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Distribution of *Pratylenchus scribneri* between Root and Soil Habitats[1]

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Abstract: The abundance of *Pratylenchus scribneri* in soil and root habitats was compared in potato and corn plots during 1986–88. Nematodes were extracted from 100-cm³ soil samples and the roots contained within the samples. The percentage of the population recovered from soil, similar among years and crops, averaged ca. 50% at the beginning and end of the growing season and ca. 20% from early to late season. Proportionately more adults and fourth-stage juveniles than younger stages were located outside roots until harvest. In a related study, nematodes were isolated from the roots, root surfaces, and soil associated with roots of whole corn and potato plants sampled from the field. Nematode population estimates calculated from the whole plant samples were generally lower than those based on soil cores, but showed similar patterns of population growth. Nematode density per gram dry weight was highest in roots, intermediate on root surfaces, and lowest in soil. Estimates of the absolute abundance of nematodes in each of the three habitats were highest in roots or soil, depending on the sampling date, and lowest on root surfaces. This study demonstrates that *P. scribneri* inhabits soil environments even when host roots are present and illustrates the importance of considering all possible habitats when estimating the size of *Pratylenchus* spp. populations.

Key words: corn, population dynamics, potato, *Pratylenchus*, recovery efficiency, rhizosphere, sampling, *Solanum tuberosum*, *Zea mays*.

Estimation of nematode populations, an important component of nematology research, has received much attention (1,4). Population estimates are used to plan and evaluate nematode management strategies and to predict potential crop losses. For endoparasites such as *Pratylenchus* spp., population estimates are commonly made by pooling independent estimates of nematodes extracted from soil and root habitats. Depending on the time of year, population estimates are sometimes based on nematodes extracted from a single habitat, usually soil before planting and after harvest and roots during the growing season. The decision as to which habitat(s) to sample depends on available resources and objectives, but it should also be influenced by the life history of the target species (4).

The biology and ecology of *Pratylenchus* spp. have been reviewed (7,15). *Pratylenchus* spp. generally can be extracted from both soil and root habitats yearround (3,6,9). In very few studies, however, have nematode counts from soil and roots been expressed in the same units and compared. The objective of this research was to measure and compare the relative distribution of nematodes among root and soil habitats before, during, and after the growing season.

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). These crops were selected because of similarities in the duration of cropping season and suitability for *P. scribneri* reproduction and because of differences in the extent of disturbance to root systems during harvesting. The research site had been cropped to potato from 1972 to 1984 and to corn in 1971 and 1985.

In 1986 and 1987, eight rows of corn (*Zea mays* cv. Wis 4763) and potato (*Solanum tuberosum* cv. Russet Burbank) were planted in adjacent strips 90 m long and separated by a 3.6-m-wide alley. Corn was planted 8 May 1986 and 30 April 1987, and potato was planted 24 April 1986 and

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TABLE 1. Extraction efficiency of centrifugal-flotation (soil) and Baermann funnel (root) techniques for *Pratylenchus scribneri* life stages.

	Extraction efficiency (%)	
	Soil	Root
J2	8.56 (3.49)	9.52 (2.10)
J3	21.82 (6.55)	24.23 (4.00)
J4	46.51 (10.47)	36.16 (7.14)
Adult	67.32 (10.69)	35.90 (7.87)

Data are the means and standard deviations of 13 soil or 7 root samples.

29 April 1987. Potato plots were hilled the first week in June. Fertilizer and pesticides were applied according to recommended practices. 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.

Field sampling and assay: The strips of continuously planted corn and potato were divided, for sampling purposes, into plots 6 m long with 3-m-wide alleys between plots. Samples were collected on nine dates at 2–4-week intervals, including the days of planting and harvest. Soil cores, 2.5 cm d, were collected from the six inner rows to a depth of 37.5 cm with a sampling tube. 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 1987, 10 cores from each of six plots were collected.

A 100-cm^3 subsample of soil from each sample was processed by a centrifugal-flotation technique (5) using nested 250-μm-pore (60-mesh) and 38-μm-pore (400-mesh) sieves. Roots retained on the 250-μm-pore sieve during the soil washing procedure were placed on Baermann funnels for 2 days at 24 C, after which 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. The recovery efficiency of the soil washing procedure was determined by extracting nematodes from pasteurized Plainfield loamy sand soil seeded with known numbers of nematodes. Baermann funnels containing roots from field samples were sampled periodically for 4 weeks to determine the number of nematodes actually present in the roots. Numbers of nematodes obtained after 48 hours of incubation were divided by the estimated total population to calculate the extraction efficiency of this procedure. Extraction rates of the soil and root assays differed for the life stages (Table 1). Counts were adjusted for extraction efficiency and expressed as nematodes per 100 cm^3 soil, nematodes per roots extracted from 100 cm^3 soil, and nematodes per gram root dry weight.

Individual plant samples: On four dates in 1987, five potato and five corn plants were removed from planted areas between plots and assayed separately for *Pratylenchus* spp. Plants were dug with a trowel (2 weeks) or shovel (4–13 weeks) using a common protocol to insure standardization among plants and sampling dates. The total volume of soil and root system removed with each plant was ca. 0.5, 2, and 7 liters for plants 2, 4–5, or > 5 weeks old, respectively. Immediately after digging each plant, the intact root system was shaken vigorously against a shovel blade for 30 seconds to remove soil adhering to roots. Root systems were then immersed in a premeasured volume of water and shaken to remove soil and nematodes adhering to root surfaces (i.e., rhizoplane). After 30 seconds, roots were removed and the water was poured through a 0.71-mm-pore sieve into a container. Soil surrounding each plant was placed in a metal tub, mixed, and sieved using a 2.36-mm-pore screen. In the laboratory, 100-cm^3 subsamples of this soil were suspended in water and poured through nested 250-μm-pore and 38-μm-pore sieves. The contents of the 38-μm-pore sieve were washed onto a Baermann funnel. This procedure was repeated to assay the water used to rinse root systems in the field. Root systems were weighed, cut into ca. 1-cm-long pieces, subsampled (1 g fresh weight), and placed on Baermann funnels. After 2 days, nematodes from all funnels were collected and the roots were placed in a drying oven. The extraction

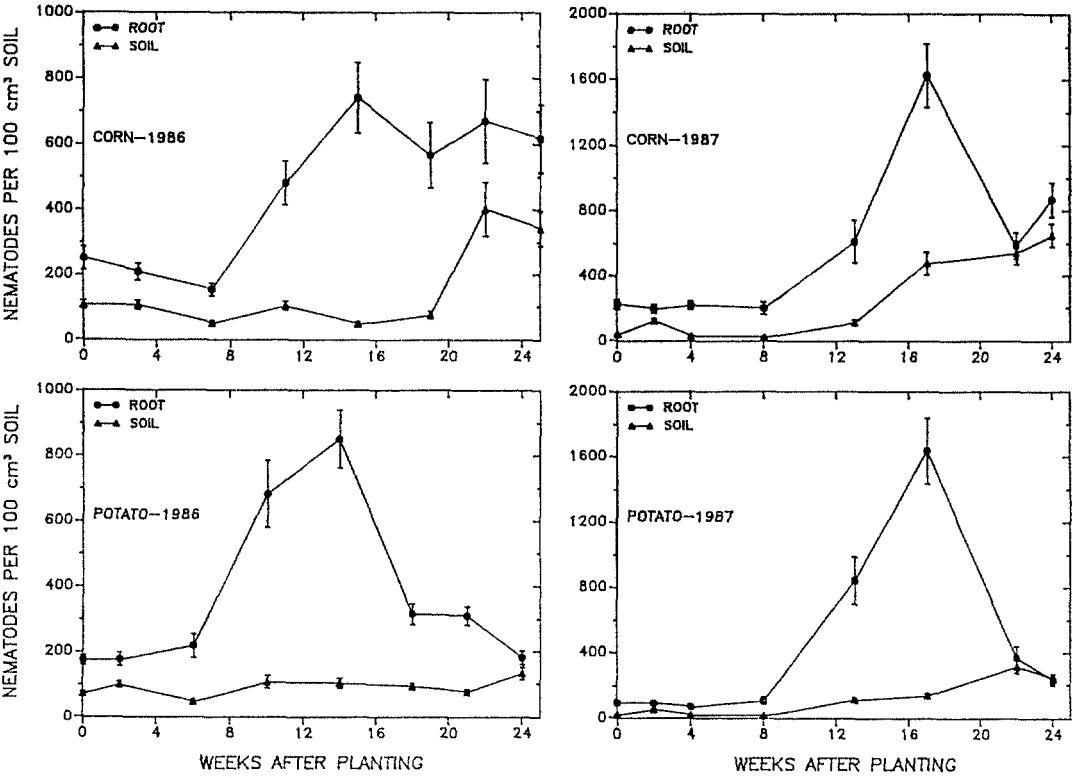

FIG. 1. Numbers of *Pratylenchus scribneri* extracted from 100 cm³ soil or from roots collected from 100 cm³ soil in corn and potato plots during 1986 and 1987.

efficiency of the root incubation procedure was the same as presented in Table 1. The efficiency of the soil incubation technique was 57% (SD = 17). Nematodes were counted as described previously and the data adjusted for extraction efficiency. To calculate the proportion of the nematode population occupying soil, root, or root surface habitats, nematode density per dry weight units were multiplied by scaling factors representing the total weight of each substrate associated with an individual plant. The study was repeated in 1988.

Data analyses: Means of adjusted counts of nematodes extracted from 100-cm³-soil samples and from roots contained therein were compared by analysis of variance (ANOVA) procedures. The proportion of the total nematode population or of each life stage occupying soil was calculated by dividing the soil counts by soil plus root counts. Because the proportion of nematodes in soil and roots did not vary with sampling depth, data for the five sampling depths were pooled to obtain a single estimate of nematode numbers 0–38 cm deep in the soil profile.

RESULTS

Field sampling: Numbers of *P. scribneri* changed ($P \leq 0.05$) in both soil and root environments over the growing season (Fig. 1). Nematode numbers in roots from 100 cm³ soil increased in all plots 10–12 weeks after planting and then decreased in September in all except the 1986 corn plots. Numbers in soil increased 12–16 weeks after planting in corn plots during 1986 and 1987 and in potato plots during 1987. More nematodes ($P \leq 0.05$) were recovered from roots than soil on all dates in the corn plots during 1986, on all but the last sampling date in potato plots during 1986, and on all but the last two sampling dates in both plots during 1987. Nematode populations were higher ($P \leq 0.05$) in corn than in potato plots at planting and harvest both years. Patterns of nematode population

TABLE 2. *Pratylenchus scribneri* from potato and corn roots extracted from 100-cm³ soil samples.

Weeks after planting†	Nematodes/g dry root weight			
	1986		1987	
	Potato	Corn	Potato	Corn
0			1,134	3,791**
2–4	1,128	2,832	1,357	2,225
5–7	1,124	1,505		
8–10		3,015	1,158	2,600**
11–13	5,130		13,063	8,714
14–16				
17–19			21,934	16,522
20–22	4,050	6,601	4,183	4,322
24–25	2,339	5,789	2,673	4,324*
$LSD_{0.05}$	1,376	1,843	3,715	2,563

Single asterisks ($P = 0.05$) and double asterisks ($P = 0.01$) indicate that the means for the two crops on each date in 1987 are significantly different according to analysis of variance.

† The 1986 corn data are for samples collected 3, 7, 11, 22, and 25 weeks after planting. The 1986 potato data are for samples collected 2, 6, 10, 21, and 24 weeks after planting. The 1987 data for both crops are for samples collected 0, 4, 8, 13, 17, 22, and 24 weeks after planting.

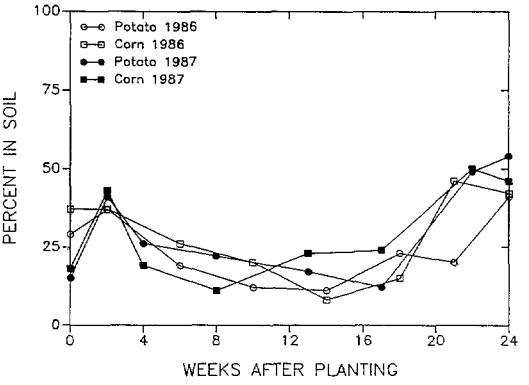

FIG. 2. Percentage of the total (root + soil) *Pratylenchus scribneri* population extracted from soil in potato and corn plots during 1986 and 1987.

growth based on nematode counts from roots in 100-cm³ soil samples were similar to those obtained from counts expressed as nematodes per gram dry root weight (Table 2).

Changes ($P \leq 0.05$) in the percentage of the total population extracted from soil over the growing season was similar among years and crops (Fig. 2). The proportion of the population inhabiting soil increased after crop growth commenced, decreased and remained at ca. 20% for about 3 months, and then increased to ca. 50% during late season.

Females comprised the predominant stage in the soil at planting, but by harvest all stages were similar in roots and soil (Table 3). The host crop had little effect on the distribution of life stages between root and soil habitats. In general, the proportion of nematodes within a life stage located outside roots was greater ($P \leq 0.05$) for fourth-stage juveniles and adults than for the younger stages until late season.

Individual plant samples: Nematode population estimates calculated from whole plant samples were generally lower than those based on soil cores, but showed similar patterns of population growth (Table 4). Nematode density per gram dry weight was highest in roots, intermediate on root

TABLE 3. *Pratylenchus scribneri* life stages associated with potato (P) or corn (C) extracted from soil during 1987.

Weeks after planting	Percentage extracted									
	J2		J3		J4		Adult		$LSD_{0.05}$	
	P	C	P	C	P	C	P	C	P	C
0	11	12	12	9	15	24	44	45	17	15
2	14	34*	48	34	38	50	51	44	19	NS
4	20	5	20	14	32	29	47	19*	NS	13
8	9	4	15	4	28	24	27	25	NS	11
13	7	4	18	19	30	33	31	31	11	13
17	5	22**	14	25*	22	24	18	28*	8	NS
22	49	57	49	42	44	47	55	50	NS	NS
24	52	61	52	41	50	40	53	44	NS	12

Single asterisks ($P = 0.05$) and double asterisks ($P = 0.01$) indicate that means within a life stage for the two crops on a single date differ significantly according to analysis of variance procedures.

TABLE 4. *Pratylenchus scribneri* extracted per gram dry weight from three habitats associated with potato and corn.

Weeks after planting	Potato			Corn		
	Bulk soil	Rhizosphere soil†	Root	Bulk soil	Rhizosphere soil†	Root
			1987			
2	0.06 ± 0.03	24 ± 17	286 ± 104	0.17 ± 0.04	63 ± 31	1,850 ± 404
4	0.10 ± 0.03	38 ± 9	685 ± 298	0.14 ± 0.03	143 ± 22	2,673 ± 839
8	0.22 ± 0.04	40 ± 11	737 ± 196	0.23 ± 0.06	128 ± 44	5,236 ± 1,552
13	0.10 ± 0.03	166 ± 39	8,725 ± 1,092	0.34 ± 0.10	181 ± 33	4,375 ± 1,186
$LSD_{0.05}$	0.10	67	1,784	NS	100	3,244
			1988			
2	0.91 ± 0.19	48 ± 19	633 ± 238	0.36 ± 0.18	3 ± 3	696 ± 282
5	0.55 ± 0.21	59 ± 19	961 ± 261	0.48 ± 0.16	10 ± 4	4,937 ± 1,613
7	0.92 ± 0.16	543 ± 111	12,491 ± 3,066	1.84 ± 1.01	88 ± 20	15,221 ± 3,640
13	2.73 ± 0.76	787 ± 117	19,522 ± 3,117	1.03 ± 0.19	139 ± 51	7,191 ± 2,148
$LSD_{0.05}$	1.23	246	6,576	NS	85	7,257

Data are means of five replications ± standard error.
† Soil tightly adhering to plant roots.

surfaces, and lowest in surrounding soil. Estimates of the proportion of the nematode population associated with each of three habitats were different for corn and potato (Table 5). There was less difference in the estimated number of nematodes occupying soil and root habitats than when considered on a weight/weight basis. The grand mean (pooled over crops and sampling dates) of the percentage of nematodes collected from root surfaces was 6%. If only nematodes located outside roots are considered, 10% (grand mean) of the nematodes were collected from root surfaces.

DISCUSSION

This study demonstrates that despite an endoparasitic lifestyle, *P. scribneri* inhabit soil environments even when host roots are available. The percentage of the total population recovered from soil was ca. 20% during the growing season and higher between growing seasons. Although the infectivity of nematodes inhabiting soil was not tested, the appearance and movement

TABLE 5. *Pratylenchus scribneri* extracted from three habitats in corn and potato plots.

Weeks after planting	Potato			Corn		
	Bulk soil	Rhizosphere soil†	Root	Bulk soil	Rhizosphere soil†	Root
			1987			
2	36 ± 14	34 ± 22	30 ± 11	38 ± 5	7 ± 5	55 ± 5
4	69 ± 10	15 ± 4	16 ± 6	56 ± 7	12 ± 3	32 ± 6
8	59 ± 10	2 ± 0.3	39 ± 9	21 ± 4	2 ± 0.4	76 ± 4
13	‡	‡	‡	15 ± 5	2 ± 0.2	83 ± 5
			1988			
2	95 ± 1	1 ± 0.4	4 ± 1	‡	‡	‡
5	66 ± 13	3 ± 0.3	31 ± 12	55 ± 9	2 ± 0.4	43 ± 8
7	38 ± 5	4 ± 0.8	58 ± 5	35 ± 9	1 ± 0.2	64 ± 9
13	30 ± 4	2 ± 0.2	68 ± 4	24 ± 8	1 ± 0.3	75 ± 9

Data are means and standard errors of five samples.
† Soil tightly adhering to plant roots.
‡ Not possible to estimate because of missing data for root weights.

of nematodes indicated that they were viable. Changes in the abundance and age structure of the portion of the population in soil also indicate that the nematodes were recent recruits, not merely remnants of the previous year's population.

These findings illustrate the importance of defining the sampling universe when estimating nematode populations. If estimates of *P. scribneri* abundance had been based on the number of nematodes extracted from 100 cm^3 soil and 1 g dry weight root, as is often done, the proportion of the population occupying soil would have seemed negligible. Scaling estimates to reflect the relative amount of each environment located in the sampling universe allows for direct comparison of habitats. Other studies using this approach (10,12) reported higher numbers of *Pratylenchus penetrans* located outside than inside roots.

Assaying roots collected during the soil washing procedure seems to be an easy and unbiased method for estimating the root substrate available for nematode colonization. An advantage to this method is that root fragments can be collected even when there is no plant present. Our finding that nematodes overwintering in dead roots represented at least 50% of the population the day crops were planted emphasized the importance of sampling roots between growing seasons.

The factors that prompt *Pratylenchus* spp., obligate plant parasites, to leave roots and move into soil were not readily apparent from this study. Conditions known to elicit the egress of *P. penetrans* from mint grown in the greenhouse—low nitrogen levels, high temperatures, and short photoperiods (11)—were not present. Numbers of nematodes in the soil generally increased late in the season when the rate of root senescence was high, but nematodes also exited roots in early and mid-season when the rate of root senescence was low. Despite large variation in the parasite load (nematodes per gram root) of individual plants and yearly crops, the proportion of the population living outside roots remained relatively constant, indicating that migration of nematodes from roots is not always in response to a depleted food source. Based on work with other parasite–host systems, there is probably a limit to the number of *Pratylenchus* spp. a root system can support (i.e., carrying capacity).

Theories to explain why an animal should leave its present location before resources are depleted (2,13) may also apply to *Pratylenchus* spp. These ecological models cannot be tested until the relationship between nematode density, host status, and nematode egress from roots is better quantified. Our current understanding of the life history of *Pratylenchus* spp. also needs to be augmented. According to our results, the older life stages are more likely to leave roots than are second-stage and third-stage juveniles until late in the season. The possibility that migration of *P. scribneri* is stage specific merits further attention.

Understanding the factors and conditions that cause *Pratylenchus* spp. to leave roots will require identification of nematode behavior outside of roots. Identifying the location of nematodes is an important step in forming hypotheses about their activities. In this study, some nematodes were closely associated with root surfaces (the actual density of nematodes in the rhizoplane was probably underestimated, since vigorous shaking to dislodge soil particles may have removed nematodes as well). Nematodes on root surfaces may be in the process of root penetration, a process that requires several hours (Wixted, unpubl.). Ectoparasitic feeding, as observed for other *Pratylenchus* spp. in the laboratory (8,14), may also occur in the field. Until there is a better understanding of the role and fate of *Pratylenchus* spp. on or close to root surfaces, population estimates of *Pratylenchus* spp. should be based on counts from both soil and root environments.

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