

# Impact of Soil Texture on the Reproductive and Damage Potentials of *Rotylenchulus reniformis* and *Meloidogyne incognita* on Cotton<sup>1</sup>

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**Abstract:** The effects of soil type and initial inoculum density (Pi) on the reproductive and damage potentials of *Meloidogyne incognita* and *Rotylenchulus reniformis* on cotton were evaluated in microplot experiments from 1991 to 1993. The equilibrium nematode population density for *R. reniformis* on cotton was much greater than that of *M. incognita*, indicating that cotton is a better host for *R. reniformis* than *M. incognita*. Reproduction of *M. incognita* was greater in coarse-textured soils than in fine-textured soils, whereas *R. reniformis* reproduction was greatest in a Portsmouth loamy sand with intermediate percentages of clay plus silt. Population densities of *M. incognita* were inversely related to the percentage of silt and clay, but *R. reniformis* was favored by moderate levels of clay plus silt (ca. 28%). Both *M. incognita* races 3 and 4 and *R. reniformis* effected suppression of seed-cotton yield in all soil types evaluated. Cotton-yield suppression was greatest in response to *R. reniformis* at high Pi. Cotton maturity, measured as percentage of open bolls at different dates, was affected by the presence of nematodes in all 3 years.

**Key words:** cotton, ecology, edaphic factor, *Gossypium hirsutum*, *Meloidogyne incognita*, nematode, plant-disease loss, reniform nematode, root-knot nematode, *Rotylenchulus reniformis*, soil texture, yield.

*Meloidogyne incognita* (Kofoid & White) Chitwood (root-knot nematode) has long been associated with cotton in North Carolina and other areas where cotton is grown (10,11,16,17,20). *Rotylenchulus reniformis* Linford & Olivera (reniform nematode), though associated with cotton in other areas (2,9), has only recently been recognized as a pathogen of cotton in North Carolina (12). Quantitative data on the population dynamics of *R. reniformis* and its impact on cotton yield are limited (12,14).

Severe root-knot nematode infestations tend to occur on sandier soils such as those found on the coastal plain of the southeastern United States. Still, this nematode is

adapted to a large range of soil textures (15,16,19,21), but several reports indicate that the reniform nematode is favored by finer textured soils (7,16,19). Knowledge about the ecological requirements of plant-pathogenic nematodes can be used to identify areas where these pests are most likely to occur, thereby facilitating the focus of educational efforts in those areas where it is needed. Much of the nematological work on cotton in the United States predates 1975. Cultivars and techniques used for managing cotton have changed in the past 20 years. Information on the population dynamics, reproductive potential, damage potential, and survival of these pests on cotton under current management systems is essential to the implementation of integrated pest management programs (1,6).

The objectives of this research were to compare the reproductive and damage potentials of *R. reniformis* and *M. incognita* on cotton, and to evaluate the effects of soil type and texture on these nematodes and associated plant growth.

## MATERIALS AND METHODS

*Inoculum preparation:* *Rotylenchulus reniformis* was cultured in the greenhouse on

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sweetpotato (*Ipomea batatas* (L.) Lam.) cv. Beauregard. The same population of *R. reniformis* was used each year. Infected roots and infested soil were prepared before initiation of the experiment in 1991 and 1992. Inoculum preparation consisted of roots cut into 1-cm pieces and infested soil from greenhouse cultures. Soil and roots were mixed, and five samples of 500 cm<sup>3</sup> soil plus roots were assayed to determine nematode density. These soil and root samples were processed by elutriation (3) and centrifugation (8) to extract vermiform nematodes from soil. Roots were collected from each sample and processed by NaOCl extraction to estimate numbers of eggs (4). Infested soil was mixed with uninfested soil in measured proportions to give the desired concentration of nematodes for each plot. Tomato (*Lycopersicon esculentum* Mill.) roots cv. Rutgers infected with *M. incognita* race 3 in 1991 and *M. incognita* race 4 in 1992 were prepared in a similar manner. A suspension containing ca. 1,000 chlamydospores of *Glomus macrocarpus* Tul. & Tul., obtained from a soybean (greenhouse) culture, also was broadcast onto the soil surface of each microplot. Nematodes and fungal spores were incorporated 15 cm deep.

*Experimental design and data collection:* The experiment in 1991 was a two-nematode species (*M. incognita* race 3, and *R. reniformis*), X nine inoculum levels (0, 310, 625, 1,250, 2,500, 5,000, 10,000, 15,000, and 20,000/500 cm<sup>3</sup> soil) factorial design arranged in randomized complete blocks with four replications in a Fuquay sand. The second experiment was conducted in 1992 and 1993. The experimental design was a 2 × 4 × 6 factorial with two nematode species, four inoculum levels of *R. reniformis* and *M. incognita* race 4, and six soil types located at a common site. Initial population levels (Pi) of 0, 1,250, 2,500 and 5,000 eggs plus second-stage juveniles (J2) per 500 cm<sup>3</sup> soil were used for *M. incognita* and 0, 625, 1,250 and 2,500 eggs + vermiforms per 500 cm<sup>3</sup> soil for *R. reniformis*. Inoculum levels in 1993 were the carryover populations from 1992 and were

quantified from soil samples collected in late April prior to cotton planting.

Numbers of eggs and J2 of *M. incognita* and eggs and vermiform stages of *R. reniformis* were determined at midseason (early September), after cotton harvest (November), and before April 1993 and May 1994. Soil samples consisted of 8 to 10 cores approximately 2.5-cm-diam. taken 20 cm deep. A 500-cm<sup>3</sup> soil sample was processed by elutriation (3) and centrifugation (8) to extract juveniles and roots from soil. Eggs were extracted from roots by the NaOCl method (4).

Statistical analysis consisted of analysis of variance (ANOVA) for a factorial design. Nematode numbers were transformed with log<sub>10</sub> (X + 1) before analysis to standardize the variance; untransformed numbers are presented in tables and figures for clarity of presentation. Regression was used to evaluate quantitative effects of inoculum level on nematode reproduction and cotton yield. The Waller-Duncan k-ratio *t* test was used to separate means for the qualitative variable soil type. Mean population densities of *R. reniformis* and *M. incognita* race 4 for midseason (Pm) and harvest (Pf) for each soil type were regressed against the percentage of silt + clay. PROC GLM of the SAS System (SAS Institute, Cary, NC) was used to develop a model for each year for slopes relating Pi to cotton yield within soil types. Heterogeneity of slopes tests were used to evaluate differences in response to a quantitative variable (inoculum level) of the two nematodes within a given soil type. Repeated-measures ANOVA was used to analyze differences in seed-cotton yield over different cotton harvests.

*Types of microplots:* In the fall of 1991 and 1992, microplots (0.76-m-diam.) located at the Central Crops Research Station near Clayton, North Carolina, were fumigated with 100 g methyl bromide + 2 g chloropicrin/m<sup>2</sup> and covered with a 0.5-mm thick polyethylene tarp for 2 weeks. The scientific classification of the soils in their native sites as well as percentages of sand, silt, clay, and organic matter for these soils

were Fuquay sand (loamy, siliceous, thermic, arenic plinthic Kandiodults—the indigenous soil), 91, 6, 3, 0.6; Norfolk sandy loam (fine-loamy, siliceous, thermic, Kandiodults), 84, 12, 4, 1.4; Portsmouth loamy sand (fine-loamy over sandy or sandy-skeletal, mixed, thermic, Typic Umbraquelts), 72, 18, 10, 3.8; muck (Medisaprists), 58, 33, 9, <30; Cecil sandy loam (clayey, kaolinitic, thermic, Typic Kanhapludults), 53, 18, 29, 2.2; and Cecil sandy clay (clayey, kaolinitic, thermic, Typic Kanhapludults), 48, 13, 39, 0.9.

**Cotton culture:** Cotton seeds were planted at the rate of 16 per plot and thinned to eight plants per plot 3 weeks after planting. Cotton cv. Deltapine 50 (DP50) was planted 13 May 1991, 4 May 1992, and 11 May 1993. Standard nutritional and pest management practices for North Carolina cotton production were employed each year. Soils were fertilized and limed according to soil-test recommendations, based on a composite sample from each soil type. Seed-cotton yield was determined for each microplot at three dates in October and November each year.

**RESULTS**

Numbers of *R. reniformis* were consistently greater than numbers of *M. incognita* race 3 in the Fuquay sand in 1991 ( $P = 0.01$ ) (Table 1). Reniform nematode Pm

and Pf in 1991 were affected by initial population density, whereas Pm and Pf of *M. incognita* race 3 were not influenced by Pi. The population density in soil and roots of both nematode species declined from midseason to cotton harvest.

Similar to 1991, Pm and Pf of *R. reniformis* were much greater than Pm and Pf of *M. incognita* race 4 in both 1992 and 1993 (Fig. 1A–D) in all six soil types ( $P = 0.01$ ). The two nematode species, however, were affected differently by soil type. Mid-season numbers of *R. reniformis* were unaffected by soil type either year, whereas soil type had a significant effect on midseason numbers of *M. incognita* ( $P = 0.10$ ) (Fig. 1A,C). Numbers of *M. incognita* were greater in the sandy soils and fewer in the Cecil sandy clay and Cecil sandy clay loam. Population densities of *M. incognita* declined from midseason to cotton harvest (Fig. 1 A–D), but the influence of soil type remained constant. Numbers of *R. reniformis* decreased slightly in most soil types in 1992 from midseason until cotton harvest (Fig. 1A,B). The population density of *R. reniformis* in 1993 increased from mid-season to cotton harvest in the Muck, Norfolk sandy loam, and Portsmouth soil types, but not in the other soil types (Fig. 1C,D). Soil type had a significant effect on *R. reniformis* Pf in both 1992 and 1993 (Fig. 1B,D). Greatest final population densities

**TABLE 1.** Influence of inoculum level (Pi) of *Rotylenchulus reniformis* (Rr) and *Meloidogyne incognita* race 3 (Mi3) per 500 cm<sup>3</sup> soil on mean midseason (Pm) and harvest (Pf) nematode population densities and standard deviation (SD) in a Fuquay sand near Clayton, North Carolina, 1991.

Pi/500 cm <sup>3</sup> soil <sup>a</sup>	September Pm (in 1,000s)				November Pf (in 1,000s)			
	Rr	SD	Mi3	SD	Rr	SD	Mi3	SD
310	208.4	48.9	24.3	15.3	96.6	60.6	2.4	1.9
625	196.5	165.2	30.2	19.7	76.8	72.7	1.4	1.4
1,250	283.6	205.3	46.1	23.4	61.1	70.7	3.1	2.2
2,500	93.5	96.1	58.9	18.5	28.5	25.3	1.6	0.4
5,000	17.7	5.4	54.9	36.3	10.7	3.1	1.5	1.3
10,000	36.0	11.8	70.5	55.7	22.9	23.8	2.4	2.5
15,000	105.6	69.0	33.7	11.1	15.1	7.2	1.1	0.5
20,000	59.8	69.7	41.5	10.6	19.7	26.9	0.8	0.8

<sup>a</sup> The relationship between Pi and midseason numbers of *R. reniformis* was adequately described by a quadratic equation where  $\log_{10} Pm = 5.23 - 0.00013 Pi + 0.000000005 Pi^2$  ( $R^2 = 0.30, P = 0.006$ ). Final population densities of *R. reniformis* were negatively related to Pi,  $\log_{10} Pf = 4.70 - 0.000063 Pi$  ( $R^2 = 0.25, P = 0.0036$ ). Population densities of *M. incognita* (Pm and Pf) were not related to initial inoculum level Pi ( $P < 0.10$ ). Standard deviation of the mean (SD) is presented.

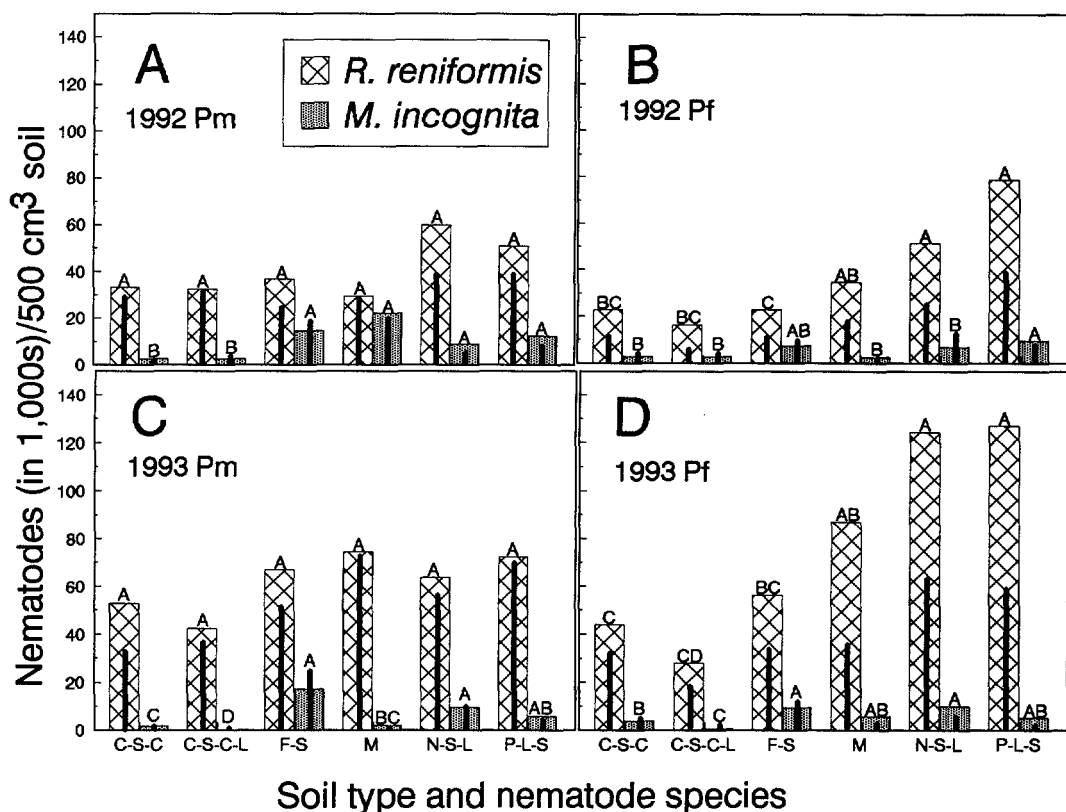


FIG. 1. Midseason (Pm) and harvest (Pf) population densities of *Rotylenchulus reniformis* and *Meloidogyne incognita* race 4 in microplots from six soil types: C-S-C Cecil sandy clay, C-S-CL Cecil sandy clay loam, F-S Fuquay sand, M Muck, N-S-L Norfolk sandy loam, and P-L-S Portsmouth loamy sand. A) 1992 Pm, B) 1992 Pf, C) 1993 Pm, and D) 1993 Pf. Numbers of *R. reniformis* were greater ( $P = 0.05$ ) than numbers of *M. incognita* race 4 at all samplings in 1992 and 1993. Means within a nematode treatment followed by the same letter are not different according to Waller-Duncan k-ratio  $t$  test ( $k$ -ratio = 50). Lines within bars are standard deviation of mean population density within a soil type. Initial inoculum level (Pi) had no effect on Pm or Pf either year.

of *R. reniformis* occurred in the Norfolk sandy loam and Portsmouth loamy sand. Lowest *R. reniformis* Pf occurred in the Cecil sandy clay and Cecil sandy clay loam, with intermediate values for the Muck soil and Fuquay sand.

The regression of *M. incognita* Pm and Pf versus silt + clay content revealed an inverse relationship ( $P = 0.01$ ) between clay + silt content (Fig. 1). A quadratic relationship provided an adequate fit ( $R^2 = 0.34$ ,  $P = 0.01$ ) as regards Pm and Pf of *R. reniformis* and clay + silt content with an optimum near 28% silt + clay of the soils tested (Fig. 2). Numbers of *R. reniformis* and *M. incognita* in the spring of 1993 and 1994 were positively correlated with the previous years' Pf ( $P = 0.10$ ). Neverthe-

less, *R. reniformis* survived overwinter at much higher levels than did *M. incognita* (Table 2).

The yield of seed cotton was suppressed by both *M. incognita* race 3 and *R. reniformis* in 1991 ( $P = 0.05$ ) (Fig. 3). The two nematode species were equal in their effects on cotton yield in the Fuquay sand. Significant ( $P = 0.01$ ) seed-cotton yield suppression in response to Pi of *M. incognita* race 4 Pi occurred in the Cecil sandy clay loam, the Muck, Fuquay sand, and Portsmouth sandy loam in 1992, whereas *R. reniformis* suppressed yield only in the Muck and Fuquay sand (Fig. 4A-D).

In contrast, seed-cotton yields were suppressed in all soil types by *R. reniformis* in 1993 (Fig. 5A-F). Seed-cotton yield was

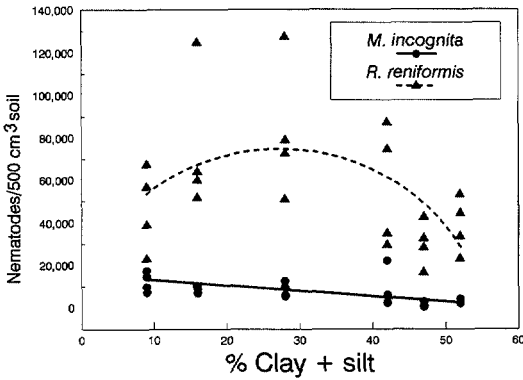


FIG. 2. Influence of the percentage of clay and silt on midseason (Pm) and harvest population densities (Pf) of *Rotylenchulus reniformis* and *Meloidogyne incognita* race 4/500 cm<sup>3</sup> soil in six soil types from 1992 and 1993. The relationship between numbers of *R. reniformis* (Y) and clay + silt percentage (X) was described by the quadratic model  $Y = 19,309 + 4,379X - 82X^2$  ( $R^2 = 0.34, P = 0.01$ ). Numbers of *M. incognita* (Y) were negatively related to the percentage of clay + silt (X):  $Y = 13,584 - 202X$  ( $R^2 = 0.36, P = 0.01$ ). Solid circles are means of *M. incognita* race 4 Pm or Pf. Solid triangles are means of *R. reniformis* Pm or Pf.

not affected by *M. incognita* in the Portsmouth loamy sand or the Muck soil type (Fig. 5C,D). Slopes of the regressions of yield vs. Pi for the two nematode species were similar, but the higher levels of *R. reniformis* encountered in 1993 resulted in the greatest cotton-yield suppression (Fig. 5A-F).

Nematodes also affected cotton yield in a subtle way. Cotton tended to mature earliest in uninoculated plots in 1991 (Fig.

6A). Most cotton was harvested from control plots at the first picking ( $P = 0.05$ ) in 1991. In contrast, at the first 1992 harvest, control plots had no open bolls, and approximately 16% to 30% of the seed cotton was picked from nematode-inoculated plots at that time (Fig. 6B). Cotton plots in 1993 with reniform nematode had lower yields than uninoculated plots or those containing *M. incognita* ( $P = 0.05$ ) (Fig. 6C). Additionally, only 59% of the cotton yield was obtained at the first harvest in plots infested with reniform nematode compared to 73% and 71% for noninfested and *M. incognita*-infested plots, respectively. Differences in the amount of cotton picked at various sample dates were significant ( $P = 0.05$ ). This variation in amounts of seed cotton available for picking at three sample dates demonstrates the effects of nematodes on cotton maturity. Differences in time of boll opening were not always consistent among treatments. Controls matured earlier in 1991 and 1993; whereas, in 1992, *R. reniformis*-inoculated cotton plants tended to open earlier. The discrepancy between years may be explained, in part, by the Pi used in these experiments.

DISCUSSION

Cotton DP 50, evidently, is a better host for *R. reniformis* than for *M. incognita* races 3 and 4. However, the extraction methods

TABLE 2. Mean initial population densities (Pi) of *Rotylenchulus reniformis* (Rr) and *Meloidogyne incognita* race 4 (Mi4) per 500 cm<sup>3</sup> soil (in 1,000s) for samples collected in April 1993 and May 1994 in six soil types in microplots at the Central Crops Research Station, Clayton, North Carolina.

Soil type	Pi 1993				Pi 1994			
	Rr	SD	Mi4	SD	Rr	SD	Mi4	SD
Cecil sandy clay	15.6 AB	10.2	0.03 D	0.03	1.1	1.1	0.0030	0.0060
Cecil sandy clay loam	7.9 BC	5.8	0.10 BC	0.10	1.2	1.5	0.0006	0.0030
Fuquay sand	9.3 C	5.7	0.08 C	0.08	0.8	0.4	0.0007	0.0030
Muck	7.8 BC	2.5	0.31 A	0.25	1.6	1.2	0.0006	0.0002
Norfolk sandy loam	13.6 AB	6.6	0.15 B	0.21	2.2	1.2	0.0000	0.0000
Portsmouth loamy sand	28.9 A	18.8	0.35 A	0.21	2.2	1.6	0.0060	0.0006
Mean	13.9	12.0	0.17	0.20	1.5	1.3	0.0008	0.0030

Means in a column followed by the same letter are not significantly different according to the Waller-Duncan k-ratio *t* test (k-ratio = 50). Inoculum level had no significant effect on nematode population densities. Numbers of *R. reniformis* were greater ( $P = 0.01$ ) than those of *M. incognita*. SD signifies the standard deviation of the mean (in 1,000s).

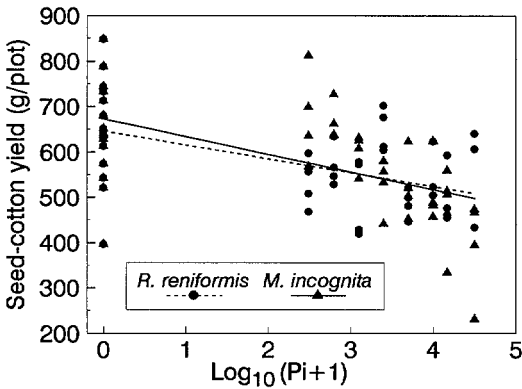


FIG. 3. Effects of initial inoculum level ( $P_i$ ) of *Meloidogyne incognita* race 3 and *Rotylenchulus reniformis* on seed-cotton yield of Deltapine 50 in 1991. Regression equation of *M. incognita* and *R. reniformis*, respectively:  $Y = 671.4 - 38.8 \log_{10} P_i$  and  $Y = 646.6 - 30.9 \log_{10} P_i$ , ( $R^2 = 0.29$ ,  $P = 0.0001$ ); slopes are not significantly different ( $P = 0.05$ ).

used may have been more efficient at recovering all population stages of *R. reniformis* than of *M. incognita*. Still, numbers of *R. reniformis* were one- to more than ten-fold greater than those of *M. incognita*. Population densities of *M. incognita* tended

to reach a relatively low equilibrium density on cotton. Perhaps certain cotton cultivars, such as DP50, restrict but do not eliminate reproduction of root-knot nematode. This genotype may represent a type of "horizontal resistance" to root-knot nematode. The population fluctuations of reniform nematode on cotton were more similar to a traditional plant-parasite interaction. High population densities of reniform nematode in 1991 tended to result in intraspecific competition, indicated by the negative correlation between  $P_i$  and  $P_f$ , which limited population size. In contrast, there was no evidence of density-dependent effects of  $P_i$  on *R. reniformis* numbers in either 1992 or 1993. Reniform nematode  $P_i$  levels were relatively low in 1992, however, and there were only four population levels. The low population density may have masked a density-dependent influence of  $P_i$  on  $P_m$  and  $P_f$  in 1992. Inoculum levels of *R. reniformis* in 1993, however, were high since they were that portion of the population that sur-

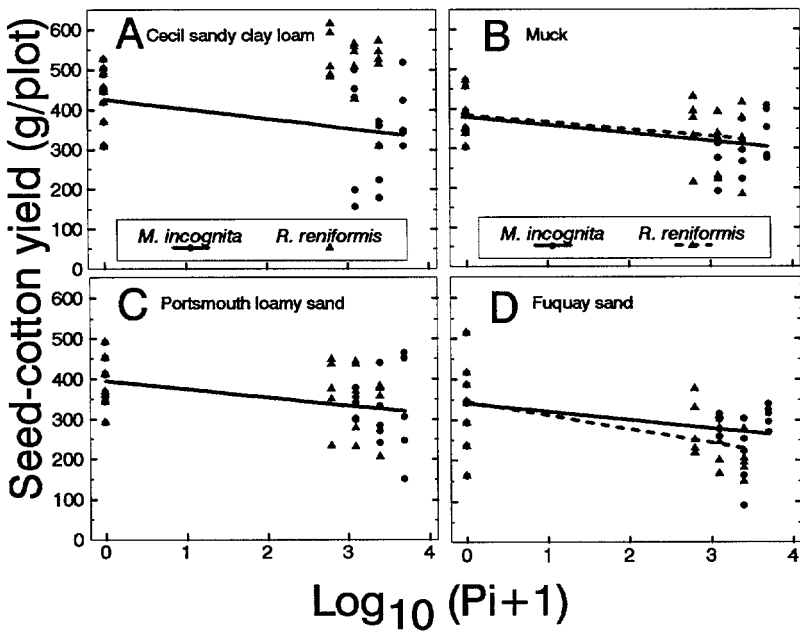


FIG. 4. Effects of initial inoculum level per  $500 \text{ cm}^3$  soil ( $P_i$ ) of *Meloidogyne incognita* race 4 and *Rotylenchulus reniformis* on seed-cotton yield of Deltapine 50 cotton in four soil types (A–D) in 1992. A) Cecil sandy clay loam regressions: *M. incognita*,  $Y = 425 - 24X$  ( $R^2 = 0.15$ ,  $P = 0.06$ ), *R. reniformis* NS. B) Muck regressions: *M. incognita*,  $Y = 380 - 21X$  ( $R^2 = 0.27$ ,  $P = 0.01$ ), *R. reniformis*  $Y = 384 - 16X$  ( $R^2 = 0.14$ ,  $P = 0.07$ ). C) Portsmouth loamy sand regressions: *M. incognita*,  $Y = 394 - 20X$  ( $R^2 = 0.17$ ,  $P = 0.05$ ), *R. reniformis* NS. D) Fuquay sand, *M. incognita*  $Y = 340 - 20X$  ( $R^2 = 0.16$ ,  $P = 0.05$ ), *R. reniformis*,  $Y = 344 - 31$  ( $R^2 = 0.32$ ,  $P = 0.01$ ).

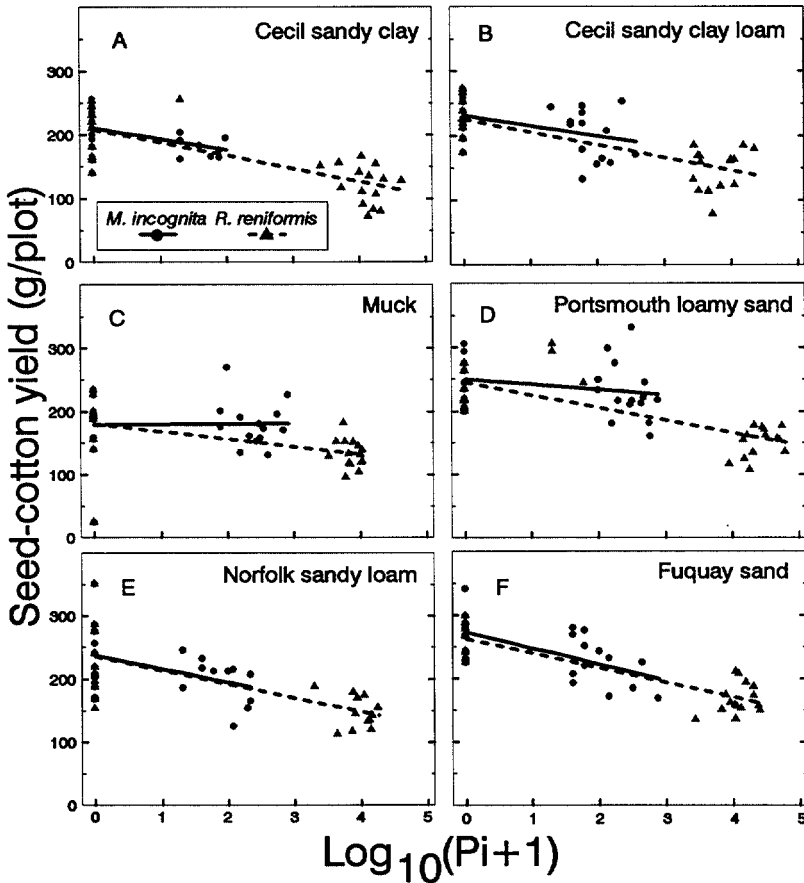


FIG. 5. Influence of initial population density ( $P_i$ ) of *Meloidogyne incognita* race 4 and *Rotylenchulus reniformis* on seed-cotton yield (grams per microplot) in six soil types in 1993. A) Cecil sandy clay regression equations: *M. incognita*,  $Y = 210 - 17X$  ( $R^2 = 0.18, P = 0.04$ ); *R. reniformis*,  $Y = 208 - 21X$ , ( $R^2 = 0.57, P = 0.01$ ). B) Cecil sandy clay loam regression equations: *M. incognita*,  $Y = 231.4 - 16.0X$  ( $R^2 = 0.17, P = 0.04$ ); *R. reniformis*,  $Y = 225 - 20X$  ( $R^2 = 0.58, P = 0.01$ ). C) Muck soil: *M. incognita*,  $Y = 178.9 - 0.66X$  ( $R^2 = 0.0003, P = 0.93$ ); *R. reniformis*,  $Y = 180.0 - 12.0X$  ( $R^2 = 0.24, P = 0.127$ ). D) Portsmouth loamy sand: *M. incognita*,  $Y = 249.7 - 8.0X$  ( $R^2 = 0.056, P = 0.2533$ ); *R. reniformis*,  $Y = 244.6 - 19.7X$  ( $R^2 = 0.056, P = 0.0001$ ). E) Norfolk sandy loam soil: *M. incognita*,  $Y = 272.1 - 25.2X$  ( $R^2 = 0.39, P = 0.0009$ ); *R. reniformis*,  $Y = 262 - 23X$  ( $R^2 = 0.78, P = 0.01$ ). F. Fuquay sand for *M. incognita*,  $Y = 236.5 - 21.3X$  ( $R^2 = 0.19, P = 0.029$ ); *R. reniformis*,  $Y = 235.3 - 22.0X$  ( $R^2 = 0.54, P = 0.0001$ ).

vived overwinter. The relatively high  $P_i$  in 1993 and small range between  $P_i$  within a soil type may have circumvented measurement of density dependence.

Cotton evidently has a high level of tolerance to *R. reniformis* or else the perennial nature of the cotton plant may allow for continued root physiological activity that permits continued reproduction and minimizes intraspecific competition. Population densities of *R. reniformis* continued to increase or maintained high levels from midseason to cotton harvest in 1992 and 1993, whereas levels of *M. incognita* race 4

declined over this time period. One possible explanation for the difference in population density maxima between these two nematode species may involve the selection of feeding sites. Root-knot nematode tends to infect the plant behind the root cap, whereas reniform nematode is less selective (5). As the cotton plant sets fruit, fewer new root tips develop, limiting feeding sites for the root-knot nematode but apparently not for the reniform nematode.

Reproduction of the two races of *M. incognita* appeared to be different when comparing 1991 densities with 1992. Re-

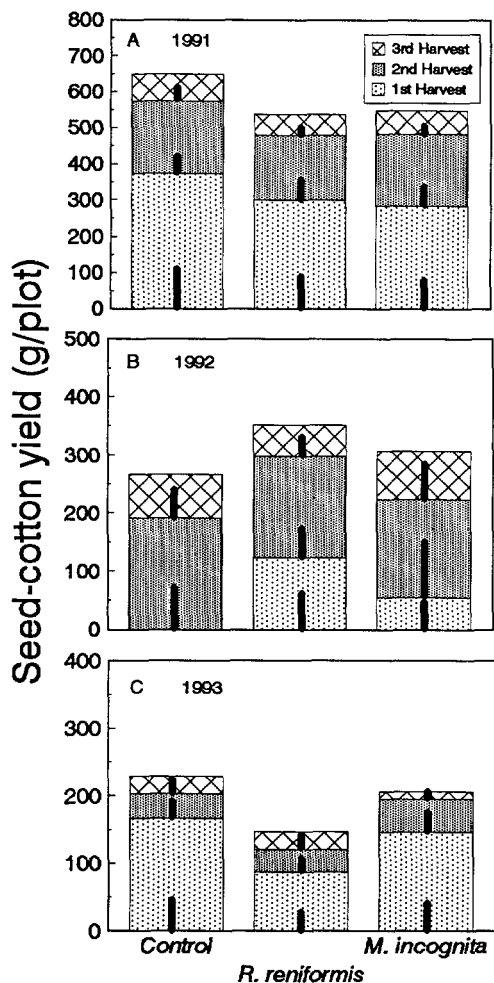


FIG. 6. Influence of *Meloidogyne incognita* and *Rotylenchulus reniformis* on seed-cotton yield, 1991-93. Lines within bars are standard deviation of the mean for each harvest date. A) 1991 yields at three harvests—cotton yields were significantly different within harvests between nematode inoculated and noninoculated plots according to repeated measures analysis of variance ( $P = 0.01$ ). The nematode inoculum level ( $P_i$ )  $\times$  date of harvest was significant. B) 1992 seed-cotton yield at three harvests—noninoculated control was significantly different from *R. reniformis* and *M. incognita*-inoculated plots for yields within harvests ( $P = 0.01$ );  $P_i \times$  date interaction, however, was not significant. C) 1993 seed-cotton yield at three harvests—noninoculated and *M. incognita*-infested plots differ from *R. reniformis*-infested plots in yield within harvests according to repeated measures analysis of variance.

searchers in North Carolina showed that race 3 *M. incognita* reproduced at higher rates than did race 4 on cotton (10,11), although research conducted in Texas

showed no differences between races 3 and 4 (27). Race 4 of *M. incognita* did not survive winter as well as *R. reniformis* in 1992 to 1993 and 1993 to 1994. Low levels of survival for *M. incognita* were due, at least in part, to the limited reproduction of *M. incognita* race 4 on cotton.

Some researchers have suggested that *R. reniformis* is more prevalent in fine-textured soils (16,19). We have made similar observations in North Carolina, where reniform nematode may be the most numerous species in a section of a field with fine-textured soil, but sandier areas of the same field tend to be dominated by other cotton pathogens such as *Hoplolaimus columbus* Sher or *M. incognita* (Koenning and Barker, unpub.). These observations combined with published reports would suggest that, although reniform nematode is not favored by clay content per se, the higher clay content may result in an environment where *R. reniformis* has a competitive advantage. The ability of *R. reniformis* to reproduce at higher levels than *M. incognita* in various soil types on cotton implies that *R. reniformis* may have greater parasitic fitness (18) on cotton. The current work was limited in its scope and does not permit testing of this last hypothesis.

Adaptation of *R. reniformis* to a wide range of soil textures would permit this nematode to exploit environments that are unsuitable for other plant-parasitic nematodes. However, the reproduction of *R. reniformis* was inhibited by the presence of *M. incognita* on sweetpotato in greenhouse research (23). Field evaluations of these two species on sweetpotato demonstrated that a competitive interaction occurs when they coexist (22). The ability of *R. reniformis* to thrive in relatively fine-textured soils may thus allow it to occupy a niche where competition is minimized.

Discrepancies between our research and reports of other researchers (16,19) about effects of soil texture on reniform nematode may be a result of (i) differences in geographic populations of *R. reniformis*, (ii) different crops and (or) cropping sequences used in various areas of the coun-



try, and (iii) other environmental factors. The latter hypothesis is favored by the current authors. Soil texture is an important factor affecting nematodes (24,25) but is still a relatively crude quantitative variable. Many other effects on nematodes are possible, including chemical, physical, mechanical, and biological components. Work on *Heterodera glycines* Ichinohe in these soil types under controlled moisture regimes established a soil type  $\times$  soil moisture level interaction (13). Soil moisture level influences soil aeration as does soil-pore size. Similarly, soils with the same soil texture may have very different soil structure, and this also may impact plant-parasitic nematodes. Further research might focus on the competitiveness of these or other plant parasites with various soils and crops.

Other research has shown that race 3 of *M. incognita* was more damaging to cotton as determined by root-gall indices than was race 4 (10). Yield loss caused by either race on Deltapine 16 cotton, however, was minimal (11), possibly because the inoculum levels used were below the damage threshold. Subsequent research, however, showed little difference in reproduction, development, or aggressiveness of the two races (27). The pathogenicity of root-knot nematode on cotton in our study is validated through the use of regression models. Races 3 and 4 of *M. incognita* appeared to have similar effects on seed-cotton yield in the Fuquay sand when comparing 1991 data with 1992 and 1993. Potentially, *M. incognita* can damage cotton in any soil type. The lower reproductive rates of *M. incognita* in finer textured soils (26), however, would tend to limit its damage potential in these soils. The influence of *M. incognita* race 4 on cotton yield in 1993 was less than in 1992 because of the relatively poor overwinter survival of this nematode compared to *R. reniformis*. Greater suppression of cotton yield in 1992 by root-knot than reniform nematode was probably due to lower inoculum levels of the latter. Cotton-yield suppression caused by *R. reniformis*, in contrast with damage caused by *M. incognita*, was evident in all soil types

because of the high reproductive rate and overwinter survival of this nematode.

Initial inoculum levels ( $P_i$ ) had significant effects on maturity (amount of seed cotton picked per harvest). The magnitude and direction of this effect was not consistent over years, however. Nematode levels were generally greater in 1991 and 1993, when cotton maturity was delayed, as compared to 1992, when cotton maturity was early as a result of nematode infestation. This result suggests that low levels of nematodes may enhance maturity, as occurred in 1992, while higher inoculum levels delay maturity, as in 1991 and 1993. The current research demonstrated that nematode infection may influence the maturity of the cotton plant. Early research on *R. reniformis* and cotton showed that cotton maturity was delayed by this nematode in field experiments comparing fumigated vs. nonfumigated plots (9). Delayed or enhanced cotton maturity can be an important factor in determining both quality and quantity of cotton harvested. Delayed maturity may require later picking, or a second picking, which may increase harvest costs. Quality of seed cotton may suffer as a result of weathering if harvest must be delayed. Finally, since nematodes tend to be unevenly distributed in fields, maturity differences would result in irregular crop maturity within a field. This last factor may complicate the growers' decisions as to the use of growth regulators or defoliants. The lack of consistency in nematode effects on plant maturity may be because cotton is actually a perennial plant grown as an annual crop. Stress imposed by nematodes may interact with other factors such as other pests, moisture, and nutrient deficiencies or excesses to either delay or enhance maturity. Measuring cotton-yield loss from season to season becomes difficult since harvest date may affect results. An early harvest may show large yield losses versus a late harvest with little or no yield loss. More research on nematode effects on maturity is warranted.

Both *R. reniformis* and *M. incognita* are capable of suppressing cotton yield, pro-

vided that inoculum density is above a damage threshold. Although root-knot nematode is more widespread than reniform nematode, the latter would appear to pose the greatest threat to cotton production because of its high reproductive potential and ability to survive the winters in North Carolina. Furthermore, the influence of nematode infection on cotton crop maturity may pose additional problems for growers and researchers trying to measure nematode effects on crop performance.

#### LITERATURE CITED

1. Barker, K. R., and J. P. Noe. 1988. Techniques in quantitative nematology. Pp. 223–226 in J. Kranz and J. Rotem, eds. *Experimental techniques in plant disease epidemiology*. Berlin: Springer-Verlag.
2. Birchfield, W., and J. E. Jones. 1961. Distribution of the reniform nematode in relation to crop failure of cotton in Louisiana. *Plant Disease Reporter* 45:671–673.
3. Byrd, D. W., Jr., K. R. Barker, H. Ferris, C. J. Nusbaum, W. E. Griffin, R. H. Small, and C. H. Stone. 1976. Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. *Journal of Nematology* 8:206–212.
4. Byrd, D. W., Jr., H. Ferris, and C. J. Nusbaum. 1972. A method for estimating numbers of eggs of *Meloidogyne* spp. in soil. *Journal of Nematology* 4: 266–269.
5. Dropkin, V. H. 1980. *Introduction to plant nematology*. New York: John Wiley.
6. Ferris, H. 1978. Nematode economic thresholds: Derivation, requirements, and theoretical considerations. *Journal of Nematology* 10:341–350.
7. Heald, C. M., and A. F. Robinson. 1990. Survey of current distribution of *Rotylenchulus* in the United States. Supplement to the *Journal of Nematology* 22: 695–699.
8. Jenkins, W. R. 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. *Plant Disease Reporter* 48:692.
9. Jones, J. E., L. O. Newsom, and E. L. Finley. 1959. Effect of the reniform nematode on yield, plant characters, and fiber properties of upland cotton. *Agronomy Journal* 51:353–356.
10. Kirkpatrick, T. L., and J. N. Sasser. 1983. Parasitic variability of *Meloidogyne incognita* populations on susceptible and resistant cotton. *Journal of Nematology* 15:302–307.
11. Kirkpatrick, T. L., and J. N. Sasser. 1984. Crop rotation and races of *Meloidogyne incognita* in cotton root-knot nematode management. *Journal of Nematology* 16:323–328.
12. Koenning, S. R., and K. R. Barker. 1994. Damage functions and cropping systems for management of *Rotylenchulus reniformis* on cotton. *Phytopathology* 84:1103 (Abstr.).
13. Koenning, S. R., and K. R. Barker. 1995. Soybean photosynthesis and yield as influenced by *Heterodera glycines* and irrigation. *Journal of Nematology* 27:51–62.
14. Noe, J. P. 1994. *Rotylenchulus reniformis* population dynamics and damage functions on cotton. *Journal of Nematology* 26:113 (Abstr.).
15. 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.
16. Robinson, A. F., C. M. Heald, S. L. Flanagan, W. H. Thames, and J. Amador. 1987. Geographic distributions of *Rotylenchulus reniformis*, *Meloidogyne incognita*, and *Tylenchulus semipenetrans* in the Lower Rio Grande Valley as related to soil texture and land use. *Annals of Applied Nematology* (*Journal of Nematology* 19, Supplement) 1:20–25.
17. Sasser, J. N. 1972. Nematode diseases of cotton. Pp. 187–214 in J. M. Webster, ed. *Economic nematology*. New York: Academic Press.
18. Shaner, G., E. L. Stromberg, G. H. Lacey, K. R. Barker, and T. P. Pirone. 1992. Nomenclature and concepts of pathogenicity and virulence. *Annual Review of Phytopathology* 30:47–66.
19. Starr, J. L., C. M. Heald, A. F. Robinson, R. G. Smith, and J. P. Krausz. 1993. *Meloidogyne incognita* and *Rotylenchulus reniformis* and associated soil textures from some cotton production areas of Texas. Supplement to the *Journal of Nematology* 25:895–899.
20. Starr, J. L., and S. L. J. Page. 1990. Nematode parasites of cotton and other tropical fibre crops. Pp. 540–556 in M. Luc, R. A. Sikora, and J. Bridge, eds. *Plant-parasitic nematodes in subtropical and tropical agriculture*. Wallington, UK: CAB International.
21. Taylor, A. L., J. N. Sasser, and L. A. Nelson. 1982. Relationship of climatic and soil characteristics to geographical distribution of species in agricultural soils. Raleigh, NC: NC State University Graphics.
22. Thomas, R. J., and C. A. Clark. 1983. Population dynamics of *Meloidogyne incognita* and *Rotylenchulus reniformis* alone and in combination, and their effects on sweet potato. *Journal of Nematology* 15:204–211.
23. Thomas, R. J., and C. A. Clark. 1983. Effects of concomitant development on reproduction of *Meloidogyne incognita* and *Rotylenchulus reniformis* on sweet potato. *Journal of Nematology* 15:215–221.
24. Wallace, H. R. 1971. Abiotic influences in the soil environment. Pp. 257–280 in B. M. Zuckerman, W. F. Mai, and R. A. Rohde, eds. *Plant-parasitic nematodes*, vol. I. New York: Academic Press.
25. Wallace, H. R. 1973. *Nematode ecology and plant disease*. New York: Crane, Russak.
26. Windham, G. R., and K. R. Barker. 1986. Effects of soil type on the damage potential of *Meloidogyne incognita* on soybean. *Journal of Nematology* 18: 331–338.
27. Veech, J. A., and J. L. Starr. 1986. Comparison of development, reproduction, and aggressiveness of *Meloidogyne incognita* races 3 and 4 on cotton. *Journal of Nematology* 18:413–415.