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# *Meloidogyne arenaria* Populations on Soybean[1]

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*Abstract:* The distribution of *Meloidogyne* spp. was determined in the Piedmont and Coastal Plains soybean production areas of South Carolina. *Meloidogyne arenaria, M. incognita,* and *M. javanica* were found in six of seven counties surveyed, with some populations consisting of two or more species. Because *M. arenaria* populations did not reproduce on peanut (*Arachis hypogaea* cv. Florunner), they were designated as Host Race 2. Severity of root galling, shoot and root growth, seed yield, and nematode reproduction were examined in fields infested with *M. arenaria* at Govan and Pelion, South Carolina, using soybean cultivars differing in host suitability to *M. arenaria.* When different responses in shoot and root growth, seed yield, and nematode reproduction in the two locations were found, soil influences were examined in duplicate field microplot experiments. Soybean growth was affected more by soil influences than by nematode populations; however, the two *M. arenaria* populations differed in amount of galling and rate of reproduction.

*Key words: Glycine max, Meloidogyne arenaria, Meloidogyne incognita, Meloidogyne javanica,* microplot, nematode, peanut root-knot nematode, soybean.

Root-knot nematodes (*Meloidogyne* spp.) are found throughout the southeastern United States, where they cause damage to a wide variety of economically important hosts, including soybean (*Glycine max* (L.) Merr.; 11,12). Host races of *Meloidogyne incognita* (Kofoid & White) and *Meloidogyne arenaria* (Neal) Chitwood differ in their abilities to reproduce on certain hosts (17,21).

In 1955, Sluth and Reynolds (16) suggested that coarse-textured soils were associated with root-knot nematode damage and that the use of detailed soil survey maps would enable growers to locate crop production areas at risk. Wallace (19) proposed that there is an optimum soil pore size for movement of each nematode species. Soil type has been shown to influence *M. incognita* reproduction and damage potential on soybean (20).

The percentage of *M. incognita* juveniles able to migrate 20 cm and penetrate tomato roots decreased as the percentage of clay and silt increased. Clay particles appeared to have a function in attracting nematodes over large distances in soil (14). Shane and Barker (15) reported that the effects of two inoculum levels of *M. incognita* on soybean height and on root and shoot fresh weights were generally detected only on plants grown in soil mixes with lower clay content.

*Meloidogyne incognita* is thought to be the predominant root-knot nematode species on soybean in South Carolina (7). However, the frequency of *M. arenaria* increased in assayed soils after 1982—especially in 1983, when a survey was initiated to determine its distribution (7). In a particularly severe disease location near Pelion (Lexington County), the size of root galls on susceptible soybean cultivars infected with *M. arenaria* was much smaller than that from a *M. arenaria* population sampled near Govan. These two South Carolina populations of *M. arenaria* have since been shown to differ in reproduction and in effects on soybean growth in microplot tests (2).

This study identifies root-knot species in seven South Carolina counties and documents differences in soybean genotype performance at two locations. The effects of nematode isolates on reproduction, galling, and plant growth are also examined.

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## MATERIALS AND METHODS

*Survey:* Soybean fields were sampled for the presence of *Meloidogyne* spp. at V6 (vegetative stage having six shoot internodes) and R3 (pod fill) stages of plant develop-

ment (6). The survey area comprised portions of seven South Carolina counties (Aiken, Calhoun, Edgefield, Lexington, Orangeburg, Richland, and Saluda) and was ca. 30 km wide in a north–south direction and 70 km long in an east–west direction, with the town of Pelion at the center. Symptomless fields and soybean fields showing symptoms of root knot (stunting, chlorosis, necrosis, poor stands, and wilting) were sampled at ca. 4-km intervals.

In fields exhibiting symptoms, samples consisted of root systems of four plants and approximately 2 liters of soil, composed of 20 cores taken 10–15 cm deep in the root zone. Sampling was confined to the periphery of symptomatic areas. In symptomless fields, cores were taken in a random zig-zag pattern. Samples were immediately placed in insulated containers and assayed within 48 hours. Gall (22) and egg mass (18) indices were recorded for each root sample. Mature females, if present, were stained (5) in root tissue and prepared for perineal-pattern examination. Each soil sample was divided for analyses as follows: 500 $cm^3$ for extraction, identification, and counting of vermiform plant-parasitic nematodes; 100 $cm^3$ for soil nutrient analysis; and 100 $cm^3$ for soil texture analysis (4). Remaining soil was placed in 15-cm pots with susceptible tomato (*Lycopersicon esculentum* Mill. cv. Rutgers) seedlings and maintained in a greenhouse. Populations of *M. arenaria* were examined for reproduction on peanut (*Arachis hypogaea* L. cv. Florunner) using either infested field soil or eggs extracted from tomato roots as inoculum.

Samples with no *Meloidogyne* spp. on root systems, in soil, or in tomato culture after 6 months were discarded. Ten perineal patterns were examined for species identification from each sample containing *Meloidogyne* spp.

*Field experiments:* In 1984, two similar tests were conducted at sites naturally infested with *M. arenaria* in Govan and Pelion. The Govan site is a Marlboro loamy sand (84% sand, 10% silt, 6% clay; pH 5.9) in the Marlboro-Faceville-Grady association. Such soils are level to gently sloping and are well-drained, with sandy clay subsoils. The Pelion site is a Lakeland sand (91% sand, 4% silt, 5% clay; pH 6.2) in the Lakeland-Norfolk-Vaucluse association. These gently sloping, excessively drained soils are located predominately in the Coastal Plain region of the southeastern United States (3). Twenty-four soybean genotypes (Table 2) were seeded in two-row plots (6-m-long), with 0.9-m spacing between rows in a randomized complete block design with three replications per genotype at both sites. Planting dates were 18 May 1984 at Pelion and 31 May 1984 at Govan.

Population densities of *M. arenaria* juveniles were recorded at planting and monthly for 4 months. Ten 15-cm-long cores collected from the root zone of both plant rows in a plot were composited, and juveniles were extracted from 500 $cm^3$ soil using elutriation (1) and centrifugal-flotation (10). Four shoots per two-row plot were harvested at 1, 2, and 3 months after planting and dried for 1 week at 65 C before weighing. Root fresh weight, and gall and egg mass indices 3 months after planting were recorded. Egg masses were stained in phloxine B (150 mg/liter) for 15 minutes (5). Gall indices were scored on a qualitative 0–10 scale as described by Zeck (22), whereas egg-mass indices were based on a quantitative 0–5 scale as described by Taylor and Sasser (18). Stand per 50 cm of plant row was counted, and seed yields were recorded after seed had dried for 1 week at 65 C.

*Microplot experiment:* Damage potential and reproduction of the Govan and Pelion isolates of *M. arenaria* populations on five soybean cultivars on two different soil types were studied in duplicate tests located approximately 100 m apart at the Edisto Research and Education Center in Blackville, South Carolina. Four replications of 10 microplots were randomly placed in a homogenous soil type of Lakeland sand (92% sand, 2% silt, 6% clay, with a coarse, sandy A horizon 60–90 cm deep) or Marlboro

loamy sand (83% sand, 7% silt, 10% clay, with an A horizon 15–20 cm deep) (3). Microplots were halves of steel drums (76 cm d, 122 cm long) pressed into the soil with a backhoe, with ca. 15 cm of the drum left above the soil surface. Care was taken not to disrupt the existing soil profile.

Before planting, each microplot was fumigated with 90 ml methyl bromide (Brom-O-Gas, Great Lakes Chemical Corp.) and covered with a polyethylene tarp. Tarps were removed after 1 week, soil was turned, and microplots were allowed to stand for 3 weeks before infestation and planting. Three or four generations of Govan and Pelion *M. arenaria* isolates were cultured on Rutgers tomato seedlings in 2-liter plastic containers in temperature-controlled water baths maintained at 25–30 C. Eggs of the appropriate isolate were extracted from galled root tissue using NaOCl (18), and 24,000 were added to 3 liters of soil taken from a microplot. A mycorrhizal fungus (*Glomus macrocarpus* Tul. & Tul.), *Bradyrhizobium japonicum* (Kirchner) Jordan, and appropriate macronutrients (N, P, K) were added to each microplot at the same concentrations indicated by soil fertility analyses (13).

After being mixed on a tarp, 3 liters infested soil was placed back into each microplot. A 250-$cm^3$ soil sample was removed from each microplot after infestation; within 48 hours it was placed in a 10-cm pot containing a Rutgers tomato seedling to assay density and viability of inoculum. After 40 days, egg masses were stained in phloxine B (150 mg/liter) for 15 minutes (5) and counted.

Each microplot was planted with one of five soybean cultivars: Centennial, Cobb, Braxton, Gordon, or Perrin. Two weeks after germination, plants were thinned to 12 per microplot. Soil moisture was held relatively constant in both sites by regular monitoring with soil moisture tensiometers and irrigating as necessary.

Soil samples were taken from the root zone at V6 and R3 soybean growth stages (6). Juveniles of *M. arenaria* were extracted (10) and counted from a 250-$cm^3$ soil sample consisting of four composited cores per microplot. Heights of four plants per plot were measured at the V6 growth stage. Gall (22) and egg mass indices (18) and root fresh weight were measured at the R3 growth stage for the two end plants in each microplot, and shoots from these plus two other plants were harvested to obtain shoot dry weight. Seed yield was recorded at harvest from the eight remaining plants.

Experimental design in each soil type was a split-split plot with four replications, each with five cultivars and two *M. arenaria* isolates. Replications were randomly assigned within soil types, soybean cultivars nested within replications, and nematode isolates nested within soybean cultivars. The microplot experiment was first conducted in 1985 and was repeated in 1986 and 1987.

## Results

*Survey:* Of 175 soybean fields sampled, 24 contained *Meloidogyne* spp. Nine field populations were not detected in later sampling attempts. Three species—*M. arenaria, M. incognita,* and *M. javanica* (Treub) Chitwood—were identified among 15 populations based on perineal patterns (Table 1). Two fields contained more than one *Meloidogyne* species. All *M. arenaria* populations were designated as Race 2 because none reproduced on Florunner peanut (18). Other plant-parasitic nematode genera found included *Criconemella, Helicotylenchus, Heterodera, Hoplolaimus, Pratylenchus, Scutellonema, Trichodorus* (*Paratrichodorus*), and *Tylenchorhynchus.*

*Field experiments:* There were differences ($P = 0.05$) within genotypes and between locations for several of the variables measured (Table 2). Grouped genotype means of all variables examined differed ($P = 0.01$) between locations, except for juvenile densities at 1 and 2 months after planting. Genotype location interactions were significant ($P = 0.05$) for gall indices and root fresh weight. Massive galls caused by the Govan population resulted in higher root fresh weight of nearly all genotypes examined. Shoot dry weight and seed yield rankings of genotypes were consistent at

TABLE 1. *Meloidogyne* spp. distribution in a seven-county sampling zone in South Carolina.

| County | Number of populations | *Meloidogyne* spp. present |
|---|---|---|
| Aiken | 2 | *M. incognita* |
| Calhoun | 1 | *M. arenaria* + *M. incognita* |
| | 1 | *M. incognita* |
| Edgefield | 1 | *M. incognita* + *M. javanica* |
| Lexington | 3 | *M. arenaria* |
| | 3 | *M. incognita* |
| | 1 | *M. javanica* |
| Orangeburg | 1 | *M. incognita* |
| | 1 | *M. arenaria* |
| Richland | 1 | *M. javanica* |

the two locations. Many genotypes had a lower ($P = 0.05$) shoot weight and seed yield at Pelion than at Govan.

*Microplot experiment:* In 1985, data were collected only from the Marlboro soil be-

TABLE 3. Mean juvenile densities, gall and egg mass indices, and shoot dry weights for five soybean cultivars grown in a Marlboro soil in microplots infested with either the Govan or Pelion isolate of *M. arenaria*, 1985.

| | Juveniles/250 cm³ soil | | Gall index† | Egg mass index‡ | Shoot dry wt. (g/plant) |
|---|---|---|---|---|---|
| | V6 | R3 | | | |
| | Data pooled by cultivar | | | | |
| Centennial | 140 a | 932 a | 5.7 a | 4.3 a | 18 a |
| Cobb | 153 a | 911 a | 5.5 a | 3.9 a | 21 a |
| Braxton | 80 a | 543 a | 4.8 a | 4.0 a | 18 a |
| Gordon | 37 a | 425 a | 4.1 a | 3.9 a | 16 a |
| Perrin | 70 a | 426 a | 5.2 a | 4.2 a | 23 a |
| | Data pooled by isolate | | | | |
| Govan | 120 a | 981 a | 5.8 a | 4.5 a | 19 a |
| Pelion | 74 a | 314 a | 4.3 b | 3.6 b | 19 a |

Data followed by the same letter in columns for each grouping are not different ($P = 0.05$) according to LSD mean separation.

† Gall index based on gall size and portion of root covered, 1–10 rating.

‡ Egg mass index based on number of egg masses present on root surface, 1–5 rating.

TABLE 2. Mean gall and egg mass indices, root fresh weights, shoot dry weights, and seed yield of soybean genotypes planted in a *Meloidogyne arenaria*-infested Marlboro loamy sand at Govan (G) and in a Lakeland sand at Pelion (P), South Carolina, 1984.

| | Gall index† | | Egg mass index‡ | | Root wt. (g/plant) | | Shoot dry wt. (g/plant) | | Seed yield (g/4 plants) | |
|---|---|---|---|---|---|---|---|---|---|---|
| Genotype | G | P | G | P | G | P | G | P | G | P |
| D76-9454 | 4.6 | 3.0 | 2.0 | 2.1 | 27 | 7* | 172 | 25 | 769 | 62* |
| SC82-1003N | 3.9 | 3.0 | 3.1 | 3.2 | 17 | 9 | 87 | 38 | 742 | 247* |
| Perrin | 4.4 | 2.6 | 1.5 | 3.2 | 24 | 9* | 145 | 26 | 1,003 | 141 |
| Kirby | 4.2 | 2.7 | 2.3 | 3.0 | 20 | 6* | 98 | 23 | 833 | 152* |
| Braxton | 5.9 | 4.2 | 1.8 | 3.4 | 19 | 9* | 70 | 25* | 544 | 202 |
| Wright | 5.0 | 3.9 | 1.7 | 2.9 | 23 | 4* | 127 | 9* | 707 | 156* |
| Gasoy 17 | 7.3 | 4.5 | 1.7 | 3.1 | 35 | 6* | 107 | 10* | 430 | 16* |
| SC82-748 | 9.6 | 3.0 | 3.3 | 3.0 | 19 | 8* | 73 | 26* | 393 | 29 |
| SC82-741 | 5.1 | 2.2 | 3.0 | 2.4 | 29 | 7* | 126 | 29* | 787 | 234* |
| F77-7450 | 4.2 | 4.3 | 2.2 | 3.4 | 20 | 8* | 99 | 18* | 622 | 153* |
| SC82-735 | 5.4 | 1.1* | 2.8 | 1.0 | 26 | 8 | 77 | 37 | 449 | 121 |
| SC8112-6-4 | 4.7 | 5.3 | 2.6 | 4.9* | 23 | 12* | 172 | 28 | 680 | 112 |
| Bossier | 5.1 | 2.8* | 2.6 | 3.2 | 18 | 10 | 96 | 28* | 468 | 139 |
| Govan | 5.2 | 2.2 | 1.5 | 2.3 | 26 | 12* | 148 | 32 | 946 | 99* |
| SC8107-4-2 | 4.2 | 2.5 | 2.2 | 2.6 | 21 | 5* | 125 | 21 | 808 | 131* |
| Cobb | 6.7 | 4.5* | 3.0 | 3.6 | 53 | 9* | 167 | 21 | 237 | 54 |
| SC82-1132 | 3.5 | 3.7 | 2.2 | 3.2 | 22 | 11 | 96 | 37 | 752 | 87* |
| SC82-400N | 3.7 | 3.4 | 2.2 | 3.0 | 18 | 8* | 103 | 27* | 758 | 80* |
| SC80-1105 | 2.7 | 3.8 | 1.8 | 3.7 | 17 | 7 | 92 | 12 | 626 | 20* |
| SC8117-6-2 | 4.0 | 4.2 | 1.8 | 4.0* | 14 | 12 | 104 | 35* | 709 | 107* |
| Gordon | 4.2 | 2.5 | 2.2 | 2.5 | 14 | 8* | 60 | 20 | 516 | 778 |
| Bedford | 5.2 | 4.4 | 2.1 | 3.8 | 17 | 10 | 86 | 29 | 184 | 234 |

* Differences between locations significant at $P = 0.05$.

† Gall index based on gall size and portion of root covered, 1–10 rating.

‡ Egg mass index based on number of egg masses present on root surface, 1–5 rating.

TABLE 4. Mean juvenile densities, gall and egg mass indices, shoot dry weights, and seed yields for five soybean cultivars grown in two soil types in microplots infested with either the Govan or Pelion isolate of *M. arenaria*, 1986.

| Soil type | Nematode isolate | Juveniles per 250 cm³ soil | | Gall index† | Egg mass index‡ | Shoot dry wt. (g/plant) | Seed yield (g/plant) |
|---|---|---|---|---|---|---|---|
| | | V6 | R3 | | | | |
| Marlboro | Govan | 98 a | 21,144 a | 7.6 a | 4.2 a | 43 a | 13 a |
| Marlboro | Pelion | 64 b | 17,418 a | 6.6 b | 4.8 a | 37 a | 14 a |
| Lakeland | Govan | 6 c | 7,132 b | 4.4 c | 4.5 a | 82 b | 32 b |
| Lakeland | Pelion | 6 c | 4,509 b | 3.2 d | 3.9 a | 91 b | 55 c |
| | | | Data pooled by soil type | | | | |
| Marlboro | — | 81 a | 19,281 a | 7.1 a | 4.5 a | 40 a | 13 a |
| Lakeland | — | 6 b | 5,901 a | 3.8 b | 4.2 a | 87 b | 44 b |
| | | | Data pooled by isolate | | | | |
| — | Govan | 52 a | 14,138 a | 6.0 a | 4.3 a | 63 a | 22 a |
| — | Pelion | 35 a | 10,963 a | 4.9 b | 4.4 a | 64 a | 34 b |

Data followed by the same letter in columns for each grouping are not different ($P = 0.05$) according to LSD mean separation.
† Gall index based on gall size and portion of root covered, 1–10.
‡ Egg-mass index based on number of egg masses present on root surface, 1–5 rating.

cause of poor germination and stand counts of all cultivars in the Lakeland soil. Differences ($P = 0.05$) in initial inoculum distribution and viability were present between *M. arenaria* populations in 1986 (26 egg masses/bioassay plant for Govan isolate vs. 47/plant for Pelion isolate) and between soil types in 1987 (39 egg masses/bioassay plant for Marlboro vs. 22/plant for Lakeland).

In 1985 in the Marlboro soil (Table 3), gall and egg mass indices were significantly greater ($P = 0.05$) in microplots infested with the Govan isolate of *M. arenaria* than in those with the Pelion isolate. No differences ($P = 0.05$) were observed in shoot growth with cultivar or nematode isolate.

The Govan population had higher gall indices than the Pelion population in both soil types in 1986 and 1987 (Tables 4, 5). The larger galls produced by the Govan population concealed many egg masses; therefore, data may not reflect actual egg mass occurrence. Shoot dry weight and seed

TABLE 5. Mean juvenile densities, gall and egg mass indices, shoot dry weights, and seed yields for five soybean cultivars grown in two soil types in microplots infested with either the Govan or Pelion isolate of *M. arenaria*, 1987.

| Soil type | Nematode isolate | Juveniles per 250 cm³ soil | | Gall index† | Egg mass index‡ | Shoot dry wt. (g/plant) | Seed yield (g/plant) |
|---|---|---|---|---|---|---|---|
| | | V6 | R3 | | | | |
| Marlboro | Govan | 112 a | 13,704 a | 7.0 a | 4.4 a | 33 a | 1.5 a |
| Marlboro | Pelion | 55 b | 17,084 a | 5.8 b | 4.4 a | 41 a | 2.5 a |
| Lakeland | Govan | 39 b | 3,434 b | 4.1 c | 3.9 a | 30 a | 0.7 a |
| Lakeland | Pelion | 22 b | 2,859 b | 3.2 d | 3.2 b | 33 a | 3.0 a |
| | | | Data pooled by soil type | | | | |
| Marlboro | — | 86 a | 15,394 a | 6.4 a | 4.4 a | 37 a | 2.0 a |
| Lakeland | — | 31 b | 3,146 b | 3.6 b | 3.5 b | 31 a | 1.9 a |
| | | | Data pooled by isolate | | | | |
| — | Govan | 76 a | 8,569 a | 5.6 a | 4.1 a | 31 a | 1.1 a |
| — | Pelion | 39 a | 9,971 a | 4.5 b | 3.8 a | 37 a | 2.7 a |

Data followed by the same letter in columns for each grouping are not different ($P = 0.05$) according to LSD mean separation.
† Gall index based on gall size and portion of root covered, 1–10.
‡ Egg-mass index based on number of egg masses on root surface, 1–5 rating.

TABLE 6. Mean plant heights and root fresh weights of five soybean cultivars grown in two soil types infested with 24,000 eggs per microplot of two populations of *Meloidogyne arenaria*.

| Soil type | Nematode isolate | Plant height (cm) 1986 | Plant height (cm) 1987 | Root fresh wt. (g) 1986 | Root fresh wt. (g) 1987 |
|---|---|---|---|---|---|
| Marlboro | Govan | 44 a | 45 a | 17 bc | 18 a |
| Marlboro | Pelion | 42 a | 46 a | 13 c | 22 a |
| Lakeland | Govan | 35 b | 29 b | 33 a | 14 ab |
| Lakeland | Pelion | 34 b | 28 b | 22 b | 8 b |
| Data pooled by soil type | | | | | |
| Marlboro | — | 43 a | 45 a | 15 a | 20 a |
| Lakeland | — | 35 b | 28 b | 27 b | 11 b |
| Data pooled by isolate | | | | | |
| — | Govan | 39 a | 37 a | 25 a | 16 a |
| — | Pelion | 38 a | 37 a | 17 b | 14 a |

Data followed by the same letter in columns for each grouping are not different ($P = 0.05$) according to LSD mean separation.

yield differences were noted only in 1986 and were greater in the Lakeland soil. Seed yield was greater ($P = 0.05$) in microplots infested with the Pelion isolate of *M. arenaria* (Table 4). In 1987, seed yields were reduced by an armyworm (*Heliothis* sp.) infestation and showed no differences among treatments (Table 5). Plant height was greater in the Marlboro soil than in the Lakeland soil in both 1986 and 1987 (Table 6). No differences were observed in plant height due to *M. arenaria* populations. In 1986, root fresh weights were greater in the Lakeland soil and in microplots containing the Govan *M. arenaria* population, whereas in 1987 root fresh weights were greater in the Marlboro soil and no differences were present due to populations.

## DISCUSSION

The observed increase in *M. arenaria*-infested fields in South Carolina could be due to previous crop management strategies that included the planting of *M. incognita*-resistant soybean and cotton cultivars. Widespread planting of such cultivars could select for and increase *M. arenaria* populations previously undetected. Moreover, most commercial soybean cultivars support reproduction of *M. arenaria*.

Environmental factors such as moisture and temperature may also influence the species composition of a population (9) and may influence plant-nematode interactions. Excessive soil drainage and drought conditions at Pelion in 1984 resulted in less growth of all soybean genotypes than at Govan; thus, differences among genotypes were diminished. Root galls at Govan were more massive and coalescing than those at Pelion. Apparent differences in galling and reproduction between the two *M. arenaria* populations could not be explained from these duplicate field tests because of environmental influences at each location.

In microplots, differences in viability of initial inoculum in 1986 (almost twice as many egg masses on bioassay plants resulted from the Pelion isolate than from the Govan isolate) did not appear to influence the greater galling of the Govan population. Because there were large differences in *M. arenaria* reproduction and root galling due to soil type in 1987, initial inoculum effects were probably minimal. Galling differed among populations, but this characteristic was also greatly influenced by soil type. In addition, differences in disease severity on soybean due to *M. arenaria* populations and differences among cultivar responses may be apparent only when inoculum levels are high (8).

## LITERATURE CITED

1. Byrd, D. W., Jr., K. R. Barker, H. Ferris, C. J. Nusbaum, W. E. Griffin, R. H. Small, and C. A. Stone. 1976. Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. Journal of Nematology 8:206–212.

2. Carpenter, A. S., and S. A. Lewis. 1986. Reproduction and virulence of four *Meloidogyne arenaria* isolates on six soybean selections. Journal of Nematology 16:602 (Abstr.).

3. Craddock, G. R., and C. M. Ellerbe. General maps of South Carolina counties. 1965. Soil association descriptions. South Carolina Agricultural Experiment Station. Clemson University, in cooperation with USDA Soil Conservation Service, Clemson, South Carolina.

4. Day, P. R. 1965. Particle fractionation and particle-size analysis. Pp. 545–567 *in* C. A. Black, ed. Methods of analysis—part I. Agronomy Monograph No. 9, American Society of Agronomy, Madison, WI.

5. Dickson, D. W., and F. B. Struble. A sieving-

staining technique for extraction of egg masses of *Meloidogyne incognita* from soil. Phytopathology 55: 497 (Abstr.).

6. Fehr, W. R., and C. E. Caviness. 1979. Stages of soybean development. Special Report 80, Cooperative Extension Service, Iowa State University, Ames.

7. Fortnum, B. A., J. P. Krausz, and N. G. Conrad. 1984. Increasing incidence of *Meloidogyne arenaria* on flue-cured tobacco in South Carolina. Plant Disease 68:244–245.

8. Hiatt, E. E. III, E. R. Shipe, and S. A. Lewis. 1988. Soybean response to two isolates of *Meloidogyne arenaria.* Journal of Nematology 20:330–332.

9. Ibrahim, I. K. A., and S. A. Lewis. 1985. Host-parasite relationships of *Meloidogyne arenaria* and *M. incognita* on susceptible soybean. Journal of Nematology 17:381–385.

10. Jenkins, W. R. 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Disease Reporter. 48:692.

11. Kinloch, R. A., C. K. Hiebsch, and H. A. Peacock. 1987. Evaluation of soybean cultivars for production in *Meloidogyne incognita*-infested soil. Supplement to the Journal of Nematology 19:32–34.

12. Kinloch, R. A., C. K. Hiebsch, and H. A. Peacock. 1987. Galling and yields of soybean cultivars grown in *Meloidogyne arenaria*-infested soil. Journal of Nematology 19:233–239.

13. Palmer, J. H., E. C. Murdock, C. L. Parks, F. H. Smith, J. W. Chapin, D. B. Smith, H. M. Harris, F. J. Wolak, and R. A. Spray. 1983. Growing soybeans in South Carolina. Cooperative Extension Service Circular 501, Clemson University, Clemson, SC.

14. Prot, J. C., and S. D. Van Gundy. 1981. Effect of soil texture and the clay component on migration of *Meloidogyne incognita* second-stage juveniles. Journal of Nematology 13:213–217.

15. 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 18:320–326.

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

17. Swanson, T. A., and S. D. Van Gundy. 1984. Variability in reproduction of four races of *Meloidogyne incognita* on two cultivars of soybean. Journal of Nematology 16:368–371.

18. Taylor, A. L., and J. N. Sasser. 1978. Biology, identification and control of root-knot nematodes (*Meloidogyne* spp.). North Carolina State University, Department of Plant Pathology, and the United States Agency for International Development. Raleigh: North Carolina State University Graphics.

19. Wallace, H. R. 1958. Movement of eelworms. I. The influence of pore size and moisture content of the soil on the migration of larvae of the beet eelworm, *Heterodera schachtii* Schmidt. Annals of Applied Biology 46:74–85.

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

21. Windham, G. L., and K. R. Barker. 1986. Relative virulence of *Meloidogyne incognita* host races on soybean. Journal of Nematology 18:327–331.

22. Zeck, W. M. 1971. A rating scheme for field evaluation of root-knot nematode infestations. Pflanzenschutz 24:141–144.