

Changes in Vertical Distribution of *Pratylenchus scribneri* under Potato and Corn¹

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Abstract: The vertical distribution of *Pratylenchus scribneri* populations was monitored under irrigated corn and potato grown in loamy sand soil. Population estimates were based on the number of nematodes recovered from 100-cm³ soil samples and the roots contained therein. Reproduction was assessed by counting the number of second-stage juveniles. An index of population maturity was computed to evaluate the age structure of populations. At no time were nematodes distributed uniformly among five soil depths from 0 to 37.5 cm deep. During the summer (June–September), changes in the total number of *P. scribneri* and the number of second-stage juveniles recovered were not consistent among the depths sampled. Early (April–June) and late (September–November) in the season, changes in the abundance, reproduction, and maturity of populations were similar among depths. The timing and pattern of increases in numbers of nematodes suggests that variation in the abundance of *P. scribneri* in the soil profile beneath potato and corn was caused primarily by reproduction rather than the movement of nematodes.

Key words: corn, maize migration, movement, population dynamics, potato, *Pratylenchus scribneri*, root-lesion nematode, *Solanum tuberosum*, spatial distribution, *Zea mays*.

Nematodes are not uniformly distributed in the soil profile (1–3,5,10,14,19). The vertical distribution of nematodes is, in part, related to the rooting pattern of the host (15). However, the distribution of nematodes is not governed solely by root resource availability (2,4,5,7,17,20). Variation in the abundance of different nematode species with depth has been related to soil type (3), temperature (3), moisture (21), and biotic factors (1).

Changes in vertical distribution of a particular nematode species occur over the course of a growing season (5,20) or calendar year (1,5). The factors responsible for these changes are difficult to identify. Two explanations are generally offered: 1) Nematodes migrate vertically to seek favorable conditions. 2) Resource allocation or edaphic conditions differentially favor nematode reproduction at various depths. Data generated from studies using controlled inoculation of nematodes support

the first hypothesis (6,12,13,16). Few data from indigenous field populations are available to determine the relative importance of migration and reproduction in establishing the vertical distribution of *Pratylenchus* spp.

To determine when changes in the vertical distribution of root-lesion nematodes occur, we monitored the distribution of *Pratylenchus scribneri* Steiner beneath two hosts for 2 years, using a scale relevant to the growth and survival of populations. *Pratylenchus scribneri* was appropriate for these studies because 20–50% of the population is present in the soil during the growing season (11). Our objectives were to determine if the vertical distribution of nematodes within a population changed during and after the growing season and if so, to test the hypothesis that these changes resulted from the relocation of nematodes.

MATERIALS AND METHODS

Plot design: An indigenous *P. scribneri* population was maintained on potato and corn at the Hancock Research Station, Plainfield, Wisconsin, in irrigated Plainfield loamy sand soil (92% sand, 5% silt, 3% clay; < 1% organic matter). These crops were selected because of similarities in length of season and suitability for *P. scrib-*

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neri reproduction and because of differences in the extent of disturbance to root systems during harvesting.

In 1986 and 1987, eight rows of *Zea mays* L. cv. Wis 4763 and eight rows of *Solanum tuberosum* L. cv. Russet Burbank were planted in adjacent strips, 90 m long, with a 3-m-wide fallow alley between crops. Corn was planted 8 May 1986 and 30 April 1987, and potato was planted 24 April 1986 and 29 April 1987. Potato plots were hilled the first week in June. Plots were managed for pests and fertility according to current recommendations for commercial corn and potato production in Wisconsin. Corn was harvested on 22 October 1986 and 15 October 1987. Potato was harvested on 30 September 1986 and 2 October 1987. There was no fall tillage of either plot. Two weeks before planting, plots were cultivated with a disk and moldboard plow.

Field sampling and assay: The following sampling plan was devised from results of a preliminary study (1985) of nematode distribution 0–75 cm deep in the soil profile. Stakes were placed in strips of continuously planted corn and potato to demarcate 10 contiguous plots, 6 m long, with 3 m between plots. Samples were collected 30 April, 21 May, 18 June, 16 July, 13 August, 12 September, 30 September, 21 October, and 5 November 1986 and 29 April, 14 May, 27 May, 23 June, 29 July, 26 August, 29 September, 14 October, and 3 November 1987. Soil cores, 2.5 cm d, were collected with a sampling tube from the six inner rows to a depth of 37.5 cm. On four dates in 1986 it was possible to insert the sampling tube to a depth of only 30 cm in corn plots. The cores were divided into five 7.5-cm sections corresponding to position in the vertical soil profile and composited by depth. In 1986, six cores from each of 10 plots were collected in the row midway between two plants. In 1987, 10 cores from each of the first six plots were collected; the remaining four plots were planted but not sampled.

A 100-cm³ subsample of soil from each sample was processed by a centrifugal-floatation technique (8) using nested 250- μ m-

pore and 38- μ m-pore sieves. Roots retained on the 250- μ m-pore sieve during the soil washing procedure were incubated on Baermann funnels for 2 days at 24 C. After nematodes were collected, roots were dried at 60 C for 48–72 hours and weighed. Numbers of *P. scribneri* per life stage were counted with a dissecting microscope, and the counts were adjusted for extraction efficiency (11).

Data analysis: Data were analyzed by PROC GLM and PROC REG procedures of SAS (18). Counts of nematodes in 100 cm³ soil and the roots recovered from 100 cm³ soil were added to obtain a single estimate of nematode abundance. Each plot was considered to be one replicate for data analyses. The distribution of nematodes between root and soil habitats is presented elsewhere (11).

Numbers of nematodes were compared among crops, years, and sampling depths by PROC GLM with main effects of replicate (plot), crop, years, and depth and their crossed effects. Separate analyses were conducted for three dates common to both years of the study; the day of planting, the day of harvest, and 1 month after harvest. Only data from the six plots used in both years of the study were analyzed. Analyses of transformed ($\log_{10} [x + 1]$) and untransformed data yielded similar results.

Numbers of nematodes were compared among dates and depths for each crop in a single year by PROC GLM. In addition to main factor effects of rep, depth and time, a depth \times time interaction term was included in the model to determine if changes in the estimated parameters were different among depths. After analyzing the entire data set (nine sampling dates), three separate analyses were conducted, each using data from three dates; less than 2 months, from 2 to 5 months, and more than 5 months after planting. The purpose of multiple analyses was to detect seasonal trends in the distribution of nematodes and to examine separately data collected in midseason when nematodes are reproducing and populations fluctuating due to natality.

The developmental maturity of the populations residing in each sampling depth was also analyzed by PROC GLM. An index of population maturity was computed as follows. The percentage of the population represented by each stage was calculated by dividing the number in each stage by the total number of nematodes in all life stages and multiplied by 100. To reflect the relative maturity of each life stage, the percentage in each stage was divided by a weighting factor ranging from 1 for adults to 4 for second-stage juveniles. Eggs were not recovered so they were not included in analyses. The weighted percentages representing each life stage were then added together. According to our index, a population comprised of all adults was 100% mature, whereas a population comprised of all second-stage juveniles was 25% mature. The maturity index of populations comprised of all life stages ranged from 25 to 100%.

RESULTS

The vertical distribution of *P. scribneri* differed with crop and year. Analyses of total nematode counts at the time of planting, harvest, and 1 month after harvest revealed significant ($P \leq 0.02$) main factor effects of crop and depth on all dates, and of year at planting and 1 month after harvest. Year \times crop, year \times depth, and crop \times depth interactions were evident on the post harvest date only. The variability in nematode abundance for multiple crops and years is illustrated by the percentage of the nematode population recovered from the top 15 cm³ soil on three dates (Fig. 1).

The number of nematodes per 100 cm³ soil varied significantly ($P \leq 0.001$) among depths and sampling dates for both potato and corn in 1986 and 1987 (Fig. 2). A significant ($P \leq 0.01$) date \times depth interaction was detected for all whole data sets except potato during 1987. When data were partitioned for separate analyses of early-season (< 2 months), midseason (2–5 months) and late-season (> 5 months)

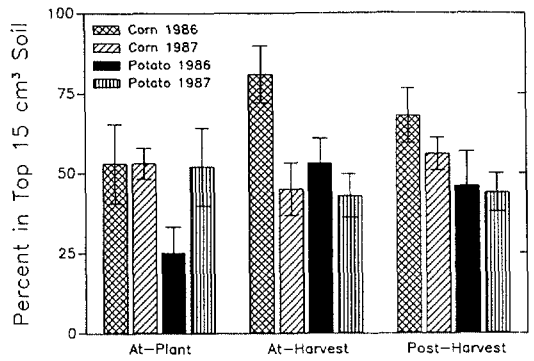


FIG. 1. Percentages of a population of *Pratylenchus scribneri* extracted from the upper 15 cm of soil in corn and potato plots on three dates in 1986 and 1987.

sampling dates, both main factor and interaction effects showed seasonal trends.

The total number of nematodes was different ($P \leq 0.01$) among depths for each of the separate analyses (Fig. 3). Early and late in the season, the numbers of nematodes decreased with depth under corn and increased with depth to 30 cm under potato. Significant ($P \leq 0.01$) main factor effects of sampling date were detected for the total number of nematodes recovered from April until June in potato plots in 1987 and in corn plots in 1986. From July until September, the total number of nematodes increased ($P \leq 0.0001$) on potato both years and on corn in 1987. Following harvest, the total number of nematodes differed ($P \leq 0.01$) among dates, declining with time on both crops in 1986, increasing on corn in 1987, and fluctuating on potato in 1987. There was no date \times depth interaction for the number of nematodes associated with either crop from April until June. From July until September, there was a date \times depth interaction ($P \leq 0.04$) for all except the 1987 potato data set; the greatest increase in nematodes occurred at depths of 7.5–22.5 cm for corn and 15.0–22.5 cm for potato. From September until November, a date \times depth interaction ($P \leq 0.007$) was detected only for the 1986 corn data; the total number of nematodes decreased in depths from 0 to 22.5 cm and were unchanged at depths greater than 22.5 cm.

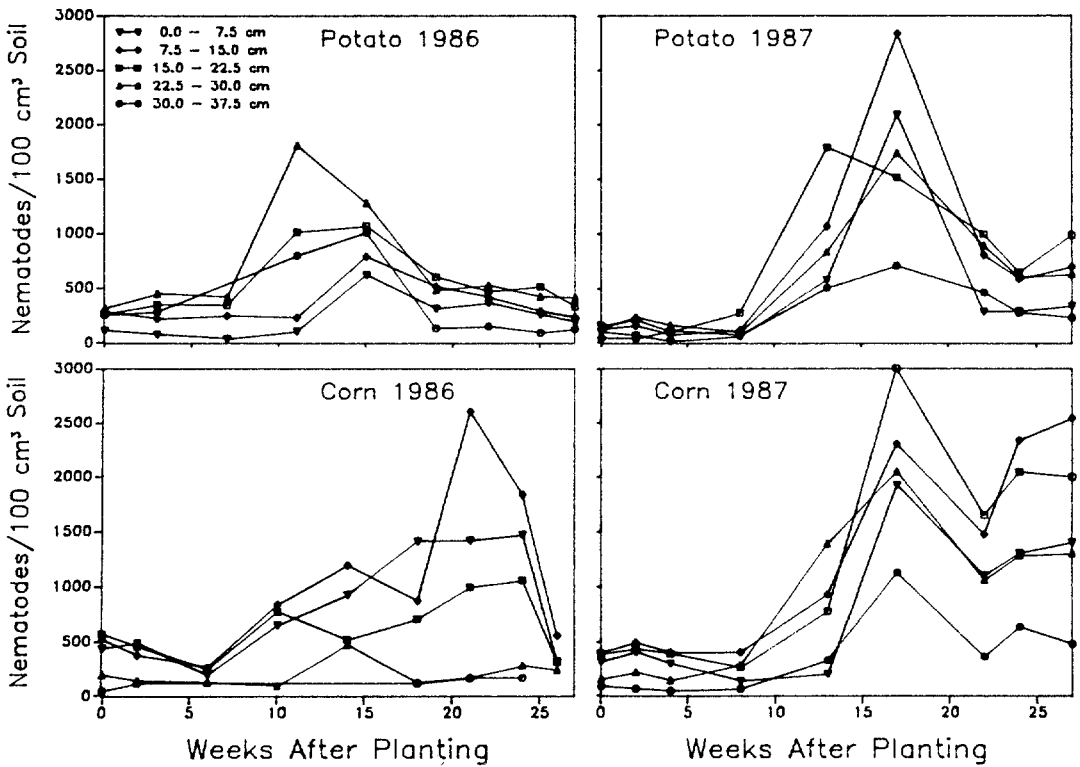


FIG. 2. Total numbers of *Pratylenchus scribneri* extracted from soil under corn and potato on nine dates in 1986 and 1987.

The number of second-stage juveniles (J2) also varied with depth and sampling date (Fig. 4). Differences in the number of J2 among depths were significant ($P \leq 0.01$) from April until June for all except the 1987 potato crop, from July until September for all except the 1987 corn crop, and from September until October for all crops. Increases in the number of J2 occurred from April until May ($P \leq 0.05$) on potato in 1986 and on corn in 1987, and from July until September ($P \leq 0.0001$) on all except the 1986 corn crop. Following harvest, the number of J2 was unchanged over time on potato, decreased ($P \leq 0.0001$) on corn in 1986, and increased ($P \leq 0.01$) on corn in 1987. Statistical interactions for the variables depth and date were the same as those reported for analyses of total number of nematodes.

The maturity of nematode populations varied less with depth and sampling date than did the total number of nematodes or J2 (Fig. 5). Early in the season, the maturity

index ($P \leq 0.0001$) differed among depths only in the corn plots in 1986. From June to September, there were differences ($P \leq 0.05$) in the maturity index among depths in both crops in 1987 but not in 1986. From September to November, populations associated with all crops except potato in 1986 were more mature at depths of 22.5–37.5 cm than at shallower depths ($P \leq 0.05$). Significant effects ($P \leq 0.001$) of sampling date on the maturity index of populations were detected for all except the 1987 potato crop early in the season, for all crops in midseason, and for only the 1987 corn crop late in the season. In general, the maturity of populations increased early and late in the season and decreased from July to September. Interaction of depth and sampling date for the maturity index was detected in only 1 of the 12 data sets (corn from April to June 1986).

There was a significant ($P \leq 0.05$) negative linear relationship between the dry weight of roots recovered per sample and

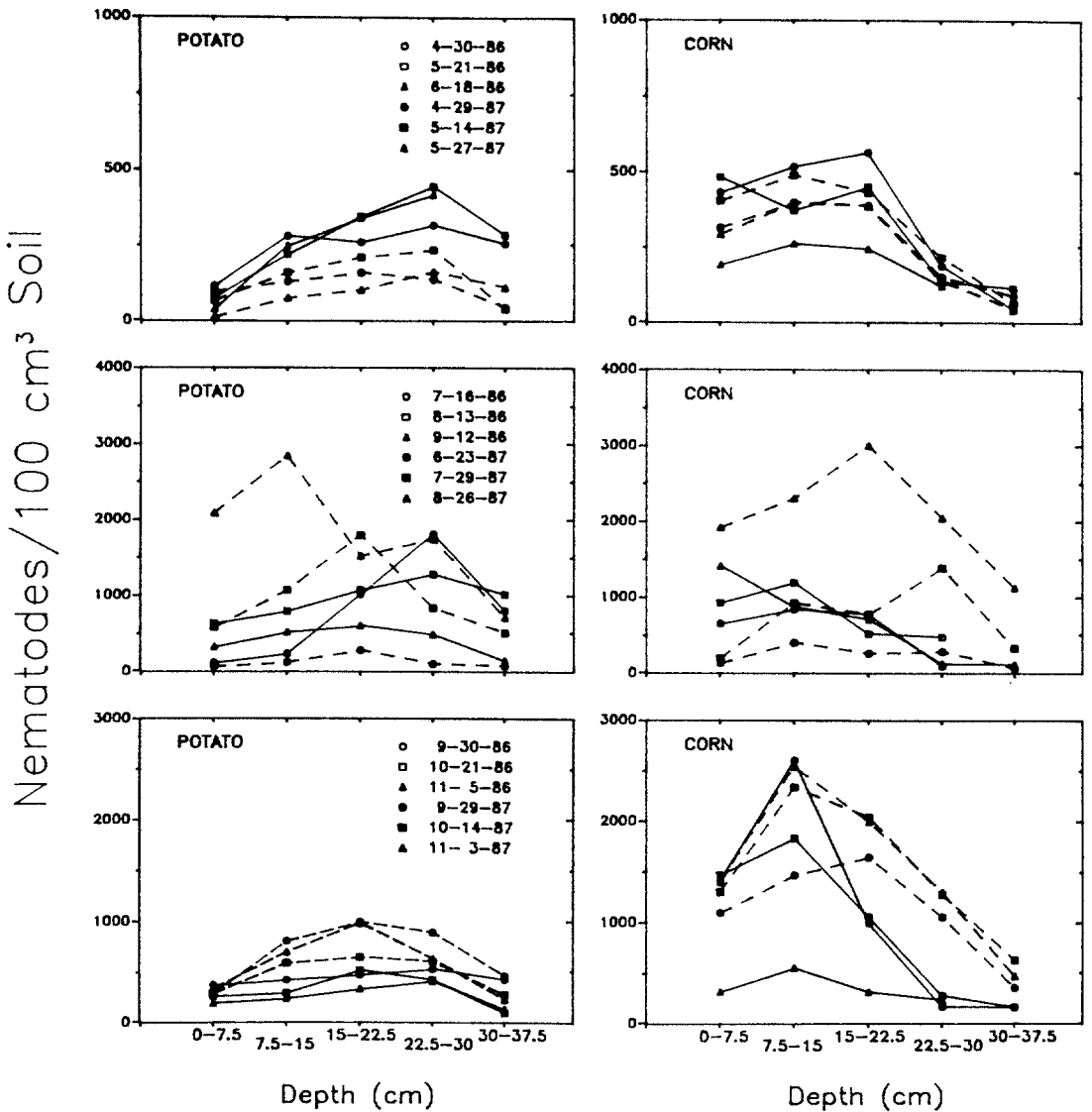


FIG. 3. Total numbers of *Pratylenchus scribneri* extracted from soil at five depths under corn and potato from samples collected early, midway, and late in the season.

depth for all crop-year combinations (Fig. 6). The distribution of nematodes and root biomass, as measured by dry root weight, was more similar among the sampling depths for corn than potato.

Weather conditions were different for 1986 and 1987. For the months of April through November, the total water (rainfall plus irrigation) received monthly by the plots was 8.0, 7.8, 24.2, 25.9, 15.8, 27.0, 4.9, and 2.9 cm in 1986 and 6.9, 11.7, 35.5, 23.0, 14.2, 7.4, 4.6, and 8.5 cm in 1987. Percentages of soil moisture by weight

were, respectively, 4-7%, 5-8%, 6-7%, 5-7%, and 5-6% for samples collected at depths of 0-7.5 cm, 7.5-15.0 cm, 15.0-22.5 cm, 22.5-30.0 cm, and 30-37.5 cm. The cumulative degree days (base 10 C) calculated from soil temperatures measured 12.5 cm beneath a sod cover on the research farm were 52, 393, 1,023, 1,773, 2,447, 2,836, 2,872, and 2,872 for the months April through November 1986 and 96, 534, 1,288, 2,208, 2,972, 3,460, 3,520, and 3,520 for the months April through November 1987.

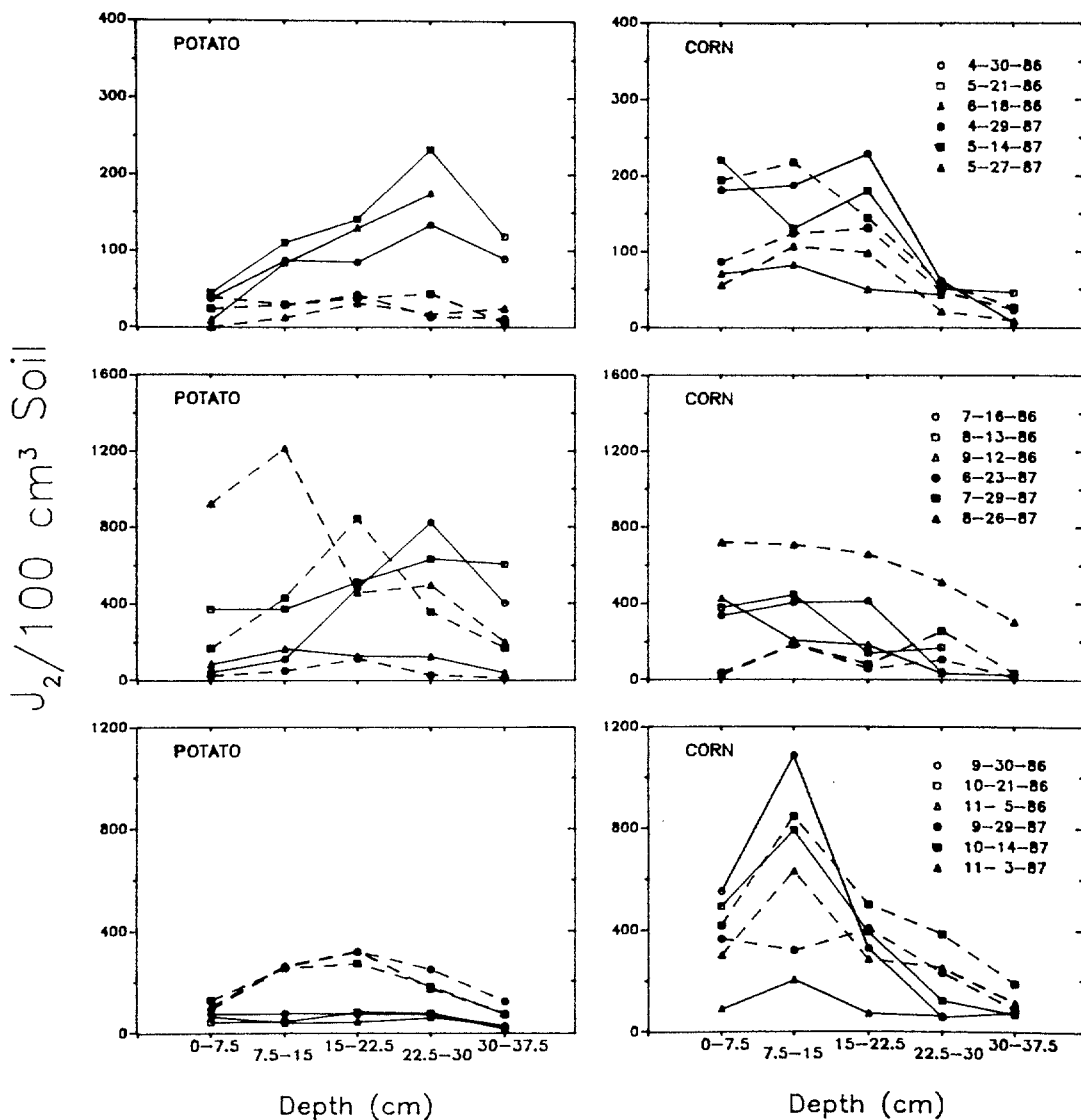


FIG. 4. Numbers of second-stage juveniles (J_2) of *Pratylenchus scribneri* extracted from soil at five depths under corn and potato from samples collected early, midway, and late in the season.

DISCUSSION

Pratylenchus scribneri associated with corn and potato were not distributed uniformly in the top 37.5 cm of the soil profile during a 2-year study, confirming findings of similar studies with other crop-nematode systems (1,2,5,20). The variation in nematode numbers among depths, evident early, midway, and late in the season, could influence estimates of nematode populations. Our study shows that even in irrigated crops, shallow sampling (less than 7.5

cm) recovers very few nematodes. Collecting soil samples to a depth of 15 cm, as is often recommended, improves population estimates but still accounts for only about half the nematodes associated with irrigated corn and potato, and even less for non-irrigated crops (19,20).

Our findings indicate that the vertical distribution of *P. scribneri* in our study system is not determined by a single factor. Both edaphic conditions and root distribution seem to play a role in setting the

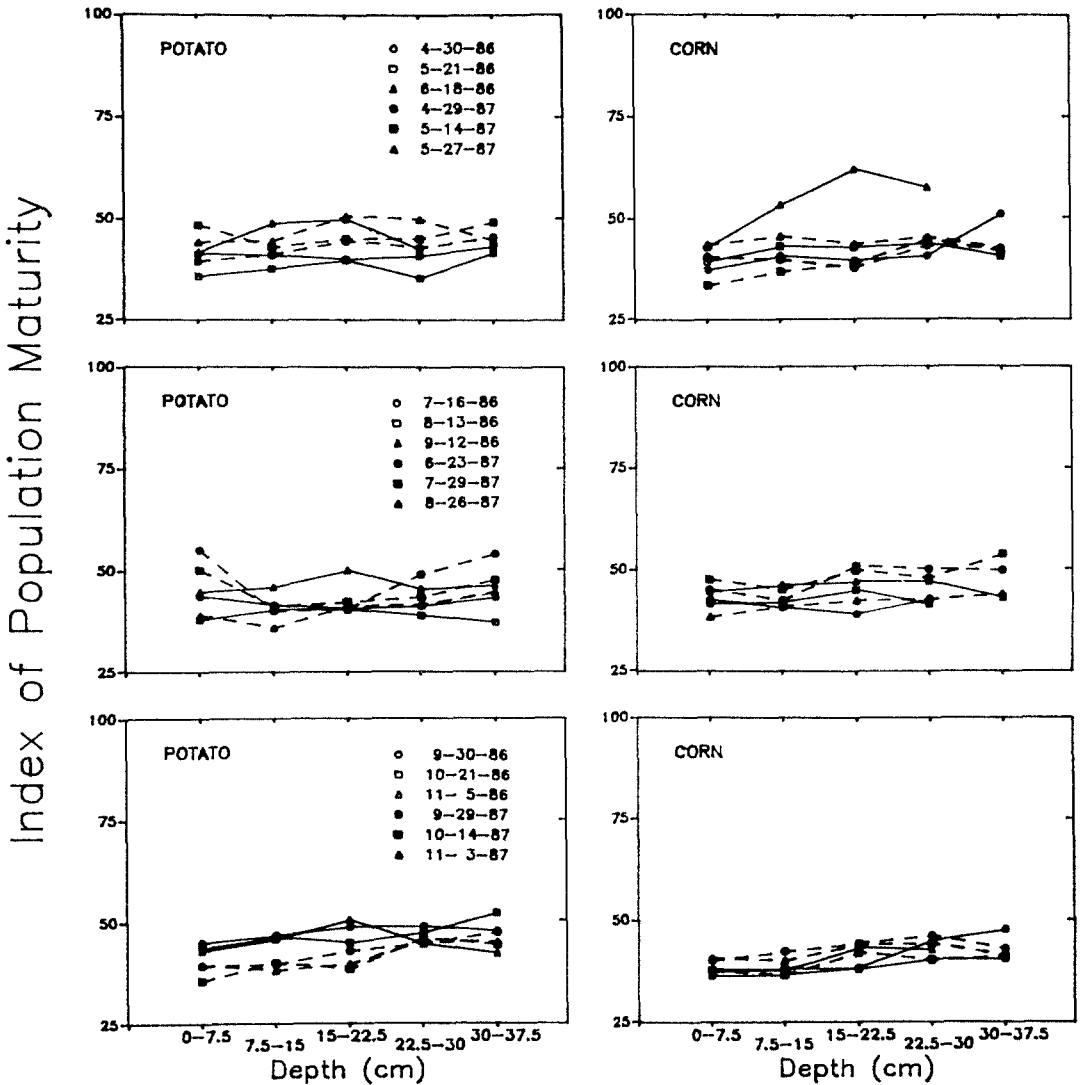


FIG. 5. Indices of the maturity of *Pratylenchus scribneri* populations extracted from soil at five depths beneath corn and potato from samples collected early, midway, and late in the season.

upper and lower boundaries, respectively, of suitable soil habitats for *P. scribneri*. Few nematodes occurred near the soil surface, despite an abundance of corn and potato roots, and few were found below 30 cm, despite temperature and moisture conditions conducive for nematode development and reproduction.

The mobility of nematodes in the soil and the role of migration in determining patterns of nematode distribution are important issues that are difficult to resolve. The movement of nematodes in a vertical

plane has been tested by capturing nematodes introduced into uninfested soil columns and noting their location relative to the point of inoculation. The upward movement of several species in a soil column has been elicited by a plant host (6) and percolation of water onto the soil surface (9,13). Downward movement is also documented (12). It is assumed, but unproven, that indigenous populations of nematodes in the soil are also mobile, moving freely up and down in the soil profile.

Three of our four data sets do not sup-

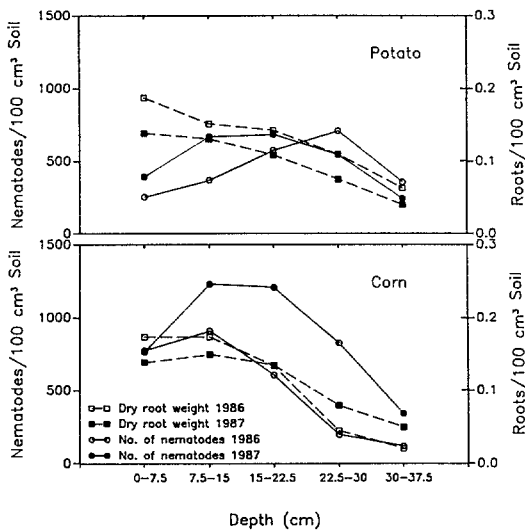


FIG. 6. Yearly averages of the number of *Pratylenchus scribneri* and dry weights of roots extracted from five soil depths under potato and corn in 1986 and 1987.

port the hypothesis that changes in the vertical distribution of *P. scribneri* populations are due to the upward or downward movement of nematodes. Rates of change in the abundance of *P. scribneri* populations were similar among soil depths in the spring and fall when nematodes would be most likely to migrate in response to changing edaphic and host-related factors. The differential increase in nematode populations recovered from different depths during summer was probably due to reproduction because 1) populations increased at all depths, 2) patterns of abundance of the youngest hatched stage (J2) were similar to those of the entire population occurring at each depth, and 3) changes in the age structure of the nematode population were consistent among depths, contrary to what would occur if fourth-stage juveniles and adults, the most likely of the four life stages to migrate downward (21), were moving from one depth to another.

Data from corn in 1986 are difficult to interpret; they neither support nor refute our hypothesis of vertical migration. In both early and late-season samples, numbers of nematodes declined 0–22.5 cm below the soil surface and remained un-

changed at depths of 22.5–37.5 cm. Because the decrease of nematodes in the upper soil layers was not concurrent with an increase in the lower layers, emigration seems an unlikely cause of the population decline. Heavy rainfall in September and a late harvest may be responsible, in part, for the anomalous results. Variation among the data sets illustrates the complexity of studying nematode populations in the field and the importance of validating hypotheses generated from controlled studies under a variety of conditions.

Our finding that the relative distribution of *P. scribneri* populations does not change with soil depth in the spring and fall is contrary to our observations of *Longidorus breviannulatus* in the same cropping system (10) and may reflect differences in behavior among nematode species. Although comparisons between studies are tenuous, at least one experiment comparing the vertical movement of different species is reported. Rossner (17) found that under controlled conditions, *Rotylenchus* and *Helicotylenchus* traveled only a short distance from the point of inoculation through a soil column, whereas *Trichodorus* and *Longidorus* moved rapidly and extensively. In our study system, *Pratylenchus* spp. can survive freezing (Forge, unpubl.) and colonize all portions of corn and potato root systems, whereas *L. breviannulatus* is sensitive to both freezing and desiccation (Mac-Guidwin, unpubl.) and feeds only on root tips. Although all nematodes move short distances to locate roots, vertical migration appears to be an important survival strategy only to those nematodes that are highly selective for feeding sites or incapable of surviving environmental extremes. Information about which species are likely to move through the soil profile and when movement occurs is valuable for estimating populations and their potential impact on plant health.

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