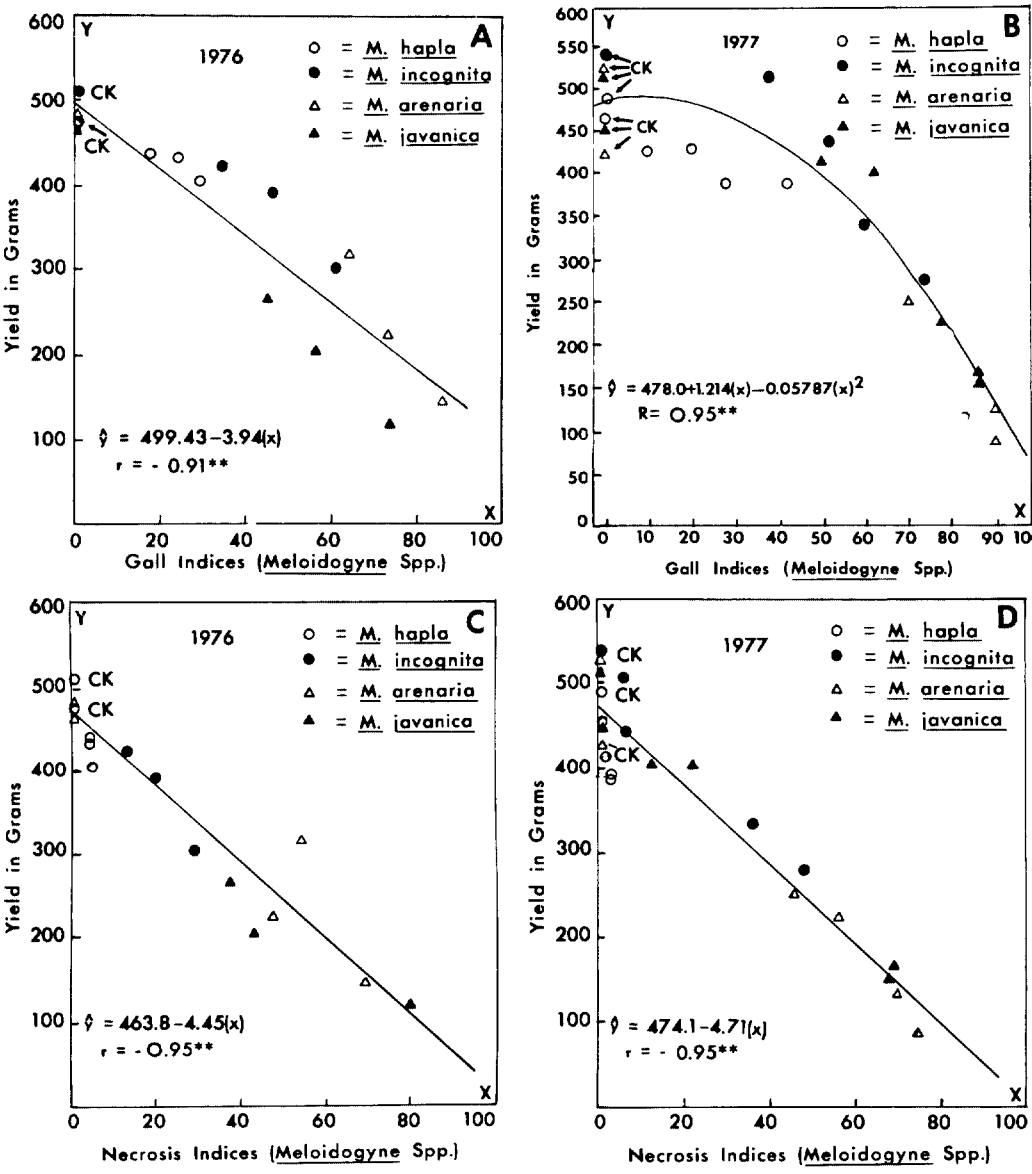

Fig. 1. Relationships of root galls and root necrosis to tobacco yields in microplots. A, B) Root-gall indices vs. yields in 1976 and 1977, respectively. C, D) Root-necrosis indices vs. yields in 1976 and 1977, respectively. All data are means of our replicates.

apparently results in these tissues being much more susceptible to invasion by secondary organisms such as *Rhizoctonia solani* (isolated from some affected plants) and other fungi. Powell (24) has found *Meloidogyne* spp. to predispose tobacco roots to numerous organisms. Thus, much of the yield loss attributed to *M. arenaria, M. javanica,* and *M. incognita* may have been brought about by secondary organisms causing extensive root decay. In contrast, *M. hapla* causes much less galling, with a maximum of approximately 50–60% of the roots usually being galled, and little necrosis. Thus, this nematode appears much less important in predisposing tobacco roots to other organisms.

The yield loss caused by *M. incognita* on resistant 'Speight G-28' was similar to earlier observations (16, C. J. Nusbaum and F. A. Todd, unpublished). Plants that received the greatest number of nematodes

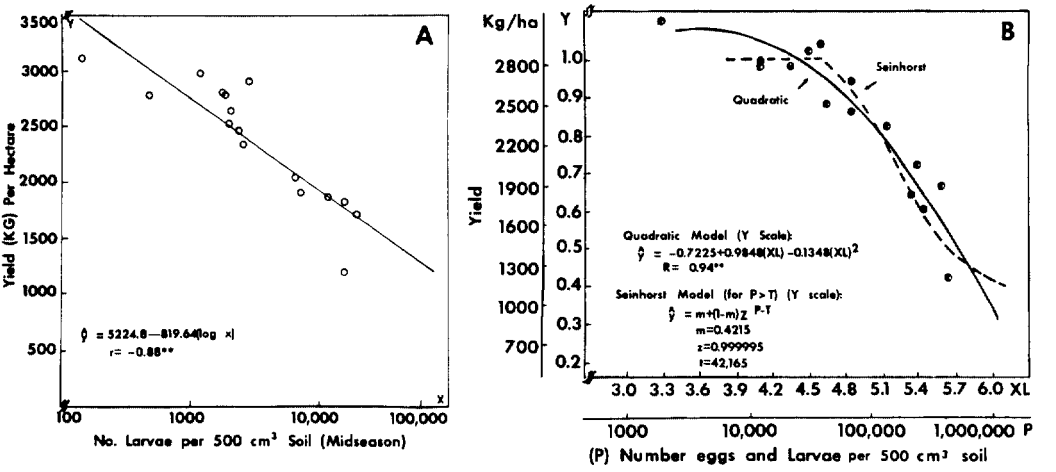

Fig. 2. Relationship of midseason counts of *Meloidogyne* to tobacco yields per ha (Johnston county, 1973). A) Number of larvae/500 cm³ soil vs. yield. B) Numbers of larvae + eggs/500 cm³ soil vs. yield (range of nematodes established with various nematicides).

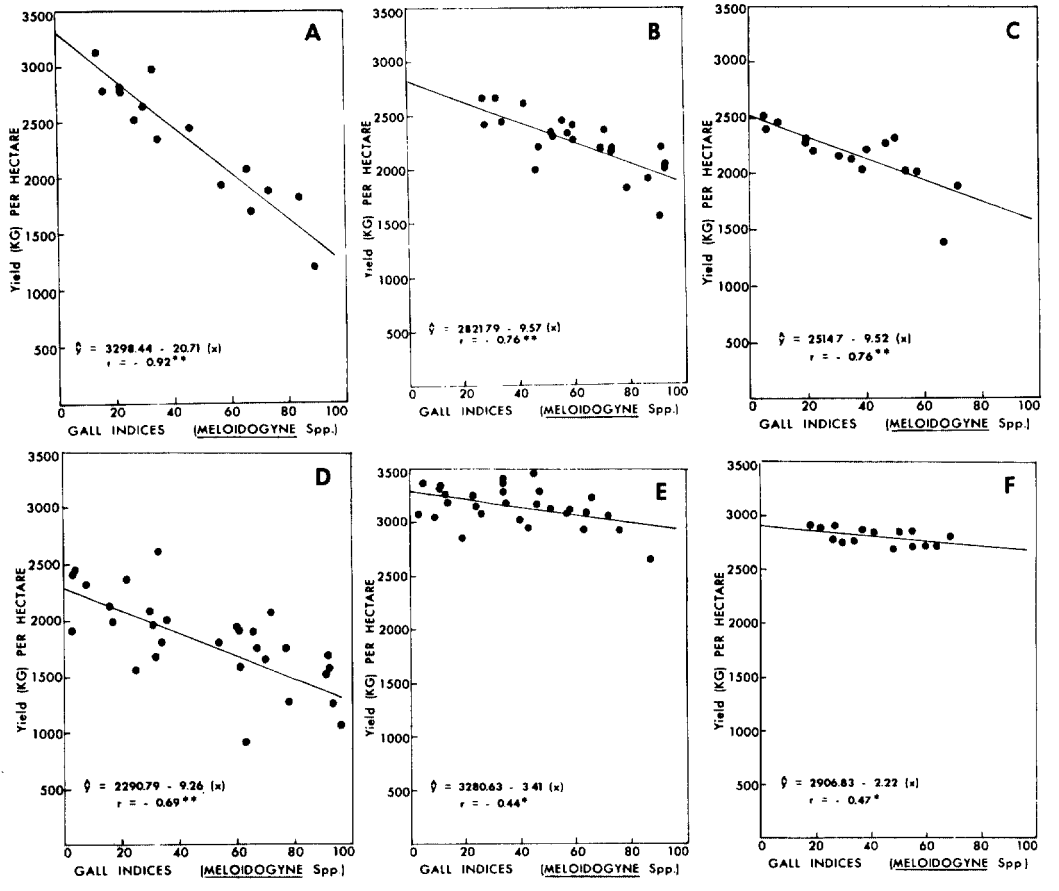

Fig. 3. Regressions of root-galling vs. tobacco yields in various field-nematicide tests. A-D) Results in coastal-plain counties: A) Johnston, 1973; B) Johnston, 1971; C) Sampson, 1974; D) Wake, 1970. E, F) Results in Piedmont counties: E) Surry, 1966; F) Yadkin, 1964.

were severely stunted shortly after transplanting but by midseason had nearly recovered. Nevertheless, there was a linear relationship between P_i and tobacco yield even though there was no nematode reproduction. This damage apparently is effected by the hypersensitive response of the resistant roots to *M. incognita* (C. J. Nusbaum, unpublished).

The differential efficacy of ethoprop on *Meloidogyne* sp. agreed with observations in field nematicide tests (Todd, unpublished). In other tests nonfumigant compounds have failed to give satisfactory control of *M. arenaria* in North Carolina, just as we observed in this microplot test. The greater reproductive potential of this species, compared to *M. hapla* and *M. incognita,* may be partially responsible for this problem. *M. javanica,* however, has an even greater reproductive rate than does *M. arenaria,* and ethoprop gave fairly good control of the former in microplots. The problem of apparent differences in tolerance of some *Meloidogyne* species to this type of nematicide needs more extensive study.

Various investigators have obtained conflicting results and conclusions on the potential of nematode assays and galling indices as predictors of tobacco yield losses. Root-gall indices obtained by Daulton (6), as presented by Oostenbrink (23), show a striking relationship between the magnitude of root galling and yield of tobacco. In contrast, Ferris (9) obtained poor correlations between yield and root galls. Other investigators (4,13,14), have found that root-gall readings near midseason are closely related to yield. Some of this variation among researchers could be partially due to the type of root-gall index used or the timing of gall determinations. For example, Zeck (30) developed a scheme to include root galls as well as necrosis. Others (1) have used schemes that are limited to actual magnitude of galled roots. We attempted to clarify this problem by developing separate disease indices for root galling and root necrosis. For growing conditions in North Carolina, both schemes have potential for determining losses caused by *Meloidogyne* spp. on tobacco. Not only did the results for a given species agree closely over a 2-yr period, but also results from nematicide tests in fields near microplot sites were very similar to those from the microplots. Nevertheless, relationships of root galling to yield at various field sites were rather variable. These differences probably were partially due to differences in soil type, rainfall, temperature, and soil microflora.

The fact that other investigators in southern states (4,13) have found a poor correlation of galling at final harvest to yield loss indicates that the timing of root-gall ratings possibly should vary with location. However, the use of root-necrosis indices for yield loss assessments at final harvest may have more promise than destructive midseason sampling in such situations. This scheme probably would not be reliable for *M. hapla,* as little root necrosis is associated with this species.

Our results also indicate that among the four common species of *Meloidogyne* attacking tobacco, the rate of reproduction may be a primary key in the relative pathogenicity of given species. To determine accurately the relative reproductive factor for each species, relatively small P_is of nematodes should be used, because of the competition among nematodes at the greater population densities. This problem can be seen in comparing the reproductive factors for the smallest inoculum level in the 1976 experiments compared to the greater inoculum levels for both years.

Our experiments indicate that the relationships between P_is of these nematodes, and associated root necrosis, with tobacco yields are adequately described by linear regressions. In contrast, midseason numbers of eggs and larvae or gall indices vs. yield are better characterized by quadratic models or others such as that of Seinhorst (25). This difference may indicate that midseason eggs or larvae, as compared to larvae coming from initial inoculum, have only a slight effect on yield. Furthermore, the striking linear regressions of root-necrosis indices vs. yield probably include the direct nematode and indirect nematode-microflora effects on yield; whereas the root-gall indices vs. yield regressions suggest that tobacco has considerable tolerance to galling, especially in the absence of root necrosis. Because nematodes often cause more damage when crops are under environmental stress, the slope of

regression models may vary over time.

The information provided herein should be of use in nematode assay programs as well as in efforts to determine yield losses to *Meloidogyne* spp. on tobacco. For example, *M. hapla* frequently is discounted as a problem on tobacco; yet relatively large populations of this nematode can result in a 10–20% loss in yield. Of equal importance is the quantification of the effects of *M. incognita* on the yield of the resistant cv. Speight G-28 and the demonstration of a low tolerance of tobacco to this nematode species in a sandy soil. The 1978 data indicate that increased organic matter may enhance tobacco's tolerance to this nematode. The greatest potential applications may lie in further development and refinement of root-gall and root-necrosis models for estimating yield losses to these pests. By developing models which would include various environmental parameters, we may be able to more accurately estimate tobacco yield losses due to root-knot nematodes in a given county or state.

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