

## Spatial and Temporal Interactions of *Meloidogyne incognita* and Soybean<sup>1</sup>

G. L. WINDHAM AND K. R. BARKER<sup>2</sup>

**Abstract:** The spatial and temporal dynamics of *Meloidogyne incognita*, relative to soybean shoot and root growth in field microplots, were determined at 11 sampling dates during a growing season. The population dynamics of *M. incognita* on soybean were dependent on initial population (Pi), soil moisture, and root spatial distribution. Final egg and juvenile population densities were greatest in plots with higher Pi. The population densities of juveniles and eggs were highest from mid- to late-season and were associated with increased soil moisture. Root spatial distributions and *M. incognita* numbers were closely related. Numbers of juveniles and eggs decreased with soil depth and distance from the center of the row. Greater numbers of juveniles and eggs were found in the upper 30 cm in the row center, and in the upper 15 cm at 10 and 20 cm from the center of the row. There were no consistent differences in root weights between nematode-infected and uninfected plants at any depth or distance from the center of the row. The optimum time for determining the relationship between Pi and soybean shoot growth was from late mid-season (September) to final harvest (14 November). The relationship between Pi and seed yield for the final harvest was best described by a quadratic model:  $\text{yield (g)} = 71.4 + 1.1(\log_{10}[\text{Pi} + 1]) - 2.3(\log_{10}[\text{Pi} + 1])^2$ , ( $R^2 = 0.99$ ,  $P = 0.03$ ).

**Key words:** *Glycine max*, *Meloidogyne incognita*, nematode, population dynamics, root-knot nematode, soybean, yield loss.

The southern root-knot nematode, *Meloidogyne incognita*, is a serious pest on soybean, *Glycine max*, in the southeastern United States (12). Soybean yield losses can be substantial, depending on cultivar susceptibility (14,18) and the aggressiveness of the *M. incognita* population (18). The potential of this nematode to damage soybean is also influenced by environmental and edaphic factors such as soil texture (17,19), temperature (13,17), and moisture (2).

Progress has been made in determining the general relationships between initial population (Pi) densities of *M. incognita* eggs and second-stage juveniles (J2) and soybean yield (11,14,19). To improve predictive capabilities and understanding of the *M. incognita*-host relationship, more

data are needed on the temporal and spatial fluctuations of *M. incognita* populations, as well as on the effects of these nematodes on soybean shoot and root growth throughout a growing season.

The objectives of this study were to determine i) the spatial and temporal distribution of *M. incognita* on soybean during a growing season and ii) the effects of *M. incognita* Pi on soybean shoot and root growth patterns.

### MATERIALS AND METHODS

The experiment was conducted in 80 × 100 cm fiberglass microplots installed to a depth of 50 cm in a Fuquay sand at Central Crops Research Station near Clayton, North Carolina. The Fuquay sand was 92% sand, 4% clay, and 4% silt at 0-15 cm; 91% sand, 4% clay, and 5% silt at 15-30 cm; and 88% sand, 5% clay, and 7% silt at 30-45 cm. Ten weeks before planting and infestation with nematodes, all plots were fumigated with 98 g methyl bromide/m<sup>2</sup>. A North Carolina isolate of *M. incognita* was increased on tomato, *Lycopersicon esculentum* cv. Manapal, in the greenhouse. Nematode inoculum was extracted with NaOCl (10) from infected roots cut into 2.5-cm segments. Pi were 0, 1,250, 5,000,

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<sup>2</sup> Former graduate student and Professor, Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695. Present address of first author: USDA ARS, Crop Science Research Laboratory, Forage Research Unit, P.O. Box 5367, Mississippi State, MS 39762.

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10,000, and 20,000 eggs/500 cm<sup>3</sup> of soil. Microplots were infested with nematode eggs to a depth of 15 cm by uniformly pouring a water suspension on each microplot and thoroughly mixing the soil with a spade. Thirty-five seed of soybean cv. Lee 68 were planted in a single row through the middle of each microplot on 26 May 1983. Soybean seed were coated with a commercial preparation of *Bradyrhizobium japonicum* ('Nitragin', Nitragin Co., Milwaukee, WI) and plots were infested with 1,000 spores of *Glomus macrocarpus*. Areas between microplots were planted with soybean to simulate field conditions.

Plant growth and nematode reproduction were determined biweekly for 18 weeks and then at ca. 3-week intervals for the last two sampling dates. Plants from 15 microplots (three per Pi treatment) were destructively sampled at each sampling date. A subsample of five shoots per microplot was arbitrarily selected to determine dry weights of cotyledons, leaflets, petioles, stems, pods, and seeds. Soybean shoots for each Pi were rated for developmental stage by the scale of Fehr et al. (6).

Root and nematode samples were collected on the same sampling times with a Giddings (Fort Collins, CO) hydraulic soil coring and sampling machine. Pairs of soil cores 5.1-cm-d were taken to a depth of 45 cm in the plant row and at 10 and 20 cm from the center of the row. Each core was split into 15-cm sections (0–15, 15–30, and 30–45 cm soil depths) for nematode assays and root extraction. Nematodes were extracted from each core section by elutriation and centrifugation (3). Root samples collected by elutriation were divided in half by weight. Half of the root sample was dried and weighed and *M. incognita* eggs were extracted from the other half with NaOCl (10).

A 5.1-cm-d by 45 cm soil core was collected from each microplot at each harvest date for soil nutrient analyses for each depth. Acidity, base saturation, cation-exchange capacity, percentage organic matter, pH, weight/volume, and levels of

exchangeable and extractable ions (calcium, copper, magnesium, manganese, phosphorus, potassium, and zinc) were determined by the Agronomic Division of the North Carolina Department of Agriculture.

Soil temperature was monitored at 15 cm with a CR21 Micrologger (Campbell Scientific, Logan, UT). Gravimetric water content, [(wet weight – oven dry weight)/oven dry weight] × 100, was determined at each sampling date. Water content was converted to soil water potential (bars) with a soil moisture characteristic curve constructed for Fuquay sand.

A randomized complete block design with three replications per treatment per sampling date was used. Paired nematode and root samples were processed separately for each microplot. Analyses of variance were performed, with orthogonal contrasts constructed to compare Pi levels for nematode reproduction and shoot and root growth parameters. Data were subjected to regression analyses to determine the relationships between Pi and root growth, shoot growth, and seed yield. The numbers of nematodes (X) were converted to log<sub>10</sub>(X + 1) to stabilize the variance in the statistical analyses.

## RESULTS

*Nematode population dynamics:* The temporal distributions of *M. incognita* J2 (Fig. 1A) and eggs (Fig. 1B) in the upper 15 cm of the soybean row followed similar trends through most of the soybean growing season. After an increase in soil moisture from 1 September to 15 September (Fig. 2), there was a large increase in the number of J2. A second peak in J2 numbers occurred on the tenth sampling date (25 October). The highest number of J2 was recovered in the 20,000 Pi treatment at the tenth sampling date (25 October). Numbers of J2 were generally lower on the last sampling date (14 November) than on 25 October.

*Meloidogyne incognita* eggs were first recovered on 23 June, 28 days after planting

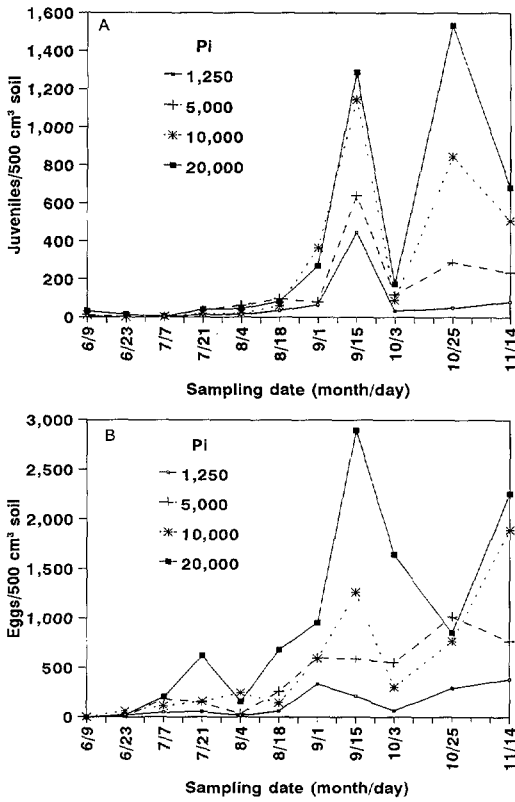


FIG. 1. Numbers of *Meloidogyne incognita* in the upper 15 cm in the soybean row as affected by initial population (Pi) during a growing season. Pi = eggs/500 cm<sup>3</sup> soil. A) Juveniles. B) Eggs.

(Fig. 1B). There was a gradual increase in egg numbers in the upper 15 cm of the soybean row through 1 September. At the next sampling date (15 September), the

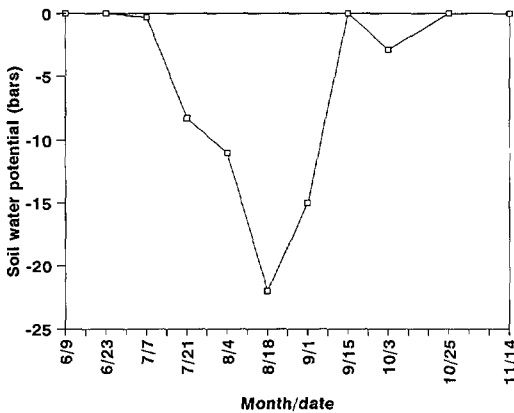


FIG. 2. Soil water potentials in a Fuquay sand at 11 sampling dates from June 1983 to November 1983.

number of eggs increased dramatically at the two highest Pi. A peak in egg numbers also occurred on the last sampling date (14 November).

*Nematode spatial distribution:* The spatial distribution patterns of *M. incognita* J2 were greatly influenced by distance from row center and depth. Spatial patterns of J2 were similar throughout the growing season, as shown in two examples herein (Fig. 3A,B). As the depth and distance from the center of the row increased, the numbers of J2 decreased. The highest densities of *M. incognita* were in the upper 30 cm of soil in the center of the row and in the upper 15 cm at 10 and 20 cm from the row. At the 30–45 cm level, highest densities were recovered mid- to late-season.

Spatial distributions of *M. incognita* eggs were similar to those for J2 during most of the growing season. Egg numbers decreased as the distance from the center of

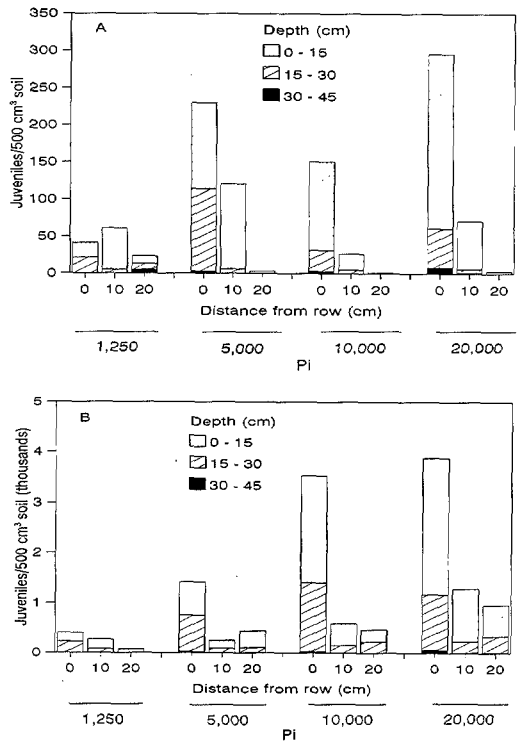


FIG. 3. Spatial distribution of *Meloidogyne incognita* juveniles relative to the center of a soybean row and initial population (Pi). Pi = eggs/500 cm<sup>3</sup> soil. A) 21 July. B) 14 November.

the row and depth increased; however, there were exceptions (Fig. 4A). On the fourth sampling date (21 July) for the two lowest *M. incognita* Pi, more eggs were extracted from cores 10 cm from the row center than in the row. Egg spatial distribution more closely resembled J2 spatial distribution, with egg numbers decreasing with increasing distance and depth from row center on the final sampling date (14 November) (Fig. 4B). Significant ( $P = 0.05$ ) differences in egg densities among Pi were detected in the upper 15 cm of soil at the center of the row late in the growing season. Reproduction differed in the upper 15 cm of the plots at 1 September and 3 October. At the 15–30 cm depth, differences ( $P = 0.05$ ) in J2 and egg population densities were detected in the row center at 3 October, and 10 cm from the row at 7 July. The lowest J2 and egg numbers were detected at the 30–45 cm depth at all distances from the row.

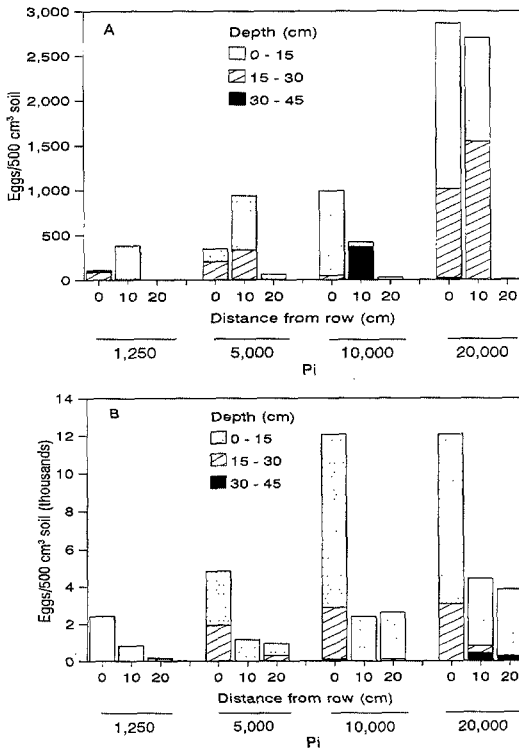


FIG. 4. Spatial distribution of *Meloidogyne incognita* eggs relative to the center of a soybean row and initial population (Pi) at two sampling dates. Pi = eggs/500 cm<sup>3</sup> soil. A) 21 July. B) 14 November.

*Plant growth responses: Meloidogyne incognita* suppressed soybean shoot dry weights through much of the growing season (Fig. 5). Differences ( $P = 0.01-0.05$ ) between the control and *M. incognita*-infested microplots were observed at eight harvest dates, beginning with the second harvest on 23 June and continuing through the final harvest on 14 November. Soybean shoot dry weight peaked on 3 October and declined thereafter as the plants senesced. Regression models described the relationship between Pi and dry shoot weights for the last four harvest dates. Linear models best described this relationship on 15 September ( $Y = 172.4 - 18.5X$ , where  $X = \log_{10}(\text{Pi} + 1)$ ,  $R^2 = 0.90$ ,  $P = 0.01$ ) and on 3 October ( $Y = 231.1 - 20.5X$ , where  $X = \log_{10}(\text{Pi} + 1)$ ,  $R^2 = 0.95$ ,  $P = 0.01$ ). Quadratic models adequately described the relationship between Pi and dry shoot weights on 25 October ( $Y = 119.6 + 38.8X - 10.4X^2$ , where  $X = \log_{10}(\text{Pi} + 1)$ ,  $R^2 = 0.96$ ,  $P = 0.02$ ) and on 14 November ( $Y = 165.2 + 2.2X - 5.8X^2$ , where  $X = \log_{10}(\text{Pi} + 1)$ ,  $R^2 = 0.99$ ,  $P = 0.01$ ).

Differences ( $P = 0.01-0.05$ ) were also observed in dry weights of specific plant parts. Leaflet dry weights generally paralleled individual plant growth. Leaflet weights from noninfested and infested microplots were significantly different at the second harvest (23 June) and later in the

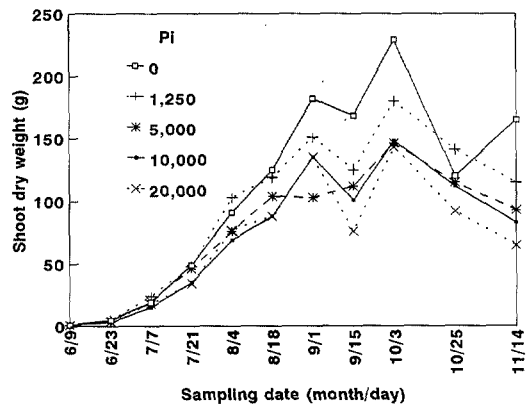


FIG. 5. Soybean shoot growth (dry weights of five plants per plot) as affected by initial populations (Pi) of *Meloidogyne incognita* over a growing season. Pi = eggs/500 cm<sup>3</sup> soil.

season from the seventh (1 September) to the ninth harvest (3 October). *Meloidogyne incognita* had a more striking effect on stem and petiole development than on leaflet development over the growing season. Differences ( $P = 0.01$ – $0.05$ ) in stem and petiole dry weights between nematode-infested and noninfested microplots were observed at the second harvest (23 June) and from the sixth (18 August) to the final harvest (14 November), with the exception of the tenth harvest. Throughout much of the growing season, the relative suppression of stem and petiole growth (weights) increased with an increase in  $P_i$ ; however, from early to mid-season, low numbers of nematodes stimulated stem and petiole development. Suppression of stem and petiole growth in *M. incognita*-infested plots increased with time.

Soybean pod and seed weights were also affected negatively by  $P_i$ . Differences ( $P = 0.05$ ) in pod weights between noninfested and *M. incognita*-infested microplots were observed at the seventh sampling date (first pod collection date, 1 September), and again at the ninth (3 October) and final (14 November) sampling dates (data not included). There was a linear relationship between  $P_i$  and pod dry weight on 1 September ( $Y = 44.4 - 4.9X$ , where  $X = \log_{10}(P_i + 1)$ ,  $R^2 = 0.98$ ,  $P = 0.01$ ) and on 14 November ( $Y = 32.2 - 4.2X$ , where  $X = \log_{10}(P_i + 1)$ ,  $R^2 = 0.97$ ,  $P = 0.01$ ). Seed yield was not significantly ( $P = 0.01$ ) affected until harvest at plant maturity (14 November), although numerical differences in seed weights were observed at the two previous sampling dates. The relationship between  $P_i$  and seed yield for the final harvest was best described by a quadratic regression model ( $Y = 71.4 + 1.1X - 2.3X^2$ , where  $X = \log_{10}(P_i + 1)$ ,  $R^2 = 0.99$ ,  $P = 0.03$ ) (Fig. 6).

*Meloidogyne incognita* had little effect on the developmental stages of soybean. Differences ( $P = 0.01$ ) in soybean development were observed only at the fourth harvest date (21 July). Average vegetative growth stages for 0, 1,250, 5,000, 10,000,

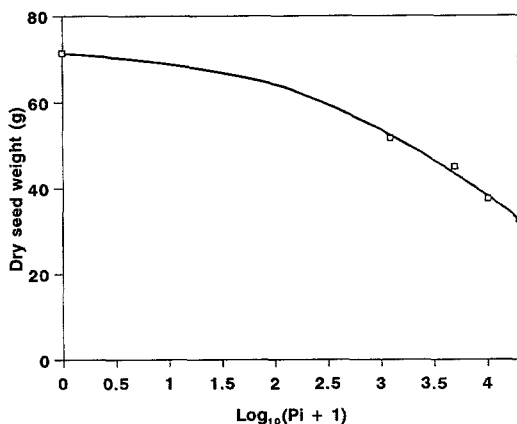


FIG. 6. Relationship between soybean yield (dry weights [g] of seed from five plants per plot) and initial population density ( $P_i$ ).  $x = \log_{10}(x + 1)$  of  $P_i$ ; quadratic regression equation:  $y = 71.4 + 1.1x - 2.3x^2$ ,  $R^2 = 0.99$ ,  $P = 0.03$ .

and 20,000 eggs per 500 cm<sup>3</sup> of soil were 9.3, 9.0, 9.0, 8.3, and 7.6, respectively. These data signify a reduction in the number of nodes per soybean plant prior to flowering.

Soybean root distribution followed similar patterns throughout the growing season, with root mass decreasing with depth and distance from the row center (Fig. 7A,B). No consistent significant differences in root weights were detected between nematode-infested and uninfested plants at any depth or distance from the row. Orthogonal contrasts of root weights from different  $P_i$  were significant ( $P = 0.05$ ) at two sampling dates (1 September and 3 October).

## DISCUSSION

The population dynamics of *M. incognita* on soybean were dependent on  $P_i$ , time after planting, environmental conditions, and root spatial distribution. Egg and J2 densities throughout the soybean growing season were closely related to  $P_i$  levels: generally, higher levels of eggs and J2 were extracted from microplots infested with the higher  $P_i$ . J2 densities, regardless of  $P_i$  were recovered at relatively low levels early in the season, as is typical for *Meloidogyne* spp. on annual row crops (5) because

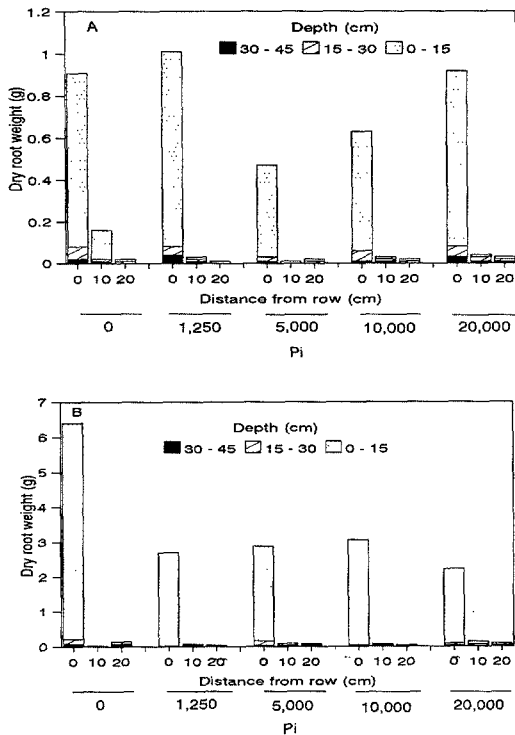


FIG. 7. Influence of *Meloidogyne incognita* initial populations (Pi) on spatial distribution of soybean roots (dry root weights) in relation to the center of the row at two sampling dates. Pi = eggs/500 cm<sup>3</sup> soil. A) 21 July. B) 15 September.

most J2 have penetrated plant roots and are not recovered in the extraction process. Egg and juvenile numbers were lower through most of the season compared with levels observed at this location in previous years (19).

Soil moisture had a marked effect on the population dynamics of *M. incognita*. Soil moisture levels were low from 21 July (-8.3 bars) to 1 September (-15 bars). *Meloidogyne incognita* egg hatch is reduced at low soil moisture levels (9). Egg hatch in our experiment would have been inhibited during the drought period from 21 July through 1 September, which would account for the low J2 population densities during this period. Two peaks in J2 population densities were observed on 15 September and on 25 October, on which dates soil moisture had increased from the previous sampling dates and apparently stim-

ulated egg hatch. Soil moisture may have also had an indirect effect on egg production, which peaked on 15 September.

Soil temperature effects on *M. incognita* population dynamics were unclear. The soil temperature remained well above the J2 activity threshold (18 C) (16) until the tenth harvest date (25 October), and then soil temperatures gradually decreased to 14 C on the last harvest (14 November). Although there was a marked decrease in J2 population densities at the last harvest, egg hatch should not have been greatly influenced because *M. incognita* egg hatch is not restricted until soil temperatures drop below 12 C (9).

Vertical distributions of plant-parasitic nematodes are usually closely related to root distribution (4), and this was the case in our study. As depth and distance from the soybean row increased, root mass and nematode numbers decreased. Although the highest J2 and egg numbers were in the upper 15 cm of soil in microplots, high numbers of *Meloidogyne* spp. were found throughout the upper 45 cm in a soybean field in a concurrent study (Windham, unpubl.). *Meloidogyne* spp. have also been recovered at greater depths (8). Microplots in our study were inoculated to a depth of 15 cm. Movement of juveniles may have been less than observed in other studies (15), with the greatest amount of inoculum remaining in the upper 30 cm of soil. The spatial distribution of *M. incognita* on soybean closely resembles that of *Heterodera glycines* on soybean in field experiments (1).

Edaphic factors also may have had an effect on *M. incognita* spatial distribution. Base saturation, cation-exchange capacity, percentage of organic matter, pH, and levels of exchangeable and extractable ions (calcium, copper, magnesium, manganese, phosphorus, and zinc) differed among soil depths, with levels decreasing with depth. The edaphic factors may have influenced J2 distribution directly, or indirectly by affecting soybean root penetration at the lower depths.

*Meloidogyne incognita* had a negligible effect on root weight, accounting for less than 1% of the variability in the root data. Soybean plants grown in low to moderate nematode Pi tended to have higher root weights compared with those at the highest Pi, although the differences were not statistically significant. Soybean roots were not severely galled by the *M. incognita* isolate used in this experiment compared with the severe galling reported in a previous study at this location (19). The effects of *M. incognita* on soybean root growth and efficiency may have been more accurately described by measuring root lengths or numbers of root tips (17). Variability observed in root weights may be attributed to the small number of samples per plot, and also to the difficulty in dividing roots in core sections. Determination of the growth of whole or half root systems from treatment plots, as was done for the shoots, may be the ideal method for obtaining the necessary measurements for modeling purposes.

The methods used for determining the effects of *M. incognita* on shoot growth and yield were more than adequate. The optimum time for determining the relationship between Pi and soybean shoot growth was from midseason (September) to harvest (harvest) for each parameter. Various soybean shoot components reflected the sensitivity of soybean to *M. incognita*.

The precision of nematode damage functions containing only preplant numbers of nematodes is limited. A number of environmental factors affect the damage potential of *M. incognita* on soybean (2,7,14,19). Soybean reactions to *M. incognita* also vary with cultivar (14) and depend on the aggressiveness of the nematode population (18). More precise estimates of soybean yield losses may be obtained by modeling soybean growth as affected by crop management practices, environmental factors, pests, and pathogens. Information collected in this study may prove useful in the development of a *M. incognita* life cycle simulator. These findings should also be

helpful in planning further research for monitoring the effects of plant-parasitic nematodes on soybean.

#### LITERATURE CITED

1. Alston, D. G., and D. P. Schmitt. 1987. Population density and spatial pattern of *Heterodera glycines* in relation to soybean phenology. *Journal of Nematology* 19:336-345.
2. Barker, K. R. 1982. Influence of soil moisture, cultivar, and population density of *Meloidogyne incognita* on soybean yield in microplots. *Journal of Nematology* 14:429 (Abstr.).
3. Barker, K. R. (Chairman). 1978. Determining nematode population response to control agents. Pp. 114-127 in E. I. Zehr, ed. *Methods for evaluating plant fungicides, nematicides, and bactericides*. St. Paul: American Phytopathological Society.
4. Barker, K. R., and J. L. Imbriani. 1984. Nematode advisory programs—Status and prospects. *Plant Disease* 68:735-741.
5. Barker, K. R., C. J. Nusbaum, and L. A. Nelson. 1969. Seasonal population dynamics of selected plant-parasitic nematodes as measured by three extraction procedures. *Journal of Nematology* 1:232-239.
6. Fehr, W. R., C. E. Caviness, D. T. Burmood, and J. S. Pennington. 1971. Stage of development descriptions for soybeans, *Glycine max* (L.) Merrill. *Crop Science* 11:929-931.
7. Ferris, H. 1981. Dynamic action thresholds for diseases induced by nematodes. *Annual Review of Phytopathology* 19:427-436.
8. Ferris, H., and M. V. McKenry. 1974. Seasonal fluctuations in the spatial distribution of nematode populations in a California vineyard. *Journal of Nematology* 6:203-210.
9. Goodell, P. B., and H. Ferris. 1989. Influence of environmental factors on the hatch and survival of *Meloidogyne incognita*. *Journal of Nematology* 21:328-334.
10. Hussey, R. S., and K. R. Barker. 1973. A comparison of methods of collecting inocula of *Meloidogyne* spp., including a new technique. *Plant Disease Reporter* 57:1025-1028.
11. Kinloch, R. A. 1982. The relationship between soil populations of *Meloidogyne incognita* and yield reduction of soybean in the coastal plain. *Journal of Nematology* 14:162-167.
12. Mulrooney, R. P. 1988. Soybean disease loss estimate for southern United States in 1987. *Plant Disease* 72:915.
13. Nardacci, J. F., and K. R. Barker. 1979. The influence of temperature on *Meloidogyne incognita* on soybean. *Journal of Nematology* 11:62-70.
14. Niblack, T. L., R. S. Hussey, and H. R. Boerma. 1986. Effects of environments, *Meloidogyne incognita* inoculum levels, and *Glycine max* genotype on root-knot nematode-soybean interactions in field microplots. *Journal of Nematology* 18:338-346.
15. Prot, J. C., and C. Netscher. 1978. Improved

detection of low population densities of *Meloidogyne*. *Nematologica* 24:129-132.

16. Roberts, P. A., S. D. Van Gundy, and H. E. McKinney. 1981. Effects of soil temperature and planting date of wheat on *Meloidogyne incognita* reproduction, soil populations, and grain yield. *Journal of Nematology* 13:338-345.

17. Shane, W. W., and K. R. Barker. 1986. Effects of temperature, plant age, soil texture, and *Meloido-*

*gyne incognita* on early growth of soybean. *Journal of Nematology* 18:320-327.

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

19. 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.