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Relationships between Soil and Levels of *Meloidogyne incognita* and Tobacco Yield and Quality[1]

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Abstract: A 2-year study with six soils and four levels of *Meloidogyne incognita* in microplots was designed to determine the effects of these parameters on nematode activity and tobacco yield and quality. Key components under study were affected by soil, nematode level, and season (year–cultivar). In 1980, low initial nematode numbers (1,250) enhanced tobacco yield in Cecil clay loam, but caused slight to moderate yield losses in the other soils. Yield losses to *M. incognita* were generally greatest in sandy and muck soils. In 1980, regression analyses of the independent parameters Pi–clay–sand vs. yield gave an R^2 of 0.40. Examples of other coefficients of determination for yield vs. selected factors were root-necrosis index, 0.40; root-gall index, 0.18; root-gall index–cation exchange capacity (CEC), 0.34; root-necrosis index–CEC, 0.56; and root-necrosis index–sand-soil acidity-calcium, 0.62. In contrast, the R^2 for Pi alone versus yield in 1981 was 0.84. Soil also affected nematode reproduction with the greatest increases occurring in the sandy soils. In both years, low nematode numbers enhanced the synthesis of sugar in tobacco, whereas leaves from all other nematode treatments had low sugar levels. A low nicotine content was associated with nematode infection. Tobacco from sandy soils had a higher nicotine content than tobacco from clay soils.

Key words: crop loss, damage threshold, *Meloidogyne incognita, Nicotiana tabacum,* physiology, population dynamics, root-knot, soil texture, tobacco quality.

The impact of soil texture on the activity of *Meloidogyne* species and the associated effects on plant growth have been under study since the work of Bessey in 1911 (6). He found that root-knot disease on susceptible plants was suppressed in fine-textured clay soil. Since that research, the generalization that root-knot nematode infestations and associated crop damage are much greater in sandy soils than in clay or heavy soils has been widely accepted (3,4,24,27). Surveys on tobacco, *Nicotiana tabacum* L., and other crops in various geographic regions of North Carolina support this contention relative to the incidence of *Meloidogyne* species (2). Further microplot experiments with a range of soil textures have shown that the reproduction of *Meloidogyne incognita* (Kofoid & White) Chitwood on soybean is greatly suppressed in clay soils relative to that in various sandy soils (29). The impact on yield in this work was closely related to nematode reproduction.

Different approaches have been utilized in studying the effects of soil texture on the development of *Meloidogyne* species under greenhouse conditions. A few investigators have used mixtures of fine and coarse soils to obtain various levels of sand, silt, and clay (1,24,25). Others have selected fields with a range of textures (4,22,29). Results with the soil mixtures have differed, probably caused by specific textures in which the plants were grown. For example, a fine-textured soil suppressed the development of root-knot on sesbania growing in a 20-liter glazed jar relative to development in a coarse-textured soil (25), whereas nematode activity in other studies has been inversely related to soil (sand) particle size (26).

The influence of soil texture on nematode activity may vary with nematode species. *Heterodera schachtii* Schmidt reproduces best on plants in a silt loam, and the greatest increase of *Meloidogyne hapla* Chitwood is in a sandy loam (22). *Globodera rostochiensis* (Wollenweber) Behrens and *H. schachtii* often occur in fine-textured soils,

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TABLE 1. Moisture-holding characteristics and particle content (in percent) of soils used in this study.

Soil	Moisture at selected bars				Particle content			
	1/10	1/3	5	15	Sand	Clay	Silt	OM
Cecil sandy clay	27.0	22.0	16.0	15.5	47.9	38.9	13.2	0.9
Cecil sandy clay loam	25.7	21.7	16.5	16.2	52.8	28.7	18.5	2.2
Fuquay sand	5.5	4.6	2.1	2.1	91	2.5	6.5	0.6
Muck (organic)	67.4	50.1	34.7	32.6	58.1	8.7	33.2	> 30
Norfolk loamy sand	10.9	8.3	4.2	4.1	83.5	4.0	12.5	1.4
Portsmouth loamy sand	18.2	14.2	8.9	8.6	71.1	10.0	18.3	2.7

whereas most ectoparasitic nematodes are favored by coarse-textured soils (14,18). *Pratylenchus hexincisus* Taylor & Jenkins reproduces rapidly on corn in a wide range of soil textures (18,31).

Nematodes and soil properties have been shown to affect the chemical composition of plant tissues. These changes may affect the quality of tobacco, although related studies have given conflicting results. One study indicated that infection of tobacco by *Meloidogyne* species may result in a lower nicotine content of the cured leaf (28). Other findings showed that infection of tobacco by *M. incognita* may give rise to elevated levels of nicotine, particularly in the leaves of young plants (8,30). An extensive study of this nematode on susceptible and resistant cultivars revealed that it may limit nicotine content of leaves of susceptible tobacco and increase quantities in a resistant cultivar (11,12).

Much research has focused on characterizations of nematode-damage functions, especially the general inverse relationships between initial nematode levels and growth and (or) yield of annual crops (3,9,20,23). Rather precise tolerance limits (23) and economic thresholds (9) have been proposed and remain worthwhile goals. Unfortunately, present understanding of the dynamics of nematode–plant systems, as affected by environmental conditions, greatly limits the practical application of ecological findings (23). Therefore, damage thresholds with broad ranges are often used (20).

Few studies have focused on the quantitative effects of soil texture on the growth and yield responses and leaf chemistry of tobacco infected with *Meloidogyne* species. Thus, this study was initiated with three objectives: 1) determine the impact of soil texture and *M. incognita* on the growth and yield of tobacco; 2) elucidate the effects of soil texture on the reproduction of this nematode on tobacco; and 3) characterize the impact of various levels of this pathogen and soils on yield and the chemistry of the cured tobacco leaf.

MATERIALS AND METHODS

Experiments were conducted in 1980 and 1981. In each experiment, six soil textures were tested in 76-cm-d fiberglass-barrier microplots (4) at the Central Crops Experiment Station, Clayton, North Carolina (Table 1). Fuquay sand at this site was removed from some microplots to a depth of 40 cm to accommodate the addition of five other soil textures (29) (Table 1). In addition to determining the physical characteristics of each soil, the chemical properties were analyzed by the Agronomic Division of the North Carolina Department of Agriculture. Parameters included were acidity, base saturation, cation exchange capacity (CEC), organic matter content, pH, and levels of various cations and anions. All microplots were fumigated with methyl bromide–2% chloropicrin (100 g/m^2) 6 weeks before establishment of each crop.

A race 3 population of *M. incognita* from North Carolina was used in each of the experiments. This nematode was increased on tomato, *Lycopersicon esculentum* Mill. cv. Manapal, in the greenhouse. Eggs used for inoculum were extracted from infected roots 10–12 weeks after inoculation (5).

TABLE 2. Correlations of initial number (Pi),† root galls, and root necrosis with tobacco yields in six soils (1980).

Soil	Base yield (g/plot without nematodes)	Loss per Pi (%)†			Correlation coefficients‡		
		1,250	5,000	20,000	Pi	Root galls	Root necrosis
Cecil sandy clay	452	6	24	43	−0.51*	−0.58**	−0.70**
Cecil sandy clay loam	440	+8	0	13	−0.21 NS	−0.17 NS	−0.37 NS
Fuquay sand	489	4	17	30	−0.51*	−0.47*	−0.75**
Muck (organic)	411	18	34	58	−0.69**	−0.62**	−0.79**
Norfolk loamy sand	563	11	11	16	0.43*	−0.46*	−0.35 NS
Portsmouth loamy sand	463	12	22	50	0.70**	−0.62**	−0.71**

† Pi = eggs/500 cm³ soil.
‡ *, ** refer to significance level of $P = 0.05$ and 0.01, respectively; NS = nonsignificant.

Eggs extracted with NaOCl (5) were used at rates of 0, 1,250, 5,000, and 20,000/500 cm³ soil. In addition to the nematode inoculum, approximately 1,000 chlamydospores of the mycorrhizal fungus *Glomus macrocarpus* Tul. & Tul. were added to each plot. The 24 treatments were arranged in a randomized complete block design with five replicates. Tobacco cultivars used were McNair 944 (1980) and Coker 319 (1981). Fertilizers, insecticides, and supplemental irrigation were provided as needed.

Nematode population levels were determined 10–12 weeks after transplanting and at the final harvest. For nematode assays, 10 cores, collected 20 cm deep with a 2.5-cm-d soil probe, were composited. *Meloidogyne incognita* eggs were extracted by elutriation and NaOCl, whereas juveniles were extracted by elutriation and centrifugation (5). In addition, root-gall development and associated root necrosis were assessed at the final harvest. A root-disease rating scale of 0–100 (with 0 = no disease and 100 = maximum disease) was used.

Additional crop response data included growth ratings on a scale of 0–10 (with 0 = poorest growth and 10 = maximum growth) and the weights and commercial value of the cured leaf (value and vigor data not included). An automated system for determining sugar and nicotine content of tobacco leaves was used (13). These compounds were extracted simultaneously from small tobacco samples with an aqueous 4% NaOH, 10% acetic acid solution. The samples were clarified with Dargo G60 (phosphorous free).

Yield, chemistry, and nematode data were subjected to analysis of variance. *Meloidogyne incognita* population data were transformed to $\log_{10}(x + 1)$ for the statistical analysis. Various regression analyses were used in some instances.

RESULTS

Effects of nematode level and soils on tobacco yields: Initial levels of nematodes and soil texture had significant but varying effects on tobacco yields in both years (Tables 2, 3). The least damage by various levels of *M. incognita* occurred in each year in a Cecil sandy clay loam. A low level of this nematode gave a slight yield enhancement of the cured leaf in this soil during the first year. The lowest yields occurred in the organic (muck) soil and the Portsmouth loamy sand. Yield responses varied from one season to the next in similar soil and nematode treatments. Yield losses to moderate levels of *M. incognita* in the Norfolk loamy sand and in the Cecil sandy clay were intermediate in 1980 and severe in 1981.

Multiple regression analysis of various soil parameters and nematode levels versus tobacco yields in 1980 accounted for a maximum of 62% of the variation. Initial levels of nematodes across all soils versus yield had an R^2 of 0.18, whereas cation exchange capacity versus yield had an R^2 of 0.23. The greatest single coefficient of determination was for root-necrosis indi-

TABLE 3. Influence of initial number (Pi)† of *Meloidogyne incognita* and soil texture on tobacco yield and nematode reproduction (1981).

Soil‡	Pi 0	Pi 1,250	Pi 5,000	Pi 20,000 (% loss)	Soil means
		Yield (g/plot)			
Cecil sandy clay	448	381	220	31 (93)	270
Cecil sandy clay loam	490	409	323	198 (60)	355
Fuquay sand	464	402	338	103 (78)	327
Muck (organic)	523	376	305	36 (93)	310
Norfolk loamy sand	578	409	340	128 (79)	364
Portsmouth loamy sand	565	443	241	42 (89)	323
Nematode–Pi means	511	403	294	90	
LSD ($P = 0.05$) Pi × soil = 74; Pi means = 30; soil means = 37					
		Midseason nematode reproduction factor (no. eggs and juveniles/Pi)			
Cecil sandy clay		85	16	5	35
Cecil sandy clay loam		106	21	6	44
Fuquay sand		107	40	10	52
Muck (organic)		40	6	2	16
Norfolk loamy sand		244	40	7	97
Portsmouth loamy sand		143	42	6	64
Nematode–Pi means		121	27	6	
LSD ($P = 0.05$) Pi × soil = 37; Pi means = 15; soil means = 21					

Means of five replicates.
† Pi = eggs/500 cm^3 soil.
‡ Based on topsoil (upper 30 cm) in microplots.

ces ($R^2 = 0.29$). When combined, initial levels of nematodes and cation exchange capacity gave an R^2 of 0.42. The greatest R^2 for disease rating and soil properties was a combination of root necrosis–sand-acidity-calcium (0.62).

The R^2 values for nematode levels versus tobacco yields for 1981 were higher than for 1980. For example, when four sets of soil data were combined (Cecil sandy clay and muck excluded), initial levels of nematodes alone versus yield gave an R^2 of 0.92. The quadratic equation for this Pi–yield relationship was $Y = 478 + 109X - 45X^2$. The model for all soils for 1981 was $Y = 439 + 110X - 45X^2$; $R^2 = 0.84$. Differences in yields for the 2 years can be depicted most clearly in loss percentages compared with the respective controls (Tables 2, 3). For the high nematode numbers, yield losses ranged from 13 to 58% in 1980 (Table 2). In 1981, these losses ranged from 60 to 93% (Table 3). These year–cultivar differences were so great they were not analyzed statistically.

Influence of soil properties on nematode reproduction and disease ratings: Reproduction of *M. incognita* at 10–12 weeks after planting, especially at lower initial levels, was greater in the Norfolk loamy sand and the Portsmouth loamy sand than in the clay and organic soils (Table 3). Tobacco growing in the Fuquay sand supported an intermediate rate of nematode reproduction. Actual rate of nematode increase at the low initial levels for 1981 ranged from two to almost eight times greater for given soils, relative to the previous year.

Root gall and root necrosis development on plants exposed to various nematode levels in the different soils varied slightly over the treatments (Table 4). There was greater root-knot development and associated root necrosis for all treatments in 1981 (Table 4) than in 1980 (data not included). This response was particularly true for the root necrosis induced by this nematode and associated fungi (4).

Impact of nematode level and soils on tobacco chemistry: The influence of *M. incognita* on sugar content of the cured tobacco leaf appeared to be population-density dependent

TABLE 4. Effects of initial number (Pi)† of *Meloidogyne incognita* and soil on root-gall and root-necrosis development of tobacco (1981).

	Pi 1,250	Pi 5,000	Pi 20,000	Soil means
Root-gall indices‡				
Cecil sandy clay	79	96	100	92
Cecil sandy-clay loam	89	97	100	95
Fuquay sand	86	86	94	87
Muck	78	77	99	85
Norfolk loamy sand	80	90	100	90
Portsmouth loamy sand	77	94	98	90
Nematode–Pi means	82	90	98	
LSD ($P = 0.05$) Pi × soil = 9; Pi means = 4; soil means = 4				
Root-necrosis indices				
Cecil sandy clay	51	92	100	81
Cecil sandy clay loam	65	81	87	78
Fuquay sand	58	69	85	71
Muck	61	63	98	74
Norfolk loamy sand	57	76	98	77
Portsmouth loamy sand	66	91	98	85
Nematode–Pi means	60	79	94	
LSD ($P = 0.05$) Pi × soil = 16; Pi means = 6; soil means = 8				

Means of five replicates.
† Pi = eggs/500 cm³ soil.
‡ Disease indices, root galls, and root necrosis based on scale of 0 = healthy to 100 = entire root (galled or necrotic).

(Table 5). In 1980, low levels of this pathogen resulted in more reducing sugars than occurred in leaves from healthy plants. In contrast, high initial inoculum densities suppressed reducing sugars. However, all levels of nematode suppressed sugar synthesis in tobacco leaves in 1981. The negative effects of moderate and high nematode levels were much greater than in 1980.

Reducing sugars of cured tobacco leaf also were affected by soil ($P = 0.05$). Tobacco from the Portsmouth loamy sand had the lowest reducing sugars each year, but differences among other soils varied. No single soil or disease–nematode parameter gave a high coefficient of determination when regressed against reducing sugars. A combination of calcium level and root necrosis gave an R^2 of 0.11. Organic matter–soil acidity–root necrosis had an R^2 of 0.17.

The presence of *M. incognita* had a negative impact on nicotine content of the cured tobacco leaf in both years (Table 5). Nematode level did not have a consistent effect on this compound. Nicotine content of cured leaves from all treatments was much greater in 1980 than in 1981.

The soil in which tobacco was grown also had a striking effect on cured-leaf nicotine in both years. The friable, fertile Norfolk loamy sand supported growth of tobacco with the highest level of nicotine in both years. The Portsmouth loamy sand and the organic muck soil produced the lowest nicotine content in the cured tobacco in 1981. The Cecil sandy clay also produced tobacco with low nicotine in 1980. A number of soil parameters regressed against nicotine content gave R^2 values of 0.2 or better. Initial nematode levels as well as final numbers of juveniles regressed against nicotine gave somewhat lower R^2 values. Root gall indices when combined with clay, phosphorus, or calcium levels versus nicotine gave R^2 values > 0.35. The combination of percentage of sand and clay–cation exchange capacity and in gall indices versus nicotine gave one of the higher R^2 values > 0.46.

DISCUSSION

In this study, tobacco yield varied greatly with initial numbers of *M. incognita,* soil, and season. In previous research, no single parameter such as textural components or soil chemistry was identified as a key character responsible for the greater losses often associated with *M. incognita* in sandy soils (3,4). Still, in the present work (1980), tobacco growing in a clay loam with low numbers of nematodes had a slightly greater yield than did the uninoculated controls. This response supports observations on the suppressive effects of clay soils on damage caused by this nematode (6). Although losses in cured leaf yield to *M. incognita* in this soil were much greater in 1981 than in 1980, they still were less than those in the other soils. The lowest yields may have occurred in the muck soil, especially at high nematode levels, because this soil was quite dry in this abnormal location. The "season" effects on yield losses caused by *M. incognita* were greater than nematode lev-

TABLE 5. Impact of levels of *Meloidogyne incognita* and soil on sugar and nicotine content of tobacco.

Nematode level (Pi)†	Cecil clay	Cecil loam	Fuquay sand	Muck	Norfolk loamy sand	Portsmouth loamy sand	Nematode–Pi means
			Sugar 1980				
0 control	19.3	13.1	13.3	18.8	13.9	14.2	15.4
1,250	20.2	15.6	18.6	18.9	14.2	18.0	17.6
5,000	18.3	13.1	19.7	14.2	16.7	13.3	15.9
20,000	12.9	14.6	14.6	10.1	12.9	8.2	12.2
Soil means	17.7	14.1	16.6	15.5	14.4	13.4	
LSD ($P = 0.05$) Pi × soil = 4.6; soil means = 2.4; Pi = 1.7							
			Sugar 1981				
0 control	19.0	20.0	22.8	24.7	20.9	21.7	21.5
1,250	17.5	18.5	22.7	20.8	17.5	16.2	18.9
5,000	7.4	10.9	14.5	10.3	10.0	5.9	9.8
20,000	3.9	7.1	3.8	1.7	1.2	1.8	3.3
Soil means	12.0	14.1	15.9	14.4	12.4	11.4	
LSD ($P = 0.05$) Pi × soil = 4.2; soil means = 2.1; Pi = 1.7							
			Nicotine 1980				
0 control	3.2	5.2	5.7	4.0	5.9	5.1	4.9
1,250	2.8	3.8	4.4	4.8	4.5	4.4	3.8
5,000	2.5	3.8	3.8	3.6	5.4	3.6	3.7
20,000	2.9	3.9	3.3	4.1	4.3	3.8	4.1
Soil means	2.9	4.2	4.3	4.1	5.0	4.2	
LSD ($P = 0.05$) Pi × soil = 1.0; soil means = 0.5; Pi = 0.4							
			Nicotine 1981				
0 control	1.9	2.4	2.2	1.8	2.4	2.3	2.2
1,250	1.6	1.9	1.9	1.5	2.5	1.5	1.8
5,000	1.6	1.5	1.9	1.7	2.3	1.6	1.8
20,000	1.6	1.5	2.0	1.1	1.8	0.8	1.5
Soil means	1.7	1.8	2.0	1.5	2.2	1.5	
LSD ($P = 0.05$) Pi × soil = 0.6; soil means = 0.3; Pi = 0.2							

Means of five replicates.
† Pi = eggs/500 cm^3 soil.

els or edaphic factors. The greater yield losses in 1981 may have resulted partially from cultivar sensitivity, growing conditions, and (or) condition of nematode inoculum. In any case, this high season-to-season variation continues to pose problems in developing damage and economic thresholds for these nematodes.

The differential rates of reproduction of *M. incognita* in the different soils undoubtedly were major factors accounting for much of the different growth and yield responses of tobacco to this nematode. Although these trends are similar and in agreement with earlier researchers (4,6,18,19,24), some poorly understood deviations were observed. For example, the friable, highly fertile Norfolk loamy sand supported the second highest rate of nematode reproduction in 1980, yet the crop exhibited only limited damage. During the second year, this soil again supported extremely high rates of nematode reproduction, and the tobacco was severely damaged. These data give credence to the proposal that soil bulk density, temperature, and moisture, either alone or possibly in combination with other factors, may be keys to identifying the environmental components responsible for the seasonal variations and yield losses to nematodes (15). Although inoculum levels were identical for both years, their effectiveness the second year apparently was much greater. The cultivar Coker 319 (used in 1981) also may be somewhat more sensitive to *M. incognita*

than McNair 944 (used in 1980). These differences (inoculum effectiveness and cultivars) may account for the greater reproduction rates in all of the soils and the greater losses in yield to this nematode. The elevated rate of reproduction probably was responsible for the very high root necrosis indices observed during the second year.

Meloidogyne incognita suppresses photosynthesis in plants by limiting nutrient uptake and (or) translocation (17). Thus, it was not surprising that moderate-to-high levels of this pathogen resulted in lower sugar content in the cured tobacco leaf. The elevated sugar level in leaves from plants with low numbers of nematodes for 1980, however, may be related to the plants' compensatory responses to root damage caused by this parasite. A few studies have documented enhanced growth of plants infected by this organism (3). The absence of this stimulatory effect in 1981 probably was due to greater inoculum potential than in 1980. Recent studies on the impact of macronutrients facilitating plants to overcome damage by this nematode (17) suggest that the general nutrient levels of the soils, including the Norfolk loamy sand, may have been partially responsible for the differential yield responses as well as sugar content.

Data from our experiments on nicotine content of cured tobacco leaf generally support previous reports (11,12,28); i.e., nematode infection suppresses nicotine synthesis. Other investigations in which low initial levels of nematodes were used for short-term experiments have indicated that nematodes enhance synthesis and translocation of nicotine to tobacco leaves (8,30). This divergence in results probably is due to the limited damage and increased root proliferation caused by the nematodes in the short-term studies. Experiments on resistant cultivars by different investigators indicate an elevated level of nicotine in the leaves can be associated with this nematode (8). This response, in contrast to susceptible cultivars, also may be due to the limited damage caused by this pathogen on those resistant plants.

The restriction of new feeder roots by *M. incognita* may be a key factor in this nematode's negative effect on nicotine synthesis. Synthesis of nicotine is dependent upon continued growth and development of root tips and not upon the general metabolic activity of the root tissue (16). Also, the tobacco root does not serve as a storage site for this compound. The nicotine half life in *N. tabacum* and *N. rustica* was reported to be from 22 to 28 hours (21). The half life in the root tip of low alkaloid tobacco was found to be only 4 hours (10). This phenomenon was suggested as the regulatory mechanism for nicotine in low alkaloid tobacco (10). Thus, the suggestion that nicotine levels may be correlated with resistance in tobacco (8) may not be well founded. In our study, soils that supported tobacco with the highest nicotine content also had the greatest final nematode populations. In contrast, the clay soils, particularly the Cecil sandy clay, supported growth of tobacco with low nicotine content and some of the lower rates of nematode development.

The highly variable effects of season and soil on tobacco chemistry were somewhat surprising. However, seasonal variation in nicotine content in cured tobacco leaves occurs often (7). Differences between 1980 and 1981 may be due in part to the cultivars utilized. Synthesis of this compound does vary with cultivar and season (7,28). Also, the more effective inoculum potential of the eggs used in 1981, relative to that in 1980, may have had a greater impact on nutrient uptake and plant metabolism.

Nematode population density level and soil properties impact nematode activity and associated tobacco growth, yield, and chemistry. Nematode population levels and soil characteristics only partially explain the differential growth and chemistry responses in tobacco in these experiments. Although our results tended to support the generalization that nematode damage is greater in coarse-textured, sandy soils than

in fine-textured ones, exceptions were encountered. These unexpected responses may be due to differences in water-holding capacities of the soils, structure, bulk density, and possibly other characteristics. Considerable variation in growth and yield responses of tobacco across different soils and from season to season with the same basic treatments indicate that much research is still required before precise economic thresholds (9) based on predicted yields can be offered to the grower.

Literature Cited

1. Abed, F. M. A. H., and A. H. Y. Taha. 1975. The influence of soil texture on the infectivity of the root-knot nematodes, *Meloidogyne javanica* on tomato, *Lycopersicon esculentum*. Annals of Agricultural Science of Moshtohor 4:265–270.

2. Barker, K. R. 1974. Influence of geographic area and previous crop on occurrence and densities of plant-parasitic nematodes in North Carolina. Plant Disease Reporter 58:991–995.

3. Barker, K. R., and T. H. A. Olthof. 1976. Relationships between nematode population densities and crop responses. Annual Review of Phytopathology 14:327–353.

4. Barker, K. R., F. A. Todd, W. W. Shane, and L. A. Nelson. 1981. Interrelationships of *Meloidogyne* species with flue-cured tobacco. Journal of Nematology 13:67–79.

5. Barker, K. R., J. L. Townshend, G. W. Bird, I. J. Thomason, and D. W. Dickson. 1986. Determining nematode population responses to control agents. Pp. 283–296 *in* K. D. Hickey, ed. Methods for evaluating pesticides for control of plant pathogens. St. Paul, MN: American Phytopathological Society Press.

6. Bessey, E. A. 1911. Root-knot and its control. Bulletin 217, Bureau Plant Industry, United States Department of Agriculture, Washington, DC.

7. Bowman, D. T., E. A. Wernsman, T. C. Corbin, and A. G. Tart. 1984. Contribution of genetics and production technology to long-term yield and quality gains in flue-cured tobacco. Tobacco Science 28:30–35.

8. Davis, E. L., and J. R. Rich. 1987. Nicotine content of tobacco roots and toxicity to *Meloidogyne incognita*. Journal of Nematology 19:23–29.

9. Ferris, H. 1978. Nematode economic thresholds: Derivation, requirements, and theoretical considerations. Journal of Nematology 10:341–350.

10. Hall, L. W. 1975. Effects and mode of alkaloid control in four genotypes of *Nicotiana tabacum*. M.S. thesis, University of Kentucky, Lexington.

11. Hanounik, S. B., and W. W. Osborne. 1975. Influence of *Meloidogyne incognita* on the content of amino acids and nicotine in tobacco grown under gnotobiotic conditions. Journal of Nematology 7:332–336.

12. Hanounik, S. B., and W. W. Osborne. 1977. The relationships between population density of *Meloidogyne incognita* and nicotine content of tobacco. Nematologica 23:147–152.

13. Harvey, W. R., H. M. Stahr, and W. C. Smith. 1969. Automated determination of reducing sugars and nicotine alkaloids on the same extract of tobacco. Tobacco Science 13:13–15.

14. Jones, F. G. W., D. W. Larbey, and D. M. Parrott. 1969. The influence of soil structure and moisture on nematodes, especially *Xiphinema, Longidorus, Trichodorus,* and *Heterodera* spp. Soil Biology and Biochemistry 1:153–165.

15. Jones, F. G. W., and A. J. Thomason. 1976. Bulk density as an indicator of pore space in soils usable by nematodes. Nematologica 22:133–137.

16. Laschuk, C. T. 1949. Influence of the process of root formation on synthesis of alkaloids in *Nicotiana*. Doklady Academii Nauk SSSR 64:405–408.

17. MeLakeberhan, H., J. M. Webster, R. C. Brooke, and J. M. D'Auria. 1988. Effect of KNO_3 and CO_2 exchanges, nutrient concentration and yield of *Meloidogyne incognita*-infected beans. Revue de Nématologie 11:391–397.

18. Norton, D. C. 1979. Relationship of physical and chemical factors to populations of plant-parasitic nematodes. Annual Review of Phytopathology 17: 279–299.

19. O'Bannon, J. H., and H. W. Reynolds. 1961. Root-knot nematode damage and cotton yields in relation to certain soil properties. Soil Science 92:384–386.

20. Oostenbrink, M. 1972. Evaluation and integration of nematode control methods. Pp. 497–514 *in* J. W. Webster, ed. Economic nematology. New York: Academic Press.

21. Robinson, T. 1974. Metabolism and function of alkaloids in plants. Science 184:430–435.

22. Santo, G. S., and W. J. Bolander. 1979. Interacting effects of soil temperature and type on reproduction and pathogenicity of *Heterodera schachtii* and *Meloidogyne hapla* on sugarbeets. Journal of Nematology 11:289–291.

23. Seinhorst, J. W. 1979. Nematodes and growth of plants: Formalization of the nematode–plant system. Pp. 231–256 *in* F. Lamberti and C. E. Taylor, eds. Root-knot nematodes (*Meloidogyne* species). New York: Academic Press.

24. Shane, W. W., and K. R. Barker. 1986. Effects of temperature, plant age, soil texture, and *Meloidogyne incognita* on early growth of soybean. Journal of Nematology 18:320–327.

25. Sleeth, B., and H. W. Reynolds. 1955. Root-knot nematode infestation as influenced by soil texture. Soil Science 80:459–461.

26. Wallace, H. R. 1969. The influence of nematode numbers and of soil particle size, nutrients and temperature on the reproduction of *Meloidogyne javanica*. Nematologica 15:55–64.

27. Wallace, H. R. 1989. Environment and plant health: A nematological perception. Annual Review of Phytopathology 27:59–75.

28. Weybrew, J. A., G. L. Jones, T. J. Mann, W.

G. Woltz, T. B. Hutchenson, C. J. Nusbaum, and C. H. M. Van Bavel. 1953. Factors affecting the nicotine content of flue-cured tobacco. Report No. 8, North Carolina Experimental Station, Raleigh.

29. Windham, G. L., and K. R. Barker. 1986. Effects of soil type on the damage potential of *Meloidogyne incognita* on soybean. Journal of Nematology 18:331–338.

30. Zacheo, G., F. Lamberti, and R. D. Durbin. 1974. Effect of *Meloidogyne incognita* (Kofoid and White) Chitwood on the nicotine content of tobacco (*Nicotiana tabacum* L.). Nematologia Mediterranea 2: 165–170.

31. Zirakparvar, M. E., D. C. Norton, and C. P. Cox. 1980. Population increase of *Pratylenchus hexincisus* on corn as related to soil temperature and type. Journal of Nematology 12:313–318.