

# Population Density and Spatial Pattern of *Heterodera glycines* in Relation to Soybean Phenology<sup>1</sup>

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**Abstract:** Population dynamics of *Heterodera glycines* (SCN) were influenced by initial nematode population density in soil, soybean root growth pattern, soil type, and environmental conditions in two field experiments. Low initial populations (Pi) of SCN increased more rapidly during the growing season than high Pi and resulted in greater numbers of nematodes at harvest. Egg and juvenile (J2) populations increased within 2-6 weeks after planting when early-season soil temperatures were 20 C and above and were delayed by soil temperatures of 17 C or below in May and early June. Frequencies of occurrence and number of nematodes decreased with increasing depth and distance from center of the soybean row. Spatial pattern of SCN paralleled that of soybean roots. Higher clay content in the subsoil 30-45 cm deep in one field restricted soil penetration by roots, indirectly influencing vertical distribution of SCN. Shoot dry weight was a good indicator of the effect of SCN on seed yield. Root dry weight was poorly correlated with soybean growth and yield. The relationship of yield (seed weight) to Pi was best described by a quadratic equation at one site, but did not fit any regression model tested at the second site.

**Key words:** *Glycine max*, *Heterodera glycines*, population dynamics, soybean, soybean cyst nematode, yield.

The soybean cyst nematode (SCN), *Heterodera glycines* Ichinohe, is one of the most important pests on soybean, *Glycine max* (L.) Merr., in the United States. Yield losses in North Carolina due to SCN were estimated to be 4.9% in 1984 (11), greater than losses from any other pathogen on soybean. Current management practices focus on reducing the initial inoculum or preventing infection and (or) reproduction (19). Knowledge of factors affecting nematode populations, including initial inoculum density (1,14) and the soil environment (8,12,18,21), is fundamental to the understanding of nematode-plant relationships.

The relationship between numbers of nematodes and growth and yield of annual crops can be defined as a function of pre-plant densities (1,3,5,14,21). In addition, knowledge of preplant nematode population density is essential for predictions of associated problems before implementation of control measures.

Key environmental and edaphic param-

eters, such as soil texture (18,21), temperature (2,12), and moisture (4,8), influence movement and feeding of nematodes, as well as penetration and development of endoparasitic species in host roots. Completion of a generation of SCN on soybeans in the field requires 3 weeks when weekly mean temperatures range from 22 to 30 C and 4 weeks at 16-22 C (2).

Objectives of this research were to determine 1) spatial and temporal patterns and population dynamics of SCN on soybean during the growing season, 2) relationship between soybean root growth patterns and SCN spatial patterns, and 3) influence of different initial population densities of SCN on soybean phenology. Two locations with similar soils and discrete Pi ranges were selected to characterize the population dynamics and crop response across years.

## MATERIALS AND METHODS

Experiments to determine the influence of SCN population densities and spatial patterns on soybean growth and yield were conducted in two naturally infested fields in eastern North Carolina. The field used in 1983, infested with race 1 of SCN, was at the Upper Coastal Plains Research Station (UCPRS) near Rocky Mount. Soil texture at 0-15 cm was sandy loam (57% sand, 35% silt, 8% clay), at 15-30 cm was loam

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(49% sand, 34% silt, 17% clay), and at 30–45 cm was clay loam (38% sand, 30% silt, 32% clay).

Before planting, 100 plots (0.9 m × 1 m) were selected from 362 in order to give a range of Pi based on counts determined by assay of 300 cm<sup>3</sup> soil. Samples were processed by a combination of elutriation (6) and centrifugation (10). Pi ranges with 20 replications were 1) 0 eggs and 0 second-stage juveniles (J2), 2) 24–144 eggs ( $\bar{x}$  = 78, SE = 9) and 0 J2, 3) 0–648 eggs ( $\bar{x}$  = 166, SE = 44) and 23–72 J2 ( $\bar{x}$  = 28, SE = 4), 4) 912–3,168 eggs ( $\bar{x}$  = 1,693, SE = 128) and 12–228 J2 ( $\bar{x}$  = 108, SE = 13), and 5) 2,712–9,960 eggs ( $\bar{x}$  = 6,259, SE = 558) and 132–684 J2 ( $\bar{x}$  = 339, SE = 30).

Soil temperature was monitored at a depth of 15 cm, using a CR-21 micro-datalogger (Cambell Scientific, Logan, Utah). Soil moisture was monitored weekly at 15–20 cm, using a depth moisture gauge (Troxler Electronic Laboratories, Research Triangle Park, North Carolina). This apparatus gave imprecise readings which made data difficult to interpret.

In 1984, a field infested with race 2 of SCN located on a private farm near Weeksville was utilized. Textural components were 69% sand, 26% silt, and 5% clay at 0–15 cm; 68% sand, 25% silt, and 7% clay at 15–30 cm; and 66% sand, 24% silt, and 10% clay at 30–45 cm; all were sandy loam.

Before planting, 112 plots (1 m × 1 m) were selected from 423 in order to give a range of Pi based on counts determined in a way similar to those at UCPRS. Pi ranges with 28 replications were 1) 0–168 ( $\bar{x}$  = 93, SE = 8), 2) 360–492 ( $\bar{x}$  = 423, SE = 9), 3) 912–1,176 ( $\bar{x}$  = 1,023, SE = 17), and 4) 2,008–4,116 ( $\bar{x}$  = 2,664, SE = 97) eggs/300 cm<sup>3</sup> soil.

Soil temperature was monitored as at UCPRS. Soil moisture percentage ([wet weight – oven dry weight at 105 C for 24 hours]/oven dry weight) × 100, was determined for soil depths of 0–15, 15–30, and 30–45 cm each sampling date.

A single row of soybean, *Glycine max* cv. Coker 156, was planted in the center of each plot on 19 May 1983 and 10 May

1984. Rows were continuous and spaced 0.9 m (1983) or 1 m (1984) apart to approximate standard agronomic practices. Soybeans were planted with conventional tillage in 1983 and no-till in corn stubble in 1984.

During the growing season, paired soil samples (5.1 cm d) were collected to a depth of 45 cm in the plant row, 15, 30, and 45 cm from the row. Each core was divided into 15-cm sections for nematode assays and root extractions. At Weeksville, nematode assays at the lower depths (15–45 cm) were collected only in the plant row. A Giddings hydraulic soil coring and sampling machine (Fort Collins, Colorado) was used at UCPRS and a soil bucket auger at Weeksville. Soil samples were collected at approximately 2-week intervals from 19 May to 8 November at UCPRS and at approximately monthly intervals from 10 May to 12 November at Weeksville.

Nematodes were extracted from 300 cm<sup>3</sup> soil as described for preplant samples. All plant-parasitic nematodes from samples collected at planting were identified to genus and counted. Thereafter, only SCN cysts, eggs, and J2 were counted, since few other plant-parasitic nematode genera were present. Cysts were crushed with a Ten-Broeck tissue grinder to free eggs.

All soybean shoots were harvested at each sampling date, and fresh weight and numbers of plants per plot were determined. A subsample of five shoots per plot was randomly selected to determine dry weights of leaflets, stems, petioles, pods, and seeds. At maturity, soybeans were mechanically harvested for seed yields. Roots were collected on a 325- $\mu$ m-pore sieve during elutriation. Oven dried weights were obtained for all root samples.

A randomized design with two (UCPRS) and four (Weeksville) replications per Pi × sampling date was used. Paired nematode and root samples, processed separately for each replicate, were used in the analysis. Data were subjected to analysis of variance, and means were compared using the Waller-Duncan K-ratio *t*-test. Correlation coefficients were calculated for nematode num-

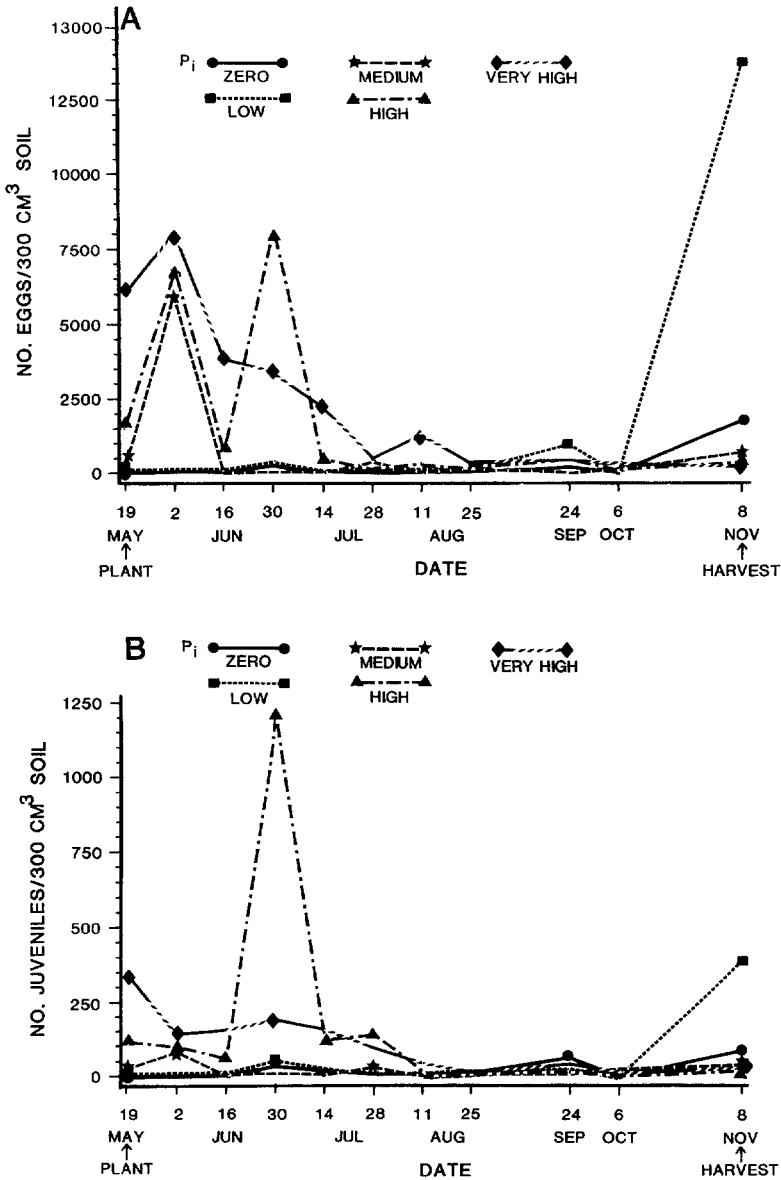


FIG. 1. Numbers of *Heterodera glycines* in the upper 15 cm in the soybean row as affected by initial population densities ( $P_i$ ) over a growing season at UCPRS, 1983. Average initial numbers of eggs were zero = 0, low = 70, medium = 150, high = 1,615, and very high = 5,980/300 cm<sup>3</sup> soil. Average initial numbers of J2 were zero = 0, low = 0, medium = 30, high = 115, and very high = 335/300 cm<sup>3</sup> soil. A) Eggs. B) J2.

bers and plant growth parameters over time. Least-squares analysis was used to determine any simple or quadratic relationships of yield to log<sub>10</sub>-transformed  $P_i$ .

**RESULTS**

*Nematode population dynamics—UCPRS:* The temporal pattern of SCN eggs and J2 in the upper 15 cm of soil in the soybean

row followed similar trends among  $P_i$  (Fig. 1A, B). Nematode numbers were most consistent with  $P_i$  in the soybean row, 0–15 cm deep, and best represented changes in nematode populations during the season. Cyst numbers were often variable within  $P_i$ ; therefore, egg and J2 population densities were used. Egg and J2 population levels were greater in soil samples between

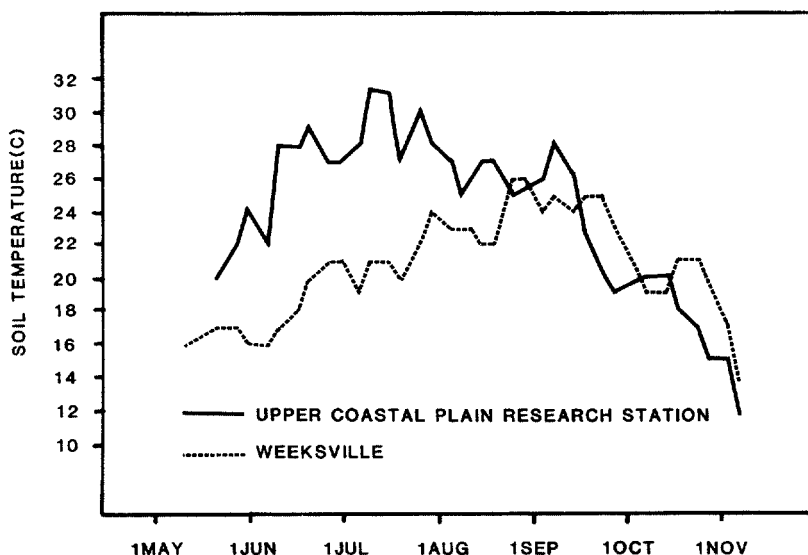


FIG. 2. Mean soil temperature (average of 5-day intervals) at 15 cm deep from May to November for UCPRS (1983) and Weeksville (1984).

2 and 6 weeks after planting and near end of season and lower from 28 July to 6 October. The greatest number of eggs early to midseason was generally in the high and very high Pi. At harvest (8 November), more eggs were present in the initially low Pi (70 eggs and 0 J2/300 cm<sup>3</sup> of soil). J2 numbers were also generally greater ( $P = 0.05$ ) in the higher Pi plots early to midseason and greater in the low Pi plots at harvest.

Mean soil temperatures, averaged at 5-day intervals, increased from 19 C in late May to 32 C in July, gradually declining late season to below 15 C by harvest (Fig. 2). Soil moisture fluctuated between 3 and 15% during the season. In July when evapotranspiration was high, soil moisture was greater in plots with higher numbers of nematodes.

The spatial pattern of SCN eggs and J2 in relation to horizontal and vertical distance from the soybean row changed during the season (Fig. 3A, B). Egg and J2 numbers were fairly low at 15–45 cm deep early in the season, increasing later in the season; however, both egg and J2 population densities and frequencies of occurrence generally decreased with depth and distance from the center of the plant row.

*Nematode population dynamics—Weeksville:* Temporal changes in SCN densities at this site differed from those at UCPRS. Egg numbers declined on the first sampling date after planting for all Pi and remained relatively low throughout the season (Fig. 4A). J2 numbers peaked in early July, 8 weeks after planting, declined until 17 September, then increased (Fig. 4B). The greatest number of J2 at harvest was in the high Pi plots.

Mean soil temperatures remained at or below 17 C in May and early June, gradually increased to a high of 27 C in August, and declined rapidly after September (Fig. 2). Soil moisture remained fairly constant in the 0–15-cm and 15–30-cm depths throughout the season at 20 and 22%, respectively, close to field capacity. At 30–45 cm deep, low soil moisture on 10 July was approximately 18%, considerably below field capacity (27%).

*Plant growth response—UCPRS:* Soybean root growth patterns were similar for the 10 sampling dates during the season. Root dry weights were greatest ( $P = 0.05$ – $0.01$ ) in the plant row in the upper 15 cm (Fig. 5). A quadratic regression equation ( $Y = 0.82 + 1.59X - 0.47X^2$ ,  $R^2 = 0.98$ ,  $P = 0.05$ ) adequately described the relation-

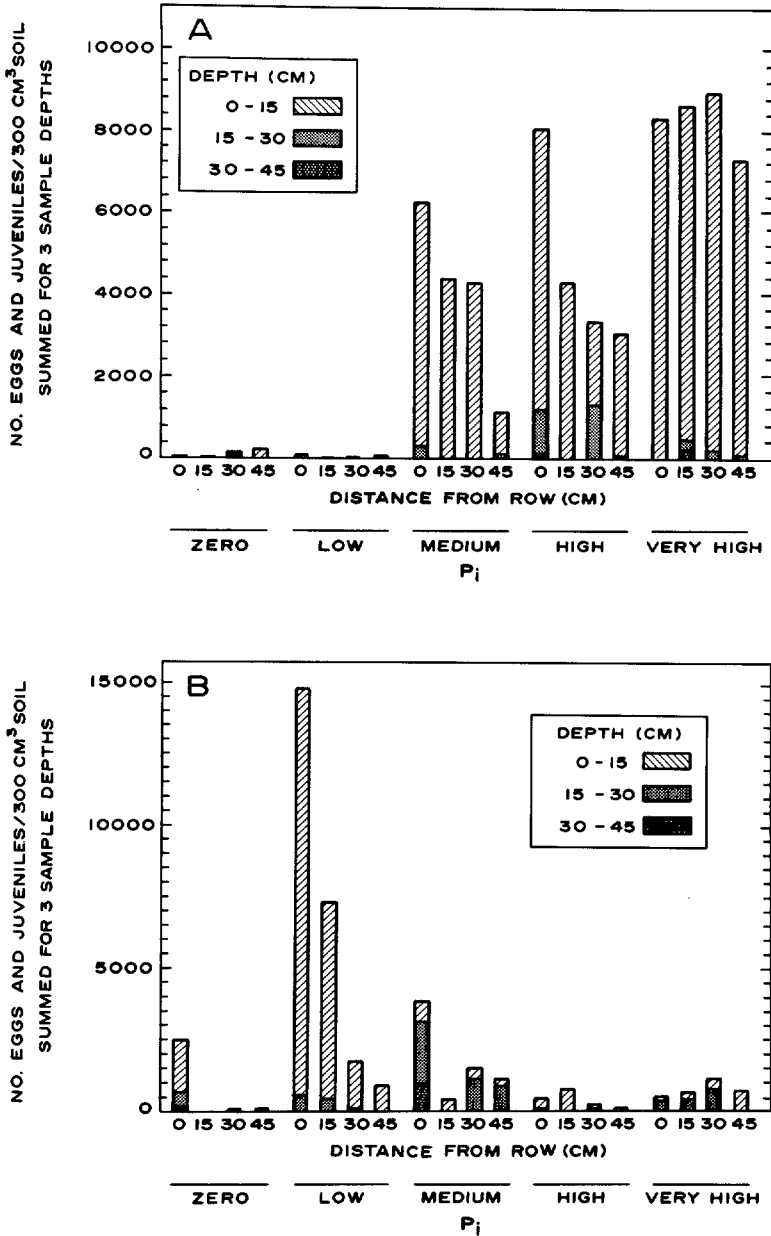


FIG. 3. Spatial distribution of *Heterodera glycines* eggs and J2 in relation to the center of a soybean row at UCPRS, 1983. Average initial numbers of eggs (Pi) were zero = 0, low = 70, medium = 150, high = 1,615, and very high = 5,980/300 cm<sup>3</sup> soil. Average initial numbers of J2 were zero = 0, low = 0, medium = 30, high = 115, and very high = 335/300 cm<sup>3</sup> soil. A) Two weeks after planting. B) Harvest.

ship between root weight in the soybean row (Y) and log<sub>10</sub> Pi + 1(X).

The influence of SCN initial population densities on soybean plant growth over the growing season was best described by differences in shoot dry weights (Fig. 6A). Differences (P = 0.05–0.01) between plots

with different Pi were observed at six of the nine sampling times. There was a general suppression of plant growth at the higher Pi on most sampling dates. A linear regression model (Y = 55.4 - 7.9X, r<sup>2</sup> = 0.97, P = 0.01) best described the relationship between log<sub>10</sub>Pi + 1(X) and dry

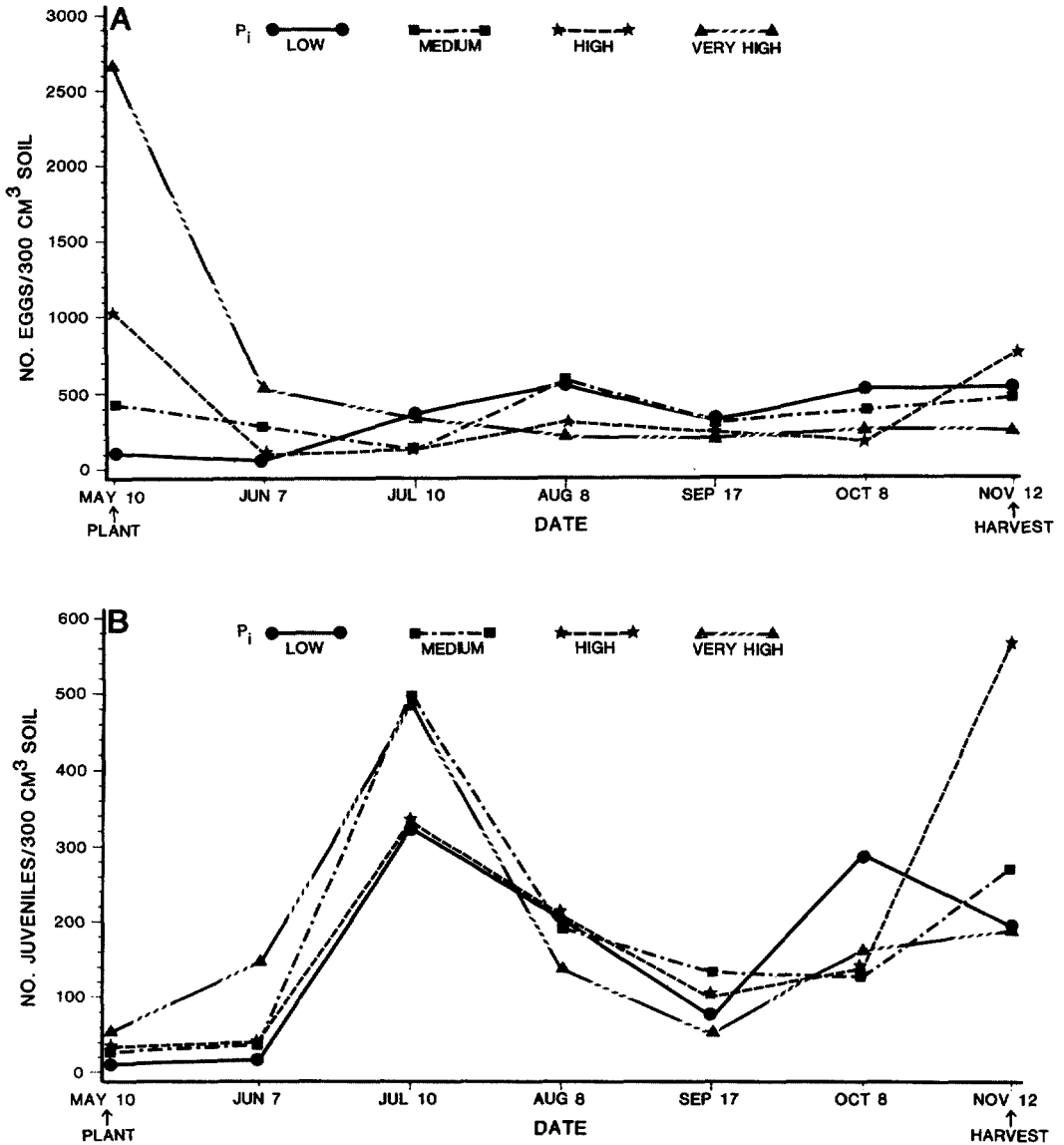


FIG. 4. Population densities of *Heterodera glycines* as influenced by initial numbers ( $P_i$ ) over a growing season at Weeksville, 1984. Average initial numbers of eggs were low = 94, medium = 424, high = 1,022, and very high = 2,664/300 cm<sup>3</sup> soil. Average initial numbers of J2 were low = 0, medium = 25, high = 33, and very high = 51/300 cm<sup>3</sup> soil. A) Eggs. B) J2.

shoot weight ( $Y$ ) at 18 weeks (24 September).

Differences ( $P = 0.05-0.01$ ) were also observed in dry weights of specific plant parts. Leaflet, petiole, and stem dry weights generally paralleled shoot growth, with greater plant weights in plots with lower  $P_i$ . Among  $P_i$  levels, differences in leaflet weights occurred at 2, 6, 8, 10, and 20

weeks and in petiole and stem weights at 8, 10, 12, and 20 weeks.

Soybean pod and seed weights of the five randomly selected plants were negatively affected by  $P_i$ . Pod dry weights generally decreased with increasing  $P_i$  but were not significant ( $P = 0.05$ ). Seed yield ( $Y$ ) suppression at harvest (8 November) fit a quadratic regression ( $Y = 128.5 + 43.5X -$

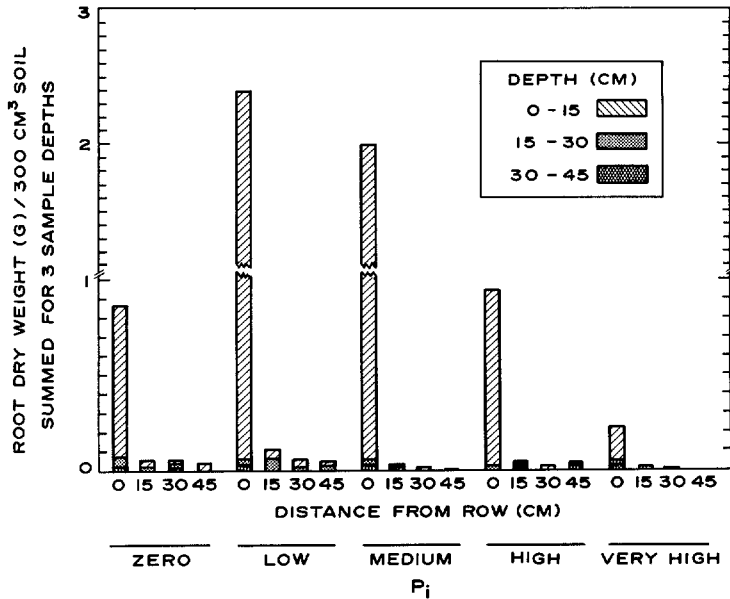


FIG. 5. Soybean root growth patterns 14 weeks after planting at UCPRS, 1983, at four distances from the center of the row and three depths from plots with different  $P_i$ . Average initial numbers of eggs were zero = 0, low = 70, medium = 150, high = 1,615, and very high = 5,980/300  $\text{cm}^3$  soil. Average initial numbers of J2 were zero = 0, low = 0, medium = 30, high = 115, and very high = 335/300  $\text{cm}^3$  soil.

$15.9X^2$ ,  $R^2 = 0.91$ ,  $P = 0.07$ ) on  $\log_{10}P_i + 1(X)$  (Fig. 7).

*Plant growth response—Weeksville:* Soybean root weights were greatest ( $P = 0.05$ – $0.01$ ) in the plant row in the upper 15 cm on all sampling dates. The relationship of  $P_i$  and time after planting to soybean growth was best measured as dry shoot weight (Fig. 6B). Shoot dry weights in July and August were highest in low and medium  $P_i$  levels, and greatest shoot weights in September were observed in the initially medium and high levels. Differences among  $P_i$  at specific times were not significant ( $P = 0.05$ ).

There were no differences ( $P = 0.05$ ) in leaflet, petiole, or stem dry weights for the four  $P_i$  levels during the growing season. Development of pods and seeds late in the season were not significantly influenced by  $P_i$  level. Lower dry pod weights were observed at the medium and high  $P_i$  levels on 8 October. Yields were suppressed at the high and very high  $P_i$ , with highest yield at the low  $P_i$  (94 eggs and 0 J2/300  $\text{cm}^3$  of soil).

## DISCUSSION

The population dynamics of SCN on soybean were influenced by initial population density in soil, root growth pattern, and edaphic and environmental conditions. Initial population density is important because it can be related to the amount of damage to annual crops caused by nematode feeding (3). Population fluctuations of SCN were dependent on  $P_i$ . Nematode numbers increased more rapidly during the season at lower  $P_i$  than at higher  $P_i$ . Damage to soybean roots early in the season by high initial numbers of nematodes may limit subsequent invasion and reproduction and, thus, inhibit late season population increases (5). In contrast, low  $P_i$  may result in little early season root damage, allowing greater vertical root growth and development and thus providing more feeding sites for the nematodes later in the season.

Soil temperature also had a major influence on SCN population changes during the growing season. Increases in egg and J2 populations in soil early in the season

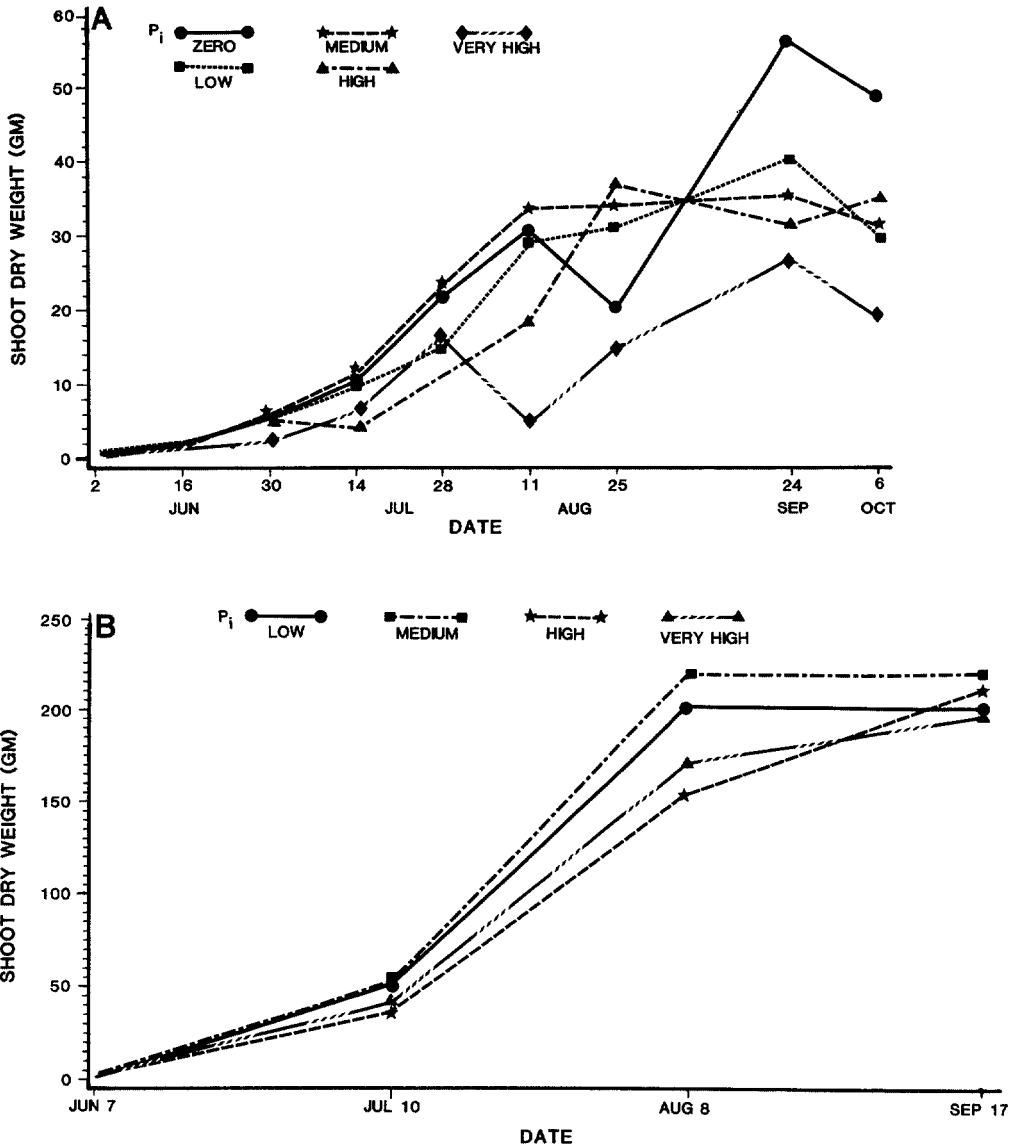


FIG. 6. Relationship of initial population densities ( $P_i$ ) of *Heterodera glycines* to soybean shoot growth (dry weights of five plants per plot). A) UCPRS, 1983. Average initial numbers of eggs were zero = 0, low = 70, medium = 150, high = 1,615, and very high = 5,980/300 cm<sup>3</sup> soil. Average initial numbers of J2 were zero = 0, low = 0, medium = 30, high = 115, and very high = 3,351/300 cm<sup>3</sup> soil. B) Weeksville, 1984. Average initial numbers of eggs were low = 94, medium = 424, high = 1,022, and very high = 2,664/300 cm<sup>3</sup> soil. Average initial numbers of J2 were low = 0, medium = 25, high = 33, and very high = 51/300 cm<sup>3</sup> soil.

were associated with soil temperatures above 17 C in May and June. Thus, mean temperatures ranging from 17 to 20 C and higher may be the threshold range for rapid invasion of soybean roots by J2, and for subsequent development and reproduction. In other studies, SCN white females were first detected in soybean roots 14 days

after inoculation at 28 and 31 C, but not until 58 days at 14 C, and new eggs were not produced at 14 C (7). A generation of SCN on soybeans in the field required up to 21 days at weekly mean soil temperatures of 22 to 30 C and up to 28 days at 16 to 22 C (2). The low midseason egg and J2 soil populations were probably due to



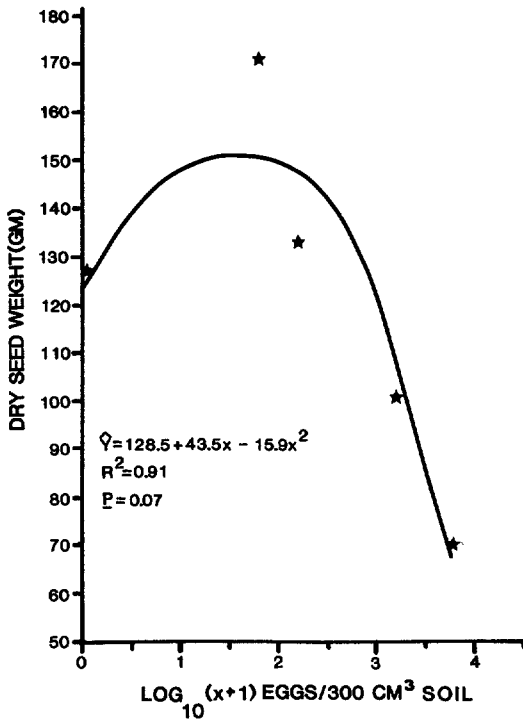


FIG. 7. Regression of soybean yield (dry seed weight) (Y) on  $\log_{10} P_i + 1$  (X) egg numbers of *Heterodera glycines* at UCPRS, 1983. Data are means of two replicates.

high mortality which occurred at soil temperatures above the optimum range of 24 to 28 C, especially above 33 C (7). Factors involved in the observed decrease in SCN soil populations during the midseason are unknown since, root infections may not be very high either (5).

Declining soil temperatures in October and November coincided with an increase in egg numbers at harvest at UCPRS. Dormancy induction in SCN eggs in the fall, with temperatures decreasing from 25 to 17 C, and increased nematode reproduction on reproductive soybeans may have accounted for the observed population buildup late in the season (9,17). Cooling soil temperatures did not appear to suppress hatch at Weeksville, as egg populations increased only slightly in the moderate  $P_i$  level late in the season.

The effects of soil moisture on nematode population dynamics were more difficult to characterize than those for temperature.

Due to widely fluctuating moisture levels at UCPRS, soil environmental conditions were probably limiting to soybean growth and nematode movement and reproduction at several times during the season. At Weeksville moisture was not limiting, resulting in optimal growth conditions for soybeans.

Nematode and root spatial patterns were closely related. The optimal activity of SCN and, therefore, highest population increases occur during May and June when roots are primarily in or near the plant row. Since root growth deep into the soil and between rows occurs later, population increase of SCN lags behind that in the row.

The relationship of soil type to nematode spatial pattern is complex, involving physical, chemical, and biotic factors inherent to each soil (13). Soil texture affects nematode movement, penetration of roots, and reproduction (18). Changes in soil texture with the soil profile at UCPRS had an impact on root growth indirectly affecting nematode spatial patterns. Soybean roots did not readily penetrate the fine-textured soil 15–45 cm deep, which resulted in low numbers of nematodes at that depth.

Shoot dry weight throughout the season was a good indicator of the suppressive effects of SCN on seed yield. Leaflet dry weight of randomly selected plants also may be a good indicator and warrants additional research. Leaf area was not measured in this study but perhaps should be considered. Both shoot and leaflet measurements were superior to root growth as damage indicators. In this study, root sampling and extraction techniques had greater error than those used for shoots. Root damage, however, may not have been expressed in weight as much as in function. Thus, malfunctioning roots, regardless of size, would affect shoot and leaflet growth.

The relationship between growth of annual plants and preplant numbers of nematodes generally has been described by regressions of yield on  $\log_{10}$ -transformed nematode population densities (3,15). Further adaptation of the regression approach

accounted for a minimum yield and tolerance limit of the crop (20). Pi provides good prediction of potential crop loss as a basis for advising growers (1,3,5,14,16,21). The accuracy of sampling methods used to detect these initial population densities for predicting damage is dependent on our knowledge of nematode temporal and spatial patterns plus the influence of environmental and edaphic factors.

#### LITERATURE CITED

1. Abawi, G. S., and B. J. Jacobsen. 1984. Effect of initial inoculum densities of *Heterodera glycines* on growth of soybean and kidney bean and their efficiency as hosts under greenhouse conditions. *Phytopathology* 74:1470-1474.
2. Alston, D. G. 1985. Development of *Heterodera glycines* life stages as influenced by temperature. M.S. thesis, North Carolina State University, Raleigh.
3. Barker, K. R., and T. H. A. Olthof. 1976. Relationship between nematode population densities and crop responses. *Annual Review of Phytopathology* 14:327-353.
4. 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.).
5. Bonner, M. J., and D. P. Schmitt. 1985. Population dynamics of *Heterodera glycines* life stages on soybean. *Journal of Nematology* 17:153-158.
6. 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.
7. Hamblen, M. L., D. A. Slack, and R. D. Riggs. 1972. Temperature effects on penetration and reproduction of soybean-cyst nematode. *Phytopathology* 62:762 (Abstr.).
8. Heatherly, L. G., L. D. Young, J. M. Epps, and E. E. Hartwig. 1982. Effect of upper-profile soil water potential on numbers of cysts of *Heterodera glycines* on soybeans. *Crop Science* 22:833-835.
9. Hill, N. S. 1985. The influence of soil temperature and soybean phenology on dormancy induction of *Heterodera glycines*. M.S. thesis, North Carolina State University, Raleigh.
10. Jenkins, W. R. 1964. A rapid centrifugal-floatation technique for separating nematodes from soil. *Plant Disease Reporter* 48:692.
11. Mulrooney, R. P. 1986. Soybean disease loss estimate for Southern United States in 1984. *Plant Disease* 70:893.
12. Nardacci, J. F., and K. R. Barker. 1979. The influence of temperature on *Meloidogyne incognita* on soybean. *Journal of Nematology* 11:62-70.
13. Noe, J. P., and K. R. Barker. 1985. Relation of within-field spatial variation of plant-parasitic nematode population densities and edaphic factors. *Phytopathology* 75:247-252.
14. Noel, G. R., P. V. Bloor, R. F. Pozdol, and D. I. Edwards. 1980. Influence of *Heterodera glycines* on soybean yield components and observations on economic injury levels. *Journal of Nematology* 12:232-233 (Abstr.).
15. Oostenbrink, M. 1966. Major characteristics of the relation between nematodes and plants. *Mededelingen Landouwhogeschool te Wageningen* 66: 1-46.
16. Rodríguez-Kábana, R., and J. C. Williams. 1981. Soybean yield losses caused by *Meloidogyne arenaria* and *Heterodera glycines* in a field infested with the two parasites. *Nematropica* 11:93-104.
17. Ross, J. P. 1963. Seasonal variation of larval emergence from cysts of the soybean cyst nematode, *Heterodera glycines*. *Phytopathology* 53:608-609.
18. Santo, G. S., and W. J. Bolander. 1979. Interacting effects of soil temperature and type on reproduction and pathogenicity of *Heterodera schachtii* and *Meloidogyne hapla* on sugar-beets. *Journal of Nematology* 11:289-291.
19. Schmitt, D. P., and G. R. Noel. 1984. Nematode parasites of soybeans. Pp. 13-59 in W. R. Nickle, ed. *Plant and insect nematodes*. New York: Marcel Dekker.
20. Seinhorst, J. W. 1965. The relation between nematode density and damage to plants. *Nematologica* 11:137-154.
21. Windham, G. 1984. Factors influencing the damage potential and population dynamics of *Meloidogyne incognita* on soybean. Ph.D. dissertation, North Carolina State University, Raleigh.