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Vertical Distribution of Plant-parasitic Nematodes in Sandy Soil under Soybean[1]

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Abstract: Vertical distribution of five plant-parasitic nematodes was examined in two north Florida soybean fields in 1987 and 1988. Soil samples were collected from 0–15 cm, 15–30 cm, and 30–45 cm deep at each site. Soil at the three depths consisted of approximately 96% sand. More than 50% of *Belonolaimus longicaudatus* population densities occurred in the upper 15-cm soil layer at planting, but the species became more evenly distributed through the other depths as the season progressed. *Criconemella sphaerocephala* was evenly distributed among the three depths in one field but was low (< 20% of the total density) in the upper 15 cm at a second site. Maximum population densities of *Pratylenchus brachyurus* were observed at 15–30 cm on most sampling dates. Vertical distributions of *Meloidogyne incognita* and *Paratrichodorus minor* were erratic and showed seasonal variation. A diagnostic sample from the upper 0–15 cm of these soybean fields revealed only a minority of the populations of most of the phytoparasitic species present.

Key words: Belonolaimus longicaudatus, Criconemella sphaerocephala, Glycine max, lesion nematode, *Meloidogyne incognita,* nematode community, *Paratrichodorus minor, Pratylenchus brachyurus,* ring nematode, root-knot nematode, sampling, soybean, sting nematode, stubby-root nematode, vertical distribution.

Nematode damage to soybean (*Glycine max* (L.) Merr.) is documented (31,32), and the development of relationships between soybean yield and nematode population density is receiving increased attention (1,16,19,21,22,28,30). Predictive models depend on reliable sampling and diagnostic methods (5,18,26), especially of the top 15–20 cm of soil, where the majority of plant-parasitic nematodes often may occur (5,18,23,26). Maximum densities at lower depths are reported for some species (4,26), and vertical distribution patterns may be further complicated by the occurrence of vertical migration during the season (4,23–26,29).

A previous study (8) with soybean (*Glycine max* (L.) Merr.) raises some concern about the vertical distribution of the members of the plant-parasitic nematode community beneath this crop. Greatest densities of *Belonolaimus longicaudatus* Rau were found within the top 30 cm of soil profile, but *Paratrichodorus christiei* (Allen) Siddiqi (= *P. minor* (Colbran) Siddiqi) (14) and especially *Pratylenchus brachyurus* (Godfrey) Filipjev & Stekhoven were often found deeper (8). Deep sampling for plant-parasitic nematodes is not a standard diagnostic procedure in Florida, where a sampling depth of 15–20 cm is usually recommended (10,17). Sampling deeper than 20 cm is costly and may be unnecessary if most of the nematode population is concentrated in the upper layer of soil. The purpose of this study was to compare nematode distribution in the top 15 cm of soil with that in the 15–30-cm and 30–45-cm layers, under cultivation of soybean on sandy soil in north Florida.

MATERIALS AND METHODS

Experiments were conducted in two adjacent 0.5-ha fields with similar cropping histories at the University of Florida Agronomy Farm in northwest Alachua County. In May 1987, eight 6-m^2, widely separated plots were established in each field. Plots were planted to 'Davis' soybean on 2 June and maintained until late October using standard agronomic practices for the region (3).

In each field, soil samples were collected from the 0–15-cm, 15–30-cm, and 30–45-cm soil layers in each of the eight plots on 4 June, 9 July, 6 August, 10 September,

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and 7 October 1987. Each sample consisted of five cores collected in a stratified random pattern with a 10-cm-d bucket auger (2). The soil from the five cores was mixed for 15 seconds in a 19-liter pail rotated by an electric motor, and a 500-cm^3 sample was removed. On each sampling date, a total of 48 samples were collected (2 fields × 3 depths × 8 plots = 48). The experiment was repeated in 1988 using similar procedures. The planting date was 10 May; samples were collected on 9 May, 2 June, 7 July, 1 August, 13 September, and 27 October 1988.

In the laboratory, nematodes were extracted from a 100-cm^3 subsample from each sample using a modified sieving-centrifugation technique (15) with a 38-μm sieve. The extraction efficiency of this method ranges from 49 to 81%, depending on nematode species and soil type (20). All plant-parasitic nematodes from the subsample were counted directly, avoiding dilutions which could result in counting error (18). Additional soil (ca. 50 g) was removed from each sample for gravimetric determination of soil moisture, expressed on a dry weight basis (7).

Soil type in the study fields was an Arredondo fine sand. Soil samples collected in June 1987 were analyzed for texture using the hydrometer method (6). For each plot on each sampling date, the abundance percentage of each nematode species present at each depth was calculated by

$$\begin{array}{c}\text{Percent of}\\ \text{species } x\\ \text{at depth } i\end{array} = \frac{\begin{array}{c}\text{Density of}\\ \text{species } x\\ \text{at depth } i\end{array}}{\begin{array}{c}\text{Total density}\\ \text{of species } x\\ \text{at three depths}\end{array}} \times 100\%$$

and reported as in other nematological studies (13,33). The percentage of abundance by depth was subjected to analysis of variance to determine if significant ($P \leq 0.05$) differences occurred with depth. Where present, differences were further examined using the Waller-Duncan *k*-ratio test (12).

TABLE 1. Soil texture by depth for 16 experimental plots in Alachua County, Florida, planted to soybean in June 1987.

Depth (cm)	Sand (%)	Silt (%)	Clay (%)
0–15	96.1 (95.2–97.0)	1.5 (0.4–2.4)	2.4 (1.5–3.5)
15–30	96.0 (92.8–97.0)	1.4 (0.3–3.0)	2.6 (1.0–7.0)
30–45	95.5 (90.8–97.0)	1.6 (1.0–2.8)	2.9 (1.5–8.0)

Data are means and ranges (in parentheses) over 16 plots (8 each in two fields).

RESULTS AND DISCUSSION

The soil texture was very similar at all depths and none of the plots in the two fields had a sand content lower then 90.8% or higher than 97.0% (Table 1). Soil moisture was under 9% at all depths, and some differences ($P \leq 0.05$) in moisture with depth were apparent, especially in the south field (Table 2).

Common plant-parasitic nematodes occurring in the fields included *B. longicaudatus*, *P. brachyurus*, *P. minor*, *Meloidogyne incognita* (Kofoid & White) Chitwood, and *Criconemella sphaerocephala* (Taylor) Luc & Raski. Individuals of a *Xiphinema* species

TABLE 2. Soil moisture at three depths in two soybean fields in Alachua County, Florida, during 1987 and 1988.

	Soil moisture (%)†					
	North field			South field		
Sampling date	0–15 cm	15–30 cm	30–45 cm	0–15 cm	15–30 cm	30–45 cm
			1987			
4 June	4.4	5.1	5.0	3.2 b	4.3 a	4.0 a
9 July	3.3 b	4.1 a	4.1 a	4.1 b	4.6 ab	4.9 a
6 Aug.	4.6	4.7‡	4.6	5.2	4.9	5.1
10 Sept.	3.5	4.1	4.2	4.2	5.1	5.0
7 Oct.	4.8	5.6	5.9	5.0 b	5.9 a	6.0 a
			1988			
9 May	5.0	4.5	4.2	5.2 a	4.2 b	3.8 b
2 June	5.7	5.0	5.1	4.6	4.9	5.3
7 July	5.5	4.8	4.5	3.3 b	3.3 b	4.0 a
1 Aug.	7.6	7.2	8.1	8.3 ab	8.8 a	8.0 b
13 Sept.	5.8	6.4	6.5	8.7	6.5	6.6

† Percent of soil moisture is computed on a dry weight basis. Data shown are means of eight replications. Numbers in a row for the same field followed by the same letter are not different ($P \leq 0.05$), according to the Waller-Duncan *k*-ratio test. No letters in a row indicates no significant differences.

‡ Mean of seven replications.

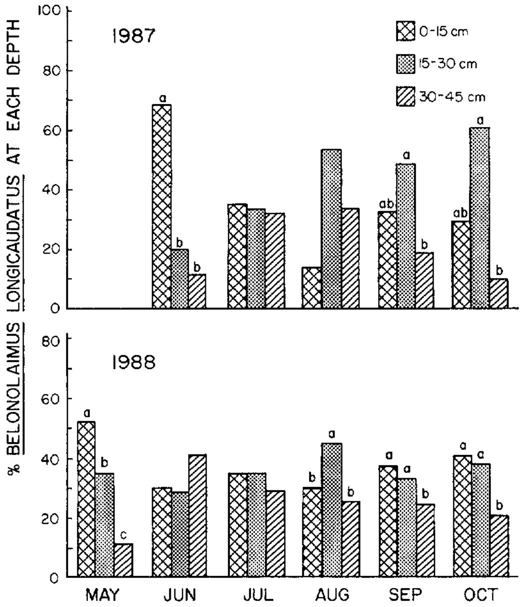

FIG. 1. Distribution of *Belonolaimus longicaudatus* population density by soil depth in the south field in 1987 and 1988. Within each month, bars with a letter in common are not different ($P \leq 0.05$) according to the Waller-Duncan *k*-ratio test. No letters indicate no significant differences in that month.

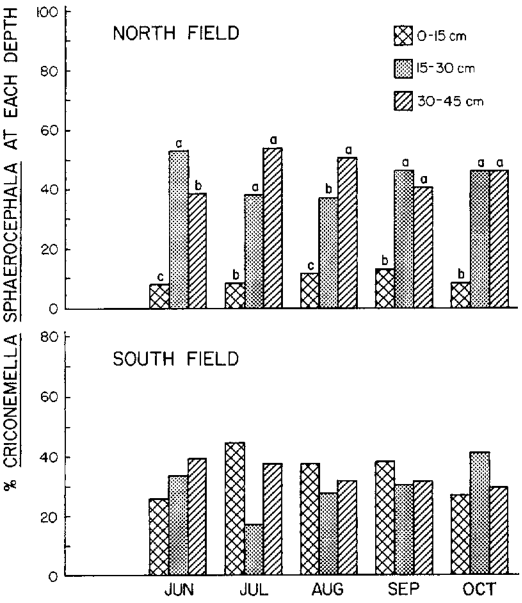

FIG. 2. Distribution of *Criconemella sphaerocephala* population density by soil depth in two fields in 1987. Within each month, bars with a letter in common are not different ($P \leq 0.05$) according to the Waller-Duncan *k*-ratio test. No letters indicate no significant differences in that month.

similar to *X. floridae* Lamberti & Bleve-Zacheo were occasionally found, but numbers were so low that a meaningful interpretation of their depth distribution was not attempted.

Numbers of *B. longicaudatus* were $<0.5/100$ cm^3 soil at any depth in the north field (data not shown). At the initial samplings in June 1987 and May 1988 in the south field, more than 50% of the population density each year was found in the upper 15 cm of soil, a higher ($P \leq 0.05$) proportion than in either of the lower depths examined (Fig. 1). As the season progressed, the population densities became more evenly distributed through the soil profile. Although there was a trend toward a maximum proportion of the population at 15–30 cm deep, particularly in 1987, proportions in the upper two layers were similar ($P \leq 0.05$), except in August 1988, when soil moisture was highest in the 15–30 cm layer (Table 2). Brodie (8) found a similar pattern of highest density of *B. longicaudatus* in the upper 0–30 cm of a somewhat less sandy (87–88% at 0–30 cm) soil in Georgia. His sample, taken in March before planting soybean in April, also showed a concentration of *B. longicaudatus* in the upper 15-cm soil layer, similar to our results with the initial samples.

Distribution of *C. sphaerocephala* was similar in 1987 (Fig. 2) and 1988 (Fig. 3), but it was different in each field. In the north field, the greatest proportion of the population usually occurred at the 30–45-cm depth. On all sampling dates except August 1988, the percentage of *C. sphaerocephala* at 30–45 cm was greater ($P \leq 0.05$) than that at 0–15 cm. On many sampling dates, only about 10% of *C. sphaerocephala* were present in the upper 15 cm of soil. In the south field, distribution of density among the three soil layers was similar, and few differences ($P \leq 0.05$) were apparent (Figs. 2, 3). An important difference between the two fields was the occurrence of high *B. longicaudatus* populations in the

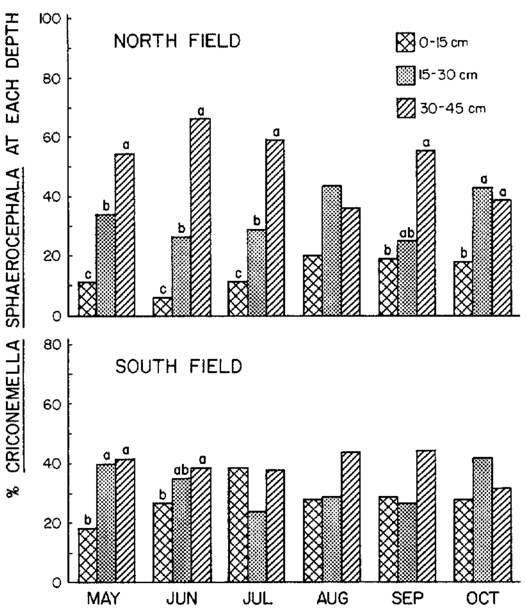

FIG. 3. Distribution of *Criconemella sphaerocephala* population density by soil depth in two fields in 1988. Within each month, bars with a letter in common are not different ($P \leq 0.05$) according to the Waller-Duncan *k*-ratio test. No letters indicate no significant differences in that month.

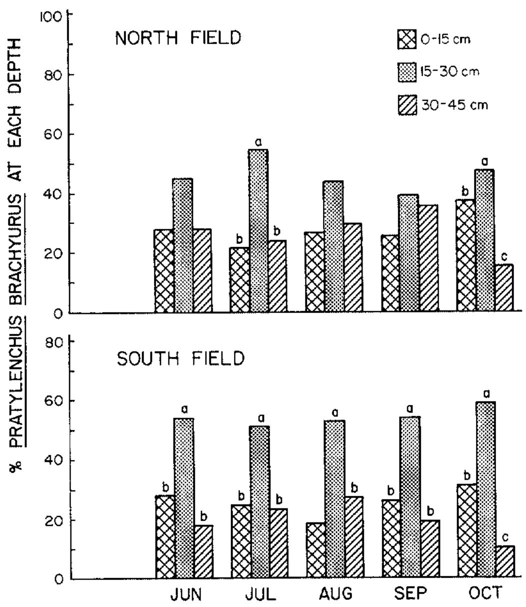

FIG. 4. Distribution of *Pratylenchus brachyurus* population density by soil depth in two fields in 1987. Within each month, bars with a letter in common are not different ($P \leq 0.05$) according to the Waller-Duncan *k*-ratio test. No letters indicate no significant differences in that month.

south field. Stunting of young soybean plants and stand reduction was attributed to *B. longicaudatus* in an adjacent site (19). It is possible that *C. sphaerocephala,* which showed a preference for deeper soil layers in the north field, was forced to feed in the upper layers in the south field because the stunted plants in that field had fewer roots and feeding sites at the lower depths. In sandy soil, the majority of soybean roots occurs in the upper 15 cm (27); a proportional decrease in plant size and root distribution throughout the profile could leave relatively few roots available for feeding below 30 cm.

High soil densities of *P. brachyurus* occurred in both fields, and on many occasions the highest percentage was found at the 15–30-cm depth (Figs. 4, 5). On every sampling date in 1987 in the south field, the 15–30-cm depth contained a higher ($P \leq 0.05$) proportion of the *P. brachyurus* density than either of the other depths examined (Fig. 4). In 1987, more than 50% of the *P. brachyurus* density was found at 15–30 cm in that field. Population distribution in the north field in 1987 was similar to that in the south field except that differences were significant ($P \leq 0.05$) only in July and October. In 1988, in both fields, a higher ($P \leq 0.05$) proportion of the population occurred in the 15–30-cm depth on two of the six sampling dates. Brodie (8) reported that maximum levels of the soil population of *P. brachyurus* occurred even deeper, at a 45–75-cm soil depth.

Second-stage juveniles of *M. incognita* were much more common in soil in the north field than in the south field. Distribution patterns with depth for *M. incognita* in the north field (Fig. 6) were erratic, and usually no differences ($P \leq 0.05$) among soil depths were evident. In May 1988, more than 70% of *M. incognita* juveniles was at 15–30 cm, whereas at the end of that season 80% was in the upper 15 cm of soil. The proportion of *M. incognita* at the 0–15-cm depth varied from 12 to 80% over the two seasons. Such wide fluctuations with depth would cause much diffi-

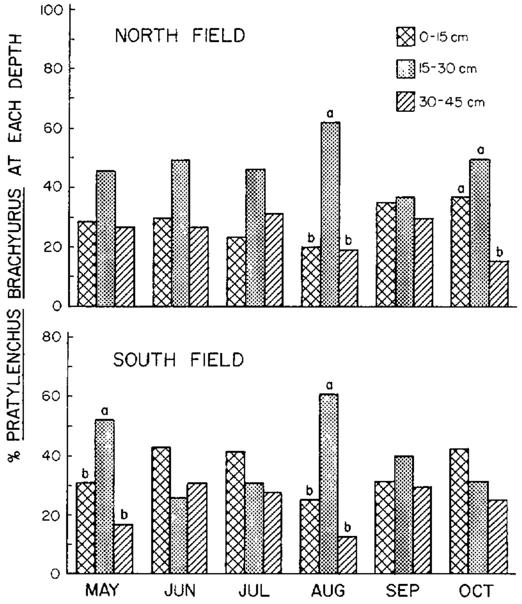

FIG. 5. Distribution of *Pratylenchus brachyurus* population density by soil depth in two fields in 1988. Within each month, bars with a letter in common are not different ($P \leq 0.05$) according to the Waller-Duncan *k*-ratio test. No letters indicate no significant differences in that month.

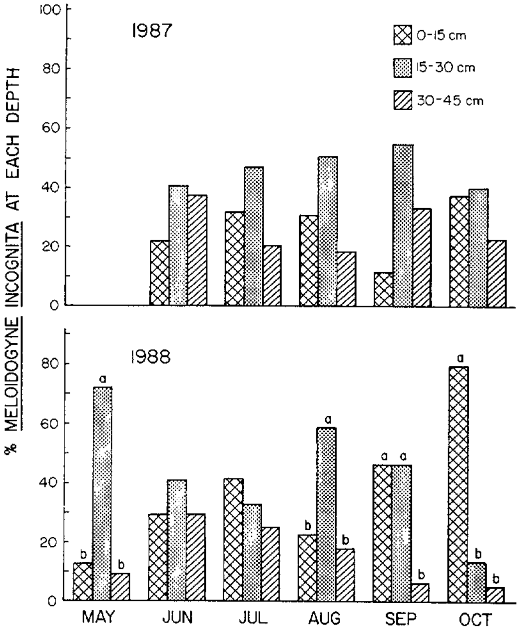

FIG. 6. Distribution of *Meloidogyne incognita* juvenile population density by soil depth in the north field in 1987 and 1988. Within each month, bars with a letter in common are not different ($P \leq 0.05$) according to the Waller-Duncan *k*-ratio test. No letters indicate no significant differences in that month.

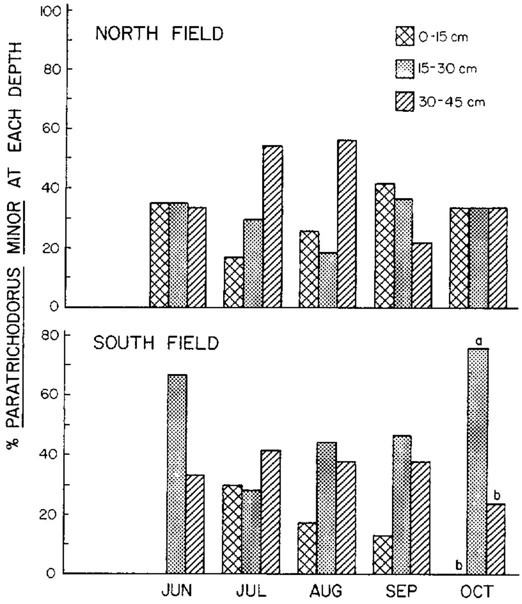

FIG. 7. Distribution of *Paratrichodorus minor* population density by soil depth in two fields in 1987. Within each month, bars with a letter in common are not different ($P \leq 0.05$) according to the Waller-Duncan *k*-ratio test. No letters indicate no significant differences in that month.

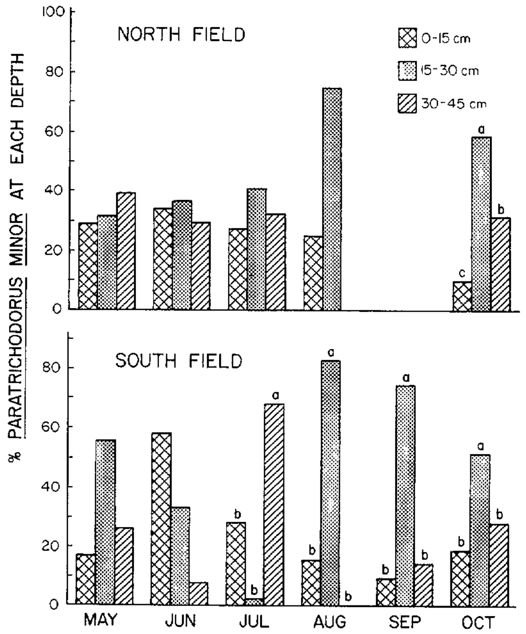

FIG. 8. Distribution of *Paratrichodorus minor* population density by soil depth in two fields in 1988. Within each month, bars with a letter in common are not different ($P \leq 0.05$) according to the Waller-Duncan *k*-ratio test. No letters indicate no significant differences in that month.

culty in assaying population densities with a sample taken only 15 cm deep. Vertical migration in *Meloidogyne* spp. occurs and can be rapid (9,24), but it must be understood in detail if reliable estimates of total population densities are to be obtained.

The general lack of differences ($P \leq 0.05$) in *P. minor* densities with depth in 1987 (Fig. 7) could be due in part to low numbers, averaging less than 10/100 cm^3 soil at any depth throughout the year. During 1987, this nematode was absent from the 0–15-cm depth in June and October in the south field. In 1988 (Fig. 8), *P. minor* was below detectable levels at all depths in September in the north field. Fewer than 10/100 cm^3 soil persisted through 1988 until October, when average densities of >20/100 cm^3 were observed at the 15–30-cm depth. The proportion of *P. minor* at this depth in October 1988 was greater ($P \leq 0.05$) than that at 0–15 or 30–45 cm in both fields (Fig. 8). On all dates when differences ($P \leq 0.05$) in the percentage of *P. minor* with depth occurred (Figs. 7, 8), the percentage present at 0–15 cm was always lower than that at one or more of the other depths. On three of four end-of-season sampling dates, densities were concentrated at the 15–30-cm depth.

Most plant-parasitic nematode population densities on soybean were concentrated at soil depths below 15 cm. Only in a few cases (initial *B. longicaudatus* densities, Fig. 1; final *M. incognita* density in one field, Fig. 6; *P. minor* density in June 1988 in one field, Fig. 8) could more than 50% of a nematode population be estimated by a sample 0–15 cm deep. On a number of occasions, recovery of *C. sphaerocephala* at this depth was as low as 10%. Diagnostic samples collected to a recommended (10,17) depth of 15–20 cm in soybean fields would in most cases contain only a minority of parasitic nematodes. Fortunately, appropriate damage functions and recommendations usually are based on a similar sampling depth, so a similar but consistent error may be made in both diagnosis and recommendation. The situation would be far worse if diagnostic sample and damage function were obtained using different sampling depths, since different nematode numbers would apply in each case. The depth sampled is only one aspect of catch efficiency (11). Just as extraction efficiency (18) or "separation efficiency" (11) of a laboratory process can be used to estimate the total number of nematodes originally present in an extracted soil sample, the total nematode population to a given depth (e.g., 45 cm) also could be estimated from a surface sample by application of an appropriate "depth efficiency." For example, sampling to a depth of 30 cm at planting (May–June, Fig. 1) would estimate the *B. longicaudatus* density to 45 cm at an efficiency of about 88%. Detailed data sets would be required to derive appropriate depth efficiency figures for a variety of nematodes and soil profiles. In addition, whereas some nematodes, such as *C. sphaerocephala* or *P. brachyurus*, showed some degree of consistency in their vertical distribution patterns, others, such as *M. incognita* or *P. minor*, showed such wide seasonal fluctuations in their vertical distribution that seasonally corrected efficiency data would be required, almost on a month-to-month basis.

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