

Effects of Temperature, Plant Age, Soil Texture, and *Meloidogyne incognita* on Early Growth of Soybean¹

W. W. SHANE AND K. R. BARKER²

Abstract: A digitizer-microcomputer combination was utilized to determine soybean seedling response to population densities of *M. incognita* (Mi) under varied environmental conditions. Plant age, temperature, soil texture, and initial Mi inoculum (Pi) influenced the pattern of shoot and root growth. Effects of Mi on plant top growth were evident on plants inoculated 2 days after seeding, but generally were not noticeable on those receiving Mi after 4, 6, or 8 days (observations limited to 6 days after inoculation). The greatest Pi of Mi (16,700 juveniles/plant) suppressed root growth on plants inoculated at 2 or 4 days after seeding. Mi had no impact on root growth at 22 C on plants inoculated 6 or 8 days after seeding at any temperature used (22, 26, 30 C). New root initiation was inhibited on soybeans inoculated 2 days after seeding at the highest Pi at all three temperatures, but only at 30 C for a Pi of 1,670 juveniles/plant. Growth of first order lateral roots and general root length were suppressed by Mi on the youngest (2-day) plants. However, a low Pi (167 juveniles/plant) resulted in root proliferation on 4-day-old plants at 26 C. Mi was most damaging in a low clay-content soil mixture.

Key words: *Glycine max*, digitizer, host sensitivity, root-knot nematode, soybean, *Meloidogyne incognita*, modeling, penetration, root growth.

The importance of soybean as a primary source of protein and oil is increasing worldwide. Various nematode species limit productivity of this crop. Root-knot nematodes, especially *Meloidogyne incognita* (Kofoid and White) Chitwood, often cause major soybean yield suppression, but damage varies with environmental conditions (1,2,15,20).

Root-knot nematodes, *Meloidogyne* spp., may impair plant growth by inhibiting new root development, causing degeneration of existing roots, and disrupting hormonal or nutritional balances (20,23). Attempts to model plant-nematode interactions have revealed that quantitative effects of nematodes on the dynamics of root growth are not clearly known (11).

Although nematode damage thresholds have been established for some crops (1), generally it is not known if initial nematode population densities (Pi) appreciably alter early plant growth or if nematode generations later in the season are primarily re-

sponsible for yield suppression. Effects of temperature and Pi have been investigated for many plant-nematode combinations, including soybean (*Glycine max* (L.) Merr.) (15). There is little information, however, on the effects of plant age on the interactions of temperature and Pi for this crop.

Nematode population densities that do not hinder older plants may suppress development of younger plants. Sensitivity of tobacco to damage by root-knot nematodes, as indicated by foliage yield, is most pronounced with young plants (5). Seinhorst (21) noted that a greater proportion of a young root system was accessible to nematode attack compared with a more mature plant. However, a major question has been whether pathogenic nematodes under field conditions reach plant hosts in sufficient numbers to alter early plant growth. Potential impact of root-knot nematodes on early growth of small plants was indicated by research showing that root-knot juveniles can migrate as far as 50 cm in 9 days (17).

Soil characteristics can also influence plant-nematode interactions. Experiments in microplots with soils of various textures showed that the impact of *M. incognita* on tobacco growth was often less in fine-textured than in coarse soils (2). *Heterodera schachtii* Schmitt juveniles in laboratory studies moved much more freely in soil fractions with coarse textures (particles 150-500 μm d) than in fine-textured soil (20-150 μm d) (25). Thus, soil texture may

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² Former research associate and Professor, Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695. Present address of senior author: Department of Plant Pathology, Ohio State University, Columbus, OH 43210.

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also affect interactions between *M. incognita* and its hosts.

The tremendous amount of work needed to quantify root characteristics has impeded research on root systems. Methods devised to characterize plant root systems include direct measurements of fresh material (13), grid methods (16), and planimeter (19) or digitizer (7) measurements of photographs or photocopies of root systems.

Our objective was to investigate the effects of the interactions of temperature and soil texture on the impact of *M. incognita* on early growth of soybean. A microcomputer-digitizer method for measuring the effects of nematodes on root characteristics is described.

MATERIALS AND METHODS

General procedures: A greenhouse culture of *Meloidogyne incognita* was increased for inoculum on *Lycopersicon esculentum* Mill. cv. Manapel in the greenhouse. Three-week-old tomato seedlings were transplanted into 15-cm-d clay pots containing a mixture of steam-sterilized Norfolk sandy-loam and river sand (2:1) and inoculated 3 weeks later with a suspension of approximately 20,000 *M. incognita* eggs. Eggs were harvested from the plants 10–14 weeks later by a NaOCl method for chopped roots (12). Juveniles were hatched on 37- μ m-pore nylon screencloth frames (24). The first day's hatch was discarded. Hatched juveniles from each of the following 2 days were stored at 4 C in continuously aerated water and combined with that from day 4. *M. incognita* populations were established by pouring juveniles suspended in 30 ml water over the surface of soil in pots. An additional 2 cm moist soil was added to pots and watered lightly. Plants were harvested 6 days after nematode inoculation.

Glycine max (L.) Mer. cv. Ransom seeds were germinated at 27.5 C in vermiculite for 40 hours, and three seedlings were transplanted into each 15.2-cm-d plastic pot containing approximately 1,500 cm³ of a given soil mixture. Plant ages reported here include the germination period. Seedlings were grown in 'B-type' growth chambers (9) and were maintained at temperatures of 22, 26, or 30 C \pm 0.5 C. Plants were watered once daily with water at the same

TABLE 1. Soils used and their mechanical analysis (Bouyoucos (4) method of soil analysis).

Component (%)	Cecil clay : 35-mesh sand			Norfolk sandy loam : river sand
	25:75	50:50	75:25	2:1
Clay	7.5	23.8	41.6	3.6
Silt	8.0	15.0	22.4	12.9
Sand	84.5	61.2	36.0	83.5

temperature as the growth chamber. Light was provided by T-12 1,500-mA cool-white fluorescent and krypton-filled incandescent lights. The photoperiod consisted of 9 hours of fluorescent and incandescent lights (430 hlx) followed by 3 hours of incandescent lights (41 hlx).

Plant age, inoculum density, and temperature: Soil containing 2-, 4-, 6-, or 8-day-old seedlings was inoculated with 0, 500, 5,000, or 50,000 juveniles/pot. Each pot contained a mixture of steam-sterilized Norfolk sandy-loam and river sand (2:1) (Table 1). Plants were kept at 22, 26, or 30 C. Each treatment combination was replicated three times in a completely randomized design.

Numbers of nematodes within roots were estimated at harvest time for a minimum of five plants per treatment combination. Root systems were gently washed free of soil and immersed in 1.0% sodium hypochlorite in water for 3 minutes. Nematodes within roots then were stained for counting with acid fuchsin (6). Roots were pressed between glass plates for observation under a stereoscopic microscope. Nematode numbers in plants from pots receiving 5,000 or 50,000 juveniles were estimated from a subsample of macerated roots.

Soil texture, inoculum density, and temperature: Three soil textures were prepared by combining Cecil clay subsoil with 35-mesh silica sand in ratios of 1:3, 1:1, or 3:1 (Table 1). The Cecil clay subsoil had been previously sterilized with methyl bromide, and lime at 2.2 kg/m³ soil was added. Soybean seedlings were germinated and transplanted, as described above, into the three soils at 26 C. The soil was inoculated 20 hours later with 0, 5,000, or 50,000 juveniles per pot with treatments replicated eight times.

Measurement of roots: Washed roots were

TABLE 2. Expanded Fehr scale (10) for soybean early developmental stages.

Stage designation	Stage description
V 0.1	Unifoliolate not at all developed, cotyledons separated.
V 0.2	Unifoliolate leaves opening.
V 0.3	Unifoliolate leaves half expanded.
V 0.5	Unifoliolate leaves expanded, trifoliolate at next node not opened.
V 1.0*	Completely unrolled leaf at the unifoliolate node.†
V 1.5	Trifoliolate at 1st trifoliolate node expanded, trifoliolate at next node not opened.
V 2.0*	Completely unrolled leaf at the first trifoliolate node.
V 2.5	Second trifoliolate expanded, trifoliolate at next node not opened.
V 3.0*	Completely unrolled leaf at second trifoliolate node.

* Whole numbers indicate stages from the Fehr scale.

† A leaf is considered completely unrolled when the leaf at node immediately above it has unrolled sufficiently so the two edges of each leaflet are no longer touching.

photocopied to preserve a two-dimensional picture of root characteristics. A high quality photocopy was needed for resolution of small roots. Numbers and lengths of first-order lateral roots (those attached to the main root axis) were obtained from the photocopies with the use of Tektronix 4051 Graphic System and 4956 Graphics Tablet (Tektronic, Inc., Beaverton, Oregon). A hand-held cursor was used to trace each rootlet so that its length could be approximated by the sum of straight line segments as measured on the two-dimensional coordinate system of the graphics tablet (digitizer). A microcomputer program allowed storage of root length data directly on magnetic tape. Data were subsequently transferred to a larger computer for statistical analysis.

RESULTS

Plant age, inoculum density, and temperature: Each of the three plants per pot at harvest time was infected with approximately 12% of the total number of juveniles added, regardless of plant age at time of inoculation and inoculum dosage.

Early plant development, as measured by an expanded scale (10) (Table 2), was affected by nematodes added 2 days after seeding only at the highest temperature. The effect was quadratic, with accelerated

TABLE 3. Effect of plant age, temperature, and *Meloidogyne incognita* on Ransom soybean height, shoot weight, and root weight.

Plant age at inoculation (days)	Juveniles/pot	Temperature (C)			
		22	26	30	
Shoot height (mm)					
2	0	70 a*	102 a	114 a	
	500	67 a	103 a	134 a	
	5,000	65 a	96 a	114 a	
4	50,000	51 b	74 b	54 b	
	0	93 a	132 a	175 a	
	500	92 a	134 a	172 a	
6	5,000	89 a	132 a	165 a	
	50,000	87 a	122 a	162 a	
	0	111 ab	171 a	196 a	
8	500	115 a	164 a	200 a	
	5,000	98 b	161 a	195 a	
	50,000	112 ab	158 a	199 a	
2	0	127 a	170 a	237 a	
	500	133 a	177 a	242 a	
	5,000	128 a	184 a	237 a	
4	50,000	129 a	161 a	235 a	
	Shoot fresh weight (g)				
	2	0	1.22 a	1.49 a	1.58 a
500		1.15 a	1.51 a	1.56 a	
5,000		1.25 a	1.30 ab	1.39 a	
4	50,000	0.88 b	1.08 b	0.98 b	
	0	1.45 a	1.66 a	1.91 a	
	500	1.53 a	1.73 a	1.86 ab	
6	5,000	1.42 a	1.81 a	1.88 a	
	50,000	1.26 a	1.56 a	1.60 b	
	0	1.55 a	2.00 a	2.25 a	
8	500	1.54 a	2.30 a	2.46 a	
	5,000	1.54 a	2.01 a	2.18 a	
	50,000	1.55 a	2.22 a	2.09 a	
2	0	2.00 a	2.73 a	2.79 a	
	500	2.01 a	2.63 a	2.87 a	
	5,000	2.00 a	2.79 a	2.77 a	
4	50,000	1.95 a	2.22 a	2.67 a	
	Root fresh weight (g)				
	2	0	0.72 a	0.89 a	0.89 a
500		0.72 a	0.91 a	0.90 a	
5,000		0.76 a	0.78 a	0.75 a	
4	50,000	0.37 b	0.44 b	0.46 b	
	0	1.12 a	1.15 ab	1.24 a	
	500	1.24 a	1.22 a	1.09 b	
6	5,000	1.08 ab	1.14 ab	1.08 b	
	50,000	0.79 b	1.02 b	0.90 c	
	0	1.29 a	1.48 a	1.53 a	
8	500	1.30 a	1.76 b	1.58 a	
	5,000	1.27 a	1.52 ab	1.37 ab	
	50,000	1.23 a	1.37 a	1.12 b	
2	0	1.88 a	2.22 a	2.00 a	
	500	1.85 a	1.97 a	2.01 a	
	5,000	1.70 a	2.07 a	1.98 a	
4	50,000	1.60 a	1.49 b	1.75 a	

* Data followed by the same letter within each age and temperature combination are not different according to Waller-Duncan *k*-ratio *t*-test (*k* = 100).

TABLE 4. Effect of plant age, temperature, and *Meloidogyne incognita* on Ransom soybean total number (N) and length of first order lateral (FOL) roots.

Plant age at time of inoculation (days)	Juveniles/pot	FOL (N)			FOL total length (cm)		
		22 C	26 C	30 C	22 C	26 C	30 C
2	0	49 a*	46 a	64 a	217 a	247 a	253 a
	500	33 ab	50 a	52 ab	126 b	241 a	181 b
	5,000	36 ab	40 a	39 b	108 b	172 b	108 c
	50,000	24 b	25 b	16 c	22 c	32 c	13 d
4	0	56 ab	49 a	48 a	297 a	314 a	266 a
	500	54 ab	76 b	54 ab	264 a	371 a	296 a
	5,000	58 a	48 a	59 b	241 a	257 ab	289 a
	50,000	47 b	59 ab	52 a	79 b	146 b	143 b

* Data followed by the same letter within each age and temperature combination are not different according to Duncan's new multiple-range test ($P = 0.05$).

plant development at 500 juveniles/pot, no influence at 5,000 juveniles/pot, and suppressed development at 50,000 juveniles/pot ($P = 0.05$). For this age and temperature combination, average plant growth stages at harvest for 0, 500, 5,000, and 50,000 juveniles/pot were 0.32, 0.48, 0.30, and 0.13, respectively.

Both plant age at time of nematode inoculation and temperature influenced the effects of *M. incognita* on soybean height and shoot and root weights (Table 3). Effects of *M. incognita* on plant height and shoot weight were evident on plants inoculated at 2 days after seeding but generally not on plants inoculated 4, 6, or 8 days after seeding within the duration of this experiment (plants were harvested 6 days after inoculation). Root growth (weight) of plants inoculated 2 and 4 days after seeding was inhibited at the highest inoculum level ($P = 0.05$). Nematodes did not affect root weight of plants inoculated 6 days after seeding at 22 C (Table 3).

Effects of *M. incognita* on numbers of first-order lateral (FOL) roots per plant generally paralleled the effects on root weight (Table 4). Emergence of new root tips was suppressed in plants inoculated 2 days after seeding at 50,000 juveniles/pot at all three temperatures and also at 5,000 juveniles/pot at 30 C. On plants inoculated 4 days after seeding, stimulation of production of new FOL roots occurred with 500 nematodes/pot at 26 C. Suppression of root numbers was seen only with 50,000 nematodes/pot at 22 C treatment on 4-day-old plants.

Measurements of total FOL root length per plant revealed effects caused by nematodes not detected by root weight and numbers data (Table 4). Root length determinations indicated that concentrations of 500 juveniles/pot suppressed root growth at 22 and 30 C. Inoculum at 5,000 juveniles/pot suppressed total FOL root length on plants inoculated 2 days after seeding at all three temperatures. Root length was suppressed at all three temperatures on plants inoculated with 50,000 juveniles 4 days after seeding.

Effects of plant age on the impact of *M. incognita* were evident in the lengths of individual FOL roots (Fig. 1). Proliferation of small roots (1.5–4.4 cm long) was detected in 4-day-old plants at 26 C when inoculated with 500 juveniles/pot (Fig. 1D). In other cases, high numbers of short FOL roots were caused by direct growth inhibition of FOL root expansion by high nematode population densities (50,000 juveniles/pot) (Fig. 1B). At Pi 50,000 juveniles/per pot, root growth of plants inoculated 4 days after seeding was most severely inhibited at 22 C (Fig. 1A, C, E); no FOL roots longer than 10.4 cm were observed. Inhibition of root growth by 500 juveniles/pot was evident only at 22 C on plants inoculated 2 days after seeding (Fig. 1A). Effects of 5,000 and 50,000 juveniles/pot at 30 C on plants inoculated 2 days after seeding (Fig. 1E) were less pronounced on plants 4 days old at inoculation time (Fig. 1F).

Soil texture, inoculum density, and temperature interactions: Soil texture influenced

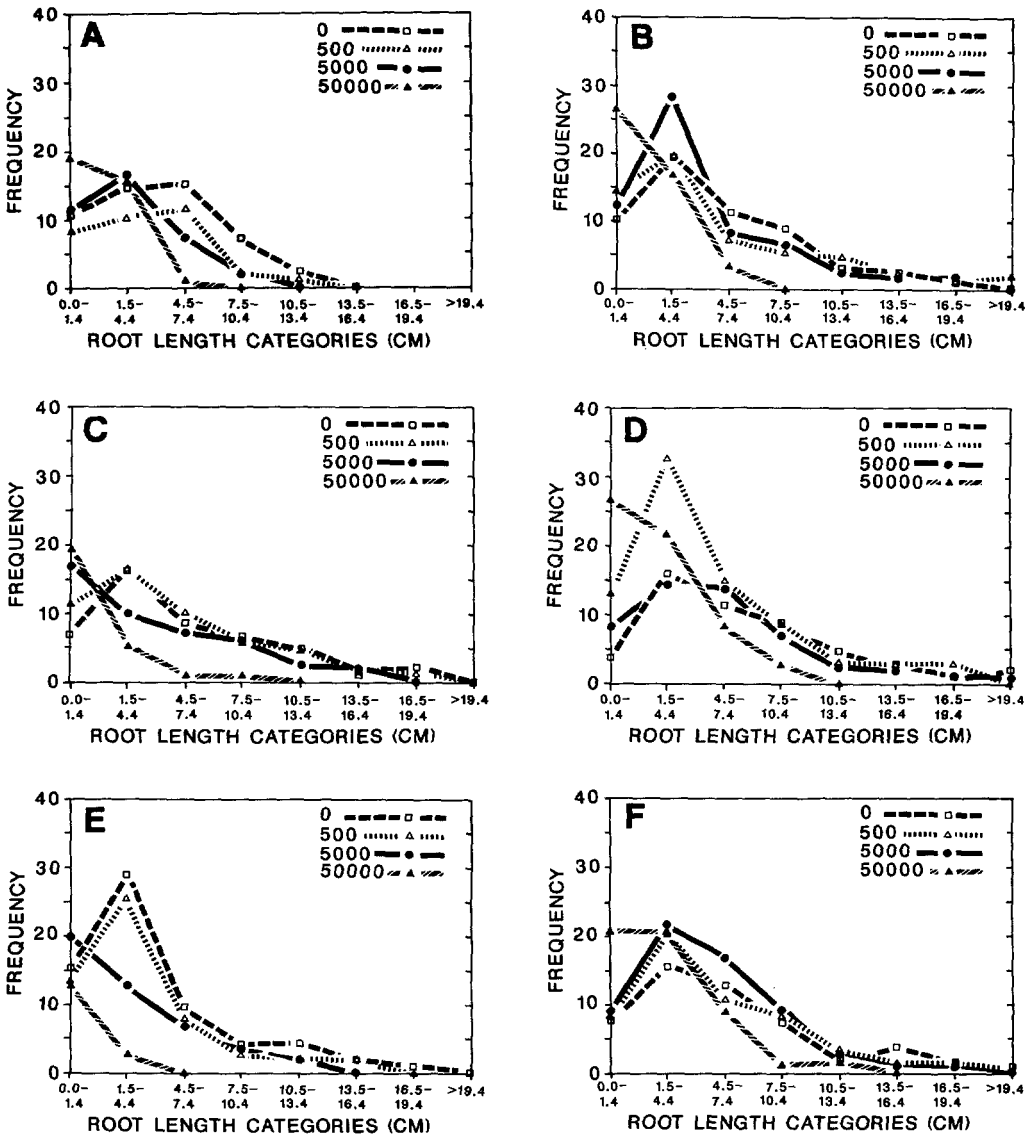


FIG. 1. Effects of different population densities of *Meloidogyne incognita* juveniles (nematodes/pot), plant ages, and temperature on frequencies and lengths of first order lateral roots on Ransom soybean. Incubation temperatures and plant age at time of inoculation as follows: A) 22 C, 2 days. B) 22 C, 4 days. C) 26 C, 2 days. D) 26 C, 4 days. E) 30 C, 2 days. F) 30 C, 4 days.

the impact of *M. incognita* juveniles on early root growth of soybean. Effects of 5,000 or 50,000 nematodes on plant height and on root and shoot fresh weights were generally detected only on plants grown in the lower clay content soil mixtures (Table 5).

At all temperatures in both experiments, each healthy plant developed a single main root axis from which the FOL roots arose. High concentrations of juveniles added to pots 2 days after seeding interfered with

the emergence of new root tips indirectly by halting main root axis elongation. However, juveniles added to pots 4 days after seeding generally did not prevent main axis growth. Once the main axis developed, the major effect of high concentrations of nematodes was the inhibition of FOL root elongation.

The influence of temperature on susceptibility of soybean to *M. incognita* can also be understood in terms of numbers of

TABLE 5. Effect of soil texture, temperature, and *Meloidogyne incognita* on soybean height and shoot and root fresh weight.

Texture (Cecil clay subsoil: 35-mesh sand)	Juve- niles/ pot	Temperature (C)		
		22	26	30
		Shoot height (mm)		
25:75	0	68 a*	92 a	110 a
	5,000	66 a	91 a	119 b
	50,000	67 a	89 a	107 a
50:50	0	65 a	87 a	105 a
	5,000	69 a	91 a	89 a
	50,000	66 a	89 a	97 a
75:25	0	74 a	96 a	108 a
	5,000	68 a	99 a	112 a
	50,000	71 a	96 a	110 a
Shoot fresh weight (g)				
25:75	0	1.17 a	1.13 a	1.05 a
	5,000	1.00 b	1.27 a	1.24 b
	50,000	1.06 b	1.16 a	1.03 a
50:50	0	1.05 a	1.12 a	1.09 a
	5,000	1.13 a	1.14 a	0.90 a
	50,000	1.04 a	1.16 a	0.92 a
75:25	0	1.26 a	1.25 a	1.03 a
	5,000	1.14 a	1.33 a	1.13 a
	50,000	1.10 a	1.23 a	1.02 a
Root fresh weight (g)				
25:75	0	0.79 a	0.90 a	0.90 a
	5,000	0.71 ab	1.19 b	0.92 a
	50,000	0.63 b	0.85 a	0.79 a
50:50	0	0.75 a	0.88 a	0.92 a
	5,000	0.89 a	0.93 a	0.60 b
	50,000	0.65 a	0.87 a	0.62 b
75:25	0	0.67 a	1.02 a	0.66 a
	5,000	0.69 a	0.91 a	0.73 a
	50,000	0.68 a	0.92 a	0.66 a

* Data followed by the same letter within each texture and temperature combination are not different according to Waller-Duncan *k*-ratio *t*-test (*k* = 100).

infection sites versus numbers of invading nematodes. On healthy plants, FOL roots were macroscopically visible 3 days after sowing at 27.5 C (Table 6) (temperature for initial germination phase before transfer to inoculation chambers). The average number of FOL roots per healthy plant increased markedly in days 4-6. Plants grown at 26 and 30 C had more than 50 FOL roots by day 6 in contrast to plants at 22 C which had only approximately 30 roots. As a result, the impact of high concentrations of nematodes on root development of soybeans inoculated 4 days after seeding was most obvious at the lowest temperature.

TABLE 6. Numbers of first order lateral roots per noninoculated Ransom soybean seedling under three growth temperatures.

Days after seeding	Temperature (C)		
	22	26	30
2*	0†	0	0
4	5.1	14.0	12.1
6	30.4	53.3	64.6

* Times indicated include a 40-hour germination period at 27.5 C before transplanting in growth chambers.

† Mean values are based on a minimum of five plants per temperature and time combination.

DISCUSSION

The digitizer-microcomputer combination used for measuring root lengths was fast and greatly simplified data handling, eliminating recording by hand. The photocopies of root systems provided a permanent record of nematode effects and were useful for later reference. Soybean seedlings more than 10 days old were too large to be measured without dissection.

Soybean sensitivity to *M. incognita* is greatly reduced as seedlings reach 8 days of age. This narrow developmental range of high susceptibility of soybean to *M. incognita* perhaps is partially responsible for the success of many nematicides that provide short-term protection. Reduced susceptibility is attributed to the manner and rate of root tip multiplication. High temperatures increase root tip multiplication rates which quickly dilutes the nematode concentration per root tip. However, at Pi below those that cause seedling stunting, early season high temperatures would ultimately result in more plant damage than low temperatures because of shorter nematode generation time (22).

As measured by harvest data, soybean in North Carolina can be damaged by Pi of ca. 200 *M. incognita* juveniles/500 cm³ soil, fewer in very sandy soils (Barker, unpubl.). Early infections by nematodes often go unnoticed in the field because only slight, if any, effects are apparent on top growth. Our experiments with soil texture also support the observations that the impact of early infection by Mi on soybean top and root growth is more evident in soils low in clay (1,2). The reasons underlying this phenomenon are likely to be complex since soil texture affects both host growth and nematode movement (2,25).

Our experiments show significant effects on structures of young roots with some age-temperature combinations with the equivalent of approximately 170 juveniles per 500 cm³ soil (= 500 juveniles per three plants in 1,500 cm³ soil). For example, at the 12% infection rate observed in our experiments, each plant in a pot receiving 5,000 juveniles was infected by approximately 600 juveniles. Allowing 48 hours for nematode movement and penetration, plants at 22 C inoculated 2 or 4 days after seeding would, 2 days hence, have average numbers of juveniles per root tip of 120 and 20, respectively. In this case a 2-day difference in plant age resulted in an estimated sixfold difference in the nematode concentration per root tip.

Simulation models of the soybean-*M. incognita* interaction should utilize numbers of root tips rather than plant biomass in calculation of available infection sites on seedling root systems. Root-knot nematodes penetrate healthy root tissue in the region of elongation near root tips. Infection sites should also include root-knot galls as they form because infective juveniles are also attracted to these tissues (3).

Differences in rooting morphology (18) and root dry weight (14) among soybean cultivars have been observed for relatively mature plants. Crittenden (8) associated soybean resistance to root-knot to morphological features such as long tapering tap roots that had a minimum of lateral roots. Cultivars that quickly develop numerous root tips may be able to avoid inhibition of root growth by invading nematodes. We have noted differences in FOL root development among some soybean cultivars in our tests. For example, the cultivar Lee 68 after 6 days greenhouse growth had significantly fewer FOL roots/plant (15.3) compared with Lee 74 (21.3 roots) and Ransom (23.4 roots) grown under the same conditions ($P = 0.05$) (W. W. Shane, unpubl.). Studies are needed to determine if such differences in root characteristics influence tolerance or resistance of soybean to root-knot nematodes in the field.

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