Temporal Changes in the Vertical Distribution of *Pratylenchus penetrans* under Raspberry

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Abstract: Population densities of *Pratylenchus penetrans* and the biomass of fine roots of raspberry at depths of 0–5, 5–10, 10–20, and 20–30 cm were determined every 2 weeks for 2 years. The vertical distribution of *P. penetrans* varied from season to season, but the seasonal changes were not similar for the 2 years. In most seasons, the greatest population density was in the 5 to 10-cm-depth interval. Population densities of *P. penetrans* were not consistently correlated with the vertical distribution of raspberry roots in any season.

Key words: diagnosis, nematode, population dynamics, *Pratylenchus penetrans*, raspberry, root-lesion nematode, sampling, vertical distribution.

Accurately assessing the potential for plant-parasitic nematodes to cause crop damage depends on accurate population estimates, which are based on knowledge of the horizontal and vertical distribution of the population. The vertical distribution of plant-parasitic nematodes changes through time (Bird and Ramsdell, 1985; Boag, 1981; Ferris and McKenry, 1974; MacGuidwin and Stanger, 1991) as the result of differential reproduction or mortality at particular depths (MacGuidwin and Stanger, 1991), or from directional movement induced by changes in environmental conditions or the presence of host roots (Hesling, 1967; Limber, 1980; Pinkerton et al., 1987). Knowledge of how the vertical distribution of a nematode population changes through time is important for determining if samples taken to a fixed depth are seasonally biased; apparent changes in population density could result from changes in vertical distribution.

Pratylenchus penetrans (Cobb) Filipjev and Schuurmans Stekhoven is an economically important pathogen of raspberry (*Rubus idaeus* L.) and many other perennial crops grown in temperate climates. The vertical distribution of *Pratylenchus* spp. at one time of the year, or averaged over several sampling dates, has been reported for annual hosts (Brodie, 1976; Sohlenius and Sandor, 1987) and perennial hosts (Ogiga and Estey, 1973; Sohlenius and Sandor, 1987). MacGuidwin and Stanger (1991) described temporal changes in the vertical distribution of *P. scribneri* Steiner that occurred within the growing season of corn and potato, but there are no published data on temporal changes in the vertical distribution of *Pratylenchus* spp. under any perennial crop.

In a previous study (Vrain et al., 1997), changes were described in the density, age structure, and root-versus-soil distribution of a population of *P. penetrans* parasitizing raspberry over a 2-year period. The data presented here describe temporal changes in the vertical distribution of the same population and correlations between nematode distribution and root distribution.

MATERIALS AND METHODS

The study site and sampling procedures were described previously (Vrain et al., 1997). We monitored, at four depth intervals, the population dynamics of *P. penetrans* parasitizing 8-year-old raspberry cv. Williamette in the lower Fraser Valley of British Columbia. Soil and root samples were taken every 2 weeks for 2 years from five plots located in the middle of the field. Each plot was 3.2 m long and contained 18 raspberry plants. At each sample date, 10 cores of soil, 2 cm in diam., were removed from each plot to a depth of 35 cm, at a distance of 20 to 30 cm from the center of the row. Each soil core was partitioned into four depths: 0–5,

5–10, 10–20, and 20–30 cm from the surface. For each plot, the 10 subsamples representing each depth were pooled into a single sample. All fragments of raspberry roots were hand-picked from each sample, rinsed, blotted dry, weighed, and fragments of coarse roots (dia. >0.5 cm) removed. Nematodes were extracted from fine feeder roots in a mist chamber for 7 days, and from 50 ml soil without roots in Baermann pans for 7 days. Nematode counts were adjusted according to extraction efficiencies determined previously for each extraction procedure (Vrain et al., 1997). For each sample, the number of *P. penetrans* per g root was multiplied by the estimated fine root biomass per 100 ml soil and added to the number of *P. penetrans* per 100 ml soil. The resulting dependent variable is hereafter referred to as *P. penetrans* per 100 ml soil + roots.

Data on *P. penetrans* per 100 ml soil + roots and fine root biomass per 100 ml soil were separated by year and season and averaged over the four to seven sample dates within each combination of plot, depth, season, and year. The seasonal distinctions (fall = October, November, December; winter = January, February, March; spring = April, May, June; summer = July, August, September) correspond to periods of dropping (fall), relatively stable and low (winter), rising (spring), and relatively stable, high soil temperatures (summer) (Vrain et al., 1997). Repeated measures analysis of variance (SAS Institute, Cary, NC) was used to analyze the effects of year, season, and depth on *P. penetrans* per 100 ml soil + roots and fine root biomass per 100 ml soil. Coefficients of correlations between mean nematodes per 100 ml soil + roots and mean root biomass were calculated for each combination of year and season. Nematode population data were shifted to match with root biomass data at 2 and 4 weeks earlier. For the non-shifted and two shifted data sets, means of both dependent variables were calculated for each combination of year, season, and depth. For each combination of year and season, correlation coefficients were calculated on the four pairings representing the four depths.

RESULTS AND DISCUSSION

A three-way interaction occurred between year, season, and depth ($P = 0.003$), indicating that the vertical distribution of *P. penetrans* under raspberry varied significantly from season to season, but that seasonal changes were not similar for the 2 years (Fig. 1). For the first full year of sampling (fall 1989 through summer 1990), population densities decreased monotonically with depth in fall, winter, and spring; however, in summer the greatest population density was at the 5- to 10-depth interval. This effect of season on vertical distribution was not similar in the second year (fall 1990-summer 1991); in fall 1990 the greatest population density was at the 5- to 10-cm-depth interval, and in winter 1991 and spring 1991 the greatest population densities were found in the third depth interval (10–20 cm). In summer 1991 the greatest population density was again in the 5- to 10-cm depth interval. Because the vertical distribution of *P. penetrans* under raspberry does not appear to vary with season in a predictable manner, we see no basis for developing seasonally based sampling strategies.

Because we did not sample below 30 cm, the full vertical distribution of *P. penetrans* under raspberry remains unknown. Previous studies that have included sample depths below 30 cm indicated that the vertical distribution of plant-parasitic nematodes was generally unimodal (Bird and Ramsdell, 1985; Boag, 1981; Brodie, 1976; Ferris and Mc-Kenry, 1974; Ingham et al., 1985; Ogiga and Estey, 1973; Sohlenius and Sandor, 1987). Assuming there was no second peak in population density below 30 cm for the population of *P. penetrans* considered in this study, sampling to 30 cm would capture the depth interval with the greatest population density in all seasons.

The population of *P. penetrans* in this study appeared to be concentrated closer to the soil surface than *Pratylenchus* spp. parasitizing other perennial hosts (Ogiga and Estey, 1973; Sohlenius and Sandor, 1987) and annual hosts (Brodie, 1976; MacGuidwin and Stanger, 1991). For example, an unde-
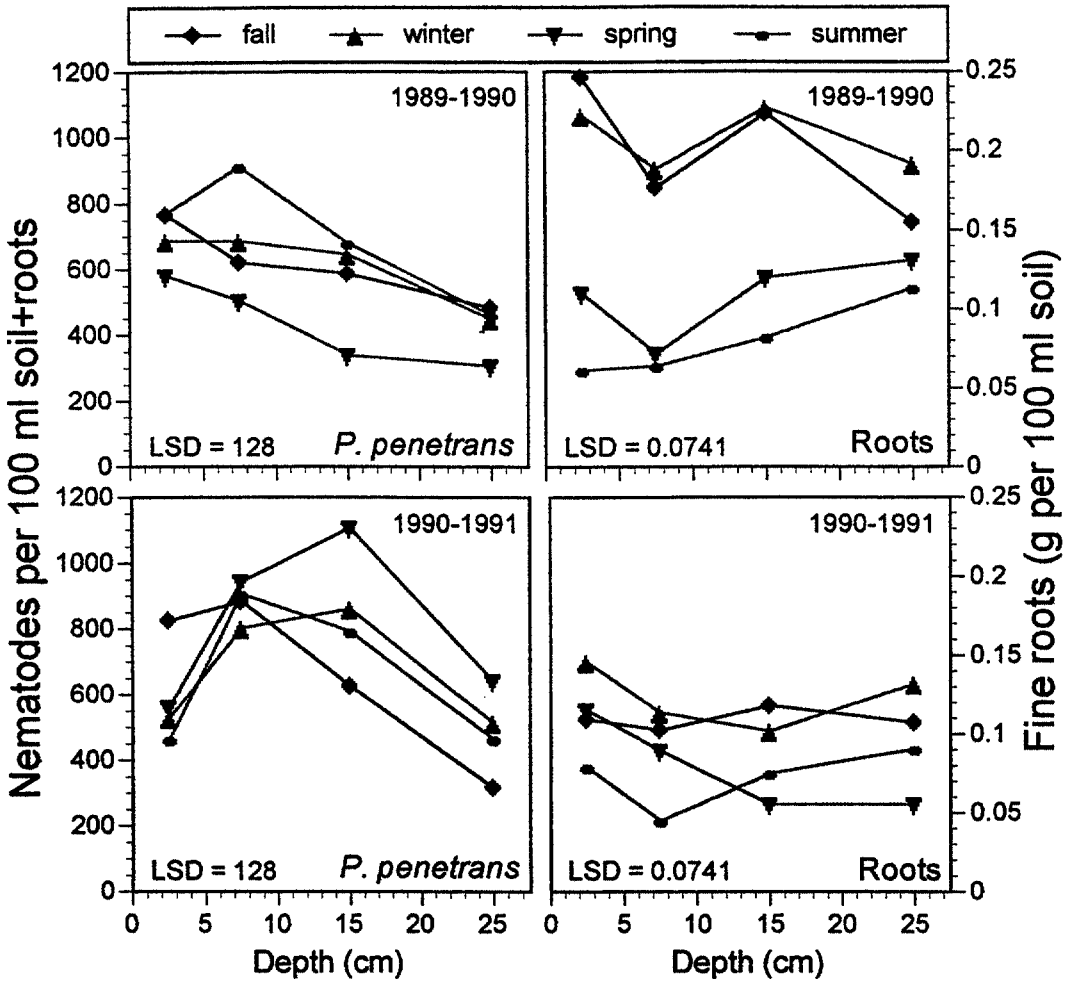
FIG. 1. Effects of depth and season on population densities of *Pratylenchus penetrans* and abundance of fine roots of raspberry through 2 years of sampling: fall 1989 through summer 1990 and fall 1990 through summer 1991.

termined species of *Pratylenchus* parasitizing apple and orchard weeds in Quebec was most abundant at depths of 40 to 60 cm (Ogiga and Estey, 1973). Because the previous studies included different hosts, tillage practices, and locations, it is not possible to determine why *P. penetrans* parasitizing raspberry in the Fraser Valley appeared to be concentrated closer to the soil surface than *Pratylenchus* spp. under other crops elsewhere.

The observed temporal changes in vertical distribution could have been caused by mortality in, or emigration from, the 0- to 5-cm-depth interval during the second winter. Between the fall 1990 and winter 1991

sampling periods, population densities in the 0- to 5-cm-depth interval dropped from 825 to 529 *P. penetrans*/100 ml soil + roots. In contrast, population densities in the 5- to 10-, 10- to 20-, and 20- to 30-cm-depth intervals either did not change significantly (5–10 cm) or increased during the same period (Fig. 1). The estimated population density for the entire 0- to 30-cm depth also did not change during winter 1991 (Vrain et al., 1997). Population densities at 0–5 cm remained lower than at 5–10 and 10–20 cm throughout the spring and summer sampling intervals of 1991.

A similar sharp decrease in population density at 0–5 cm did not occur during win-

ter 1989–1990. Mean January temperatures at 2.5 cm were 3.8 °C and –0.5 °C in 1990 and 1991, respectively, and soil in the 0- to 5-cm interval froze in 1991 but not in 1990. The relationship between freezing and mortality should be considered as speculation; establishing a correlation between freezing and mortality in surface layers would require sampling through several winters. Significant overwinter mortality of *Pratylenchus* spp. has been observed in other studies (Olthof, 1971; Kimpinski and Dunn, 1985; MacGuidwin and Forge, 1991), but the relationship between freezing and mortality of *Pratylenchus* is not clear. MacGuidwin and Forge (1991) detected mortality of *P. scribneri* in fall before the soil froze, suggesting that a portion of the population may be sensitive to the onset of low temperatures before freezing or other factors associated with fall.

The repeated measures ANOVA of fine root abundance indicated a significant interaction between season and year ($P = 0.002$). For both years, fine root abundance was greater in fall and winter than in spring and summer (Fig. 1), but the difference between fall + winter root abundance, and spring + summer root abundance, was greater in 1989–1990 than in 1990–1991.

Seasonal changes in the vertical distribution of *P. penetrans* do not appear to correspond to changes in the vertical distribution of fine roots. In fall 1989, the vertical distribution of *P. penetrans* was positively correlated with the vertical distribution of fine roots 4 weeks earlier, whereas the vertical distribution of *P. penetrans* in winter 1991 was negatively correlated with the distribution of fine roots 2 and 4 weeks earlier (Table 1). The vertical distributions of other nematode species parasitizing perennial hosts also do not appear to be correlated with the vertical distributions of host roots (Boag, 1981; Ferris and McKenry, 1974; Ingham et al., 1985). There are several possible reasons for the observed lack of correlation between the vertical distribution of plant-parasitic nematodes and roots, including: (i) nematodes may not be adapted to the full range of soil environmental conditions conducive to roots (e.g., low oxygen or

TABLE 1.   Coefficients of correlations between fine root biomass and population densities of *Pratylenchus penetrans* for each season. Correlations were calculated from means for each depth. Before calculation of means, nematode population data were shifted to match with root biomass data at 0 (no lag), 2, and 4 weeks earlier.

Season	No lag	2-week lag	4-week lag
Fall 1989	0.87	0.93	0.99[a]
Winter 1990	0.43	0.36	0.39
Spring 1990	–0.63	–0.61	–0.50
Summer 1990	–0.94	–0.91	–0.87
Fall 1990	–0.31	–0.23	–0.07
Winter 1991	–0.81	–0.95[*]	–0.96[*]
Spring 1991	–0.54	–0.43	–0.20

[a]Coefficients labelled with an asterisk are statistically significant ($P \leq 0.05$; 2 degrees of freedom).

high carbon dioxide concentrations), (ii) root turnover may be sufficiently rapid for roots to be continually growing into areas of low nematode abundance, and (iii) root damage caused by the nematodes could result in apparently low root biomass in strata of high nematode abundance.

In summary, this study indicates that the vertical distribution of *P. penetrans* under raspberry changes through time but does not follow a seasonal pattern that is similar in successive years. Consequently, there is no basis for altering sampling strategies to accommodate seasonal changes in vertical distribution. The most notable changes in vertical distribution were reduced population densities near the surface (0–5 cm) and increased population densities at lower depths during winter 1991, when the soil froze at the 0- to 5-cm depth. The vertical distribution of *P. penetrans* was not consistently correlated with the vertical distribution of fine roots.

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