Journal of Nematology 34(4):409–413. 2002.

Seasonal Populations of *Pratylenchus penetrans* and *Meloidogyne hapla* in Strawberry Roots

J. A. LaMondia[1]

Abstract: Strawberry roots were sampled through the year to determine the populations and distribution of *Pratylenchus penetrans* and *Meloidogyne hapla.* Three strawberry root types were sampled—structural roots; feeder roots without secondary tissues; and suberized, black perennial roots. Both lesion and root-knot nematodes primarily infected feeder roots from structural roots or healthy perennial roots. Few nematodes were recovered from soil, diseased roots, or suberized roots. Lesion nematode recovery was correlated with healthy roots. In both 1997 and 1998, *P. penetrans* populations peaked about day 150 (end of May) and then declined. The decline in numbers corresponded to changes in total strawberry root weight and root type distribution. The loss of nematode habitat resulted from loss of roots due to disease and the transition from structural to suberized perennial roots. *Meloidogyne hapla* juvenile recovery peaked around 170 days (mid June) in 1997 and at 85, 147, 229, and 308 days (late March, late May, mid August, and early November, respectively) in 1998. There appear to be at least four generations per year of *M. hapla* in Connecticut. Diagnostic samples from an established strawberry bed may be most reliable and useful when they include feeder roots taken in late May.

Key words: black root rot, *Fragaria x ananassa,* lesion nematode, *Meloidogyne hapla,* population dynamics, *Pratylenchus penetrans, Rhizoctonia fragariae,* root-knot nematode, strawberry.

Root lesion nematodes, primarily *Pratylenchus penetrans* (Cobb) Filip & Schur.Stek., and northern root-knot nematodes, *Meloidogyne hapla* Chitwood, are the most common nematodes associated with strawberries (*Fragaria x ananassa* Duch.) in the northeastern United States (DiEdwardo, 1961; Goheen and Bailey, 1955; Goheen and Smith, 1956; LaMondia 1999a, 1999b; Townshend, 1962). These nematodes reduce crown vigor and fruit yield without producing diagnostic aboveground symptoms (Maas, 1984; Plakidas, 1964; Townshend, 1963). In the absence of microorganisms, cortical infection by *P. penetrans* may cause root necrosis and polyderm formation in the stele (Townshend, 1963). In the field, the lesion nematode has been associated with low vigor (Braun and Keplinger, 1960), stunting (Goheen and Smith, 1956), and increased black root rot (Chen and Rich, 1962; Goheen and Bailey, 1955; Goheen and Smith, 1956). In controlled growth chamber experiments, LaMondia and Martin (1989) demonstrated an interaction of *P. penetrans* and *Rhizoctonia fragariae* resulting in an increase in the severity of black root rot. The reduction in root growth as a result of high population densities of *P. penetrans* also can result in increased winter injury and crown death (LaMondia, 1999a). *Pratylenchus penetrans* may remain active in roots at low temperatures and continue to cause plant injury in late fall and early spring (Ferris, 1970).

The relationship between nematode density and yield establishes targets for management strategies (Barker and Noe, 1987; Ferris, 1981). No seasonal patterns of lesion nematode populations were observed on established 8-year-old raspberry roots, but nematodes on young perennials may be less likely to have established an equilibrium (Vrain et al., 1997).

Population levels of plant-parasitic nematodes attacking strawberries, including *P. penetrans* and *M. hapla,* show seasonal variation in numbers in roots and soil (DiEdwardo, 1961; Szczygiel and Hasior, 1972). These variations make it difficult to interpret the relation between nematode density and strawberry yield loss from samples taken at different times during the year. While population change may be dramatic throughout the year, population dynamics tend to be similar and repeatable year after year within areas of similar climate on a single crop, regardless of differences in soil moisture or precipitation (Winslow, 1964).

Strawberry roots themselves may significantly add to the variation associated with sampling for nematodes. Three distinct types of roots exist on crowns at the same time, and the relative abundance of each morphological type varies with time (Wilhelm and Nelson, 1970). All three of these root types have specific functions and are necessary for the growth and survival of the strawberry crown. New structural roots (perennial roots) are produced from crowns. The terminal branches of these roots are fine lateral or feeder roots. These feeder roots do not develop secondary tissues and have a limited life span, and are replaced several times each season. The structural roots develop secondary tissues and eventually become dark or black perennial roots. These roots appear black due to a collapse of epidermal and cortical cells. The development of secondary growth and suberized tissues results in perennial roots that act as storage organs and conduct water without mineral uptake. Lesion nematode symptoms are commonly seen on young structural roots, but the relation between *P. penetrans* and root anatomy has not previously been determined. Nematode infection may reduce overall root growth, stimulate suberized root production, or change

Received for publication 30 April 2002.
[1] Plant Pathologist/Nematologist, Department of Plant Pathology and Ecology, The Connecticut Agricultural Experiment Station Valley Laboratory, P.O. Box 248, Windsor, CT 06095.
The author thanks J. Canepa-Morrison, S. Lamoureux, and R. Horvath for technical assistance.
This research was supported in part by the North American Strawberry Growers Association.
E-mail: James.LaMondia@po.state.ct.us.
This paper was edited by James L. Starr.

the balance between root types, influencing strawberry growth and vigor.

The objectives of this study were to investigate the relation between strawberry root type, biomass, and nematode population in roots and soil over time.

Materials and Methods

Experiments were conducted at the Connecticut Agricultural Experiment Station Valley Laboratory research farm in Windsor, Connecticut (Merrimac fine loamy sand). Existing 2-year-old 'Honeoye' strawberry crowns in field plots infested with lesion nematodes, root-knot nematodes, and the black rot pathogen, *R. fragariae,* were sampled in May, June, July, and September 1997. Two or three crowns were sampled per plot, soil was removed, and entire root systems were washed free of soil at each sampling date. Nematodes were recovered from 50 cm^3 soil by sugar centrifugation (Barker and Niblack, 1990). Roots were separated into four classes: (i) black suberized perennial roots, (ii) new healthy structural roots, (iii) fine lateral (feeder) roots from perennial roots or (iv) fine lateral roots from structural roots. Roots in each class were weighed and evaluated for percentage root rot. Nematodes in roots of each type were recovered by shaker extraction for 10 days (Barker and Niblack, 1990).

A field plot previously planted with strawberries and recently in oats for 1 year was tilled and planted with Honeoye strawberry crowns in April 1997. This plot had natural populations of *P. penetrans, M. hapla,* and *R. fragariae.* Crowns were planted 10 cm apart within rows 45 cm apart. Two crowns from each plot were removed every 3 weeks from April to December 1998. Soil associated with roots was removed and nematodes extracted by sugar centrifugation. Roots were washed free of soil and separated into four classes as above. Roots in each class were weighed. Nematodes in roots of each type were recovered by shaker extraction for 7 days. Data were analyzed by analysis of variance (NCSS 2000, Number Cruncher Statistical Systems, Kaysville, UT).

Results

The morphology of the strawberry root system was in transition from structural to suberized perennial roots from June through July 1997 (Table 1). This change in root morphology was the result of secondary growth and the loss of the root cortex. The death of cortical cells caused a change in root appearance from nearly white to dark brown or black. The stele remained white in cross section, however, and resulting healthy perennial roots were woody and had numerous fine white feeder roots attached. Cortical death resulting from black root rot caused necrosis of the stele and a loss of root tissue of all types. Black root rot peaked during the fruiting period in June. Extraction of *P. penetrans* was greater from roots than from soil at each sample date ($P \leq 0.05$). Nematode population density (per g root) was greatest in feeder roots, intermediate in structural roots, and least in perennial roots ($P \leq 0.05$).

The number of *M. hapla* second-stage juveniles (J2) extracted from roots was greatest for feeder and least from perennial roots ($P \leq 0.05$). As with *P. penetrans,* numbers of *M. hapla* extracted were greater from roots than from soil at each sample date. However, J2 numbers varied over sample dates, dependent on the stage of nematode development in roots (Table 2).

As noted in 1997, the different morphological types of strawberry roots again changed dramatically over the year in 1998 (Fig. 1). The weight of structural roots peaked in early May and then declined as a result of root loss due to disease and the transition of healthy structural roots to perennial roots. Structural root growth resumed in the fall. Weight of feeder roots remained low but fairly constant over the sampled period.

More *P. penetrans* were extracted from roots than from soil throughout the year, and numbers per g root were greater in feeder than structural roots. *Pratylenchus penetrans* numbers were lowest in perennial roots. Additionally, the numbers of *P. penetrans* extracted from feeder roots attached to structural roots were higher than from feeder roots attached to perennial roots (Table 3). The correlation between percent healthy

Table 1. Numbers of *Pratylenchus penetrans* extracted from different morphological root types of 'Honeoye' strawberry and soil in 1997.

	Weight and percentage of root in each class[a]				Lesion nematode extraction from soil[b] or per g root				
	Perennial	Structural	Feeder	Root biomass	Soil	Perennial	Structural	Feeder	Pp/plant
May 5	14	56	30	5.3	2.0	3.2	34.5	107.3	829.1
June 3	18	69	13	11.8	1.0	1.5	34.2	305.0	1,741.5
July 2	79	1	20	5.9	0.7	0.0	0.0	77.5	279.0
Sept 2	80	6	14	9.1	1.2	0.0	23.9	56.7	253.7
Source (Anova)		*P* = Root in each class			*P* = Pp recovery				
Root type		0.0001			0.0001				
Sample date		0.04			0.05				
Interaction		0.0001			0.03				

[a] Classes: Black suberized perennial roots, white structural roots, and fine feeder roots.
[b] *Pratylenchus penetrans* (Pp) recovery from 50 cm^3 soil by sugar centrifugation.

TABLE 2. Numbers of *Meloidogyne hapla* second-stage juveniles (J2) extracted from different morphological root types of 'Honeoye' strawberry and soil in 1997.

	J2 extraction from soil or per g root[a]			
	Soil[b]	Perennial	Structural	Feeder
April 24	5.0	0.0	0.0	363.7
June 19	1.0	198.8	254.3	1,730.0
July 2	5.0	38.3	100.0	64.6
Sept 2	11.0	0.0	14.6	520.0
Source (Anova)		Probability level		
Root type		0.06		
Sample date		ns		
Interaction		ns		

[a] Classes: Black suberized perennial roots, white structural roots, and fine feeder roots.
[b] Nematode recovery from 50 cm^3 soil sugar centrifugation.

TABLE 3. Numbers of *Pratylenchus penetrans* extracted from different morphological root types of 'Honeoye' strawberry and soil in 1998.

	P. penetrans per g root				
Day of year	Soil[a]	Perennial roots[b]	Feeder-black	Structural roots	Feeder-structural
64	3	0	480	30	239
85	5	48	143	30	122
105	8	33	131	55	289
127	0	33	238	135	403
147	8	18	334	290	1263
168	43	68	364	93	1285
189	15	8	403	497	727
210	40	8	209	238	415
229	50	33	315	290	755
252	5	35	176	134	467
280	8	3	96	73	158
308	3	8	143	20	85
Mean	8	24	253	157	517
Source (Anova)			*P* =		
Root type			0.001		
Sample date			0.001		
Interaction			0.07		
Linear Contrasts					
Feeder vs. structural root			0.001		
Perennial vs. structural root			0.05		
Feeder on perennial vs. feeder on structural			0.001		

[a] *Pratylenchus penetrans* recovery from 50 cm^3 soil by sugar centrifugation.
[b] *P. penetrans* per g root in classes: Black suberized perennial roots, white structural roots, and fine feeder roots attached to black suberized perennial roots or white structural roots.

roots (white structural and feeder roots) and lesion nematode recovery was high ($r = 0.72$; $P = 0.01$).

Total numbers of *P. penetrans* per plant distributed among root types (calculated by multiplying nematodes per g by root biomass in g) indicate that the majority of the lesion nematode population is present in structural roots despite the fact that nematode density per g of root may be greatest in feeder roots (Fig. 2). *Pratylenchus penetrans* numbers per plant fell sharply through June and July as roots became diseased or underwent secondary growth.

Meloidogyne hapla J2 population density was greatest in feeder roots, especially early in the season (Table 4). Most of the population resided in feeder roots, despite the fact that this root class represented a small proportion of the root system (Fig. 3). *Meloidogyne hapla* J2 numbers had four distinct peaks throughout the year, and J2 were consistently extracted from structural roots later in the year. Recovery of *M. hapla* J2 peaked at around 170 days (mid June) in 1997 and at 85 days (late March), 147 days (late May), 229 days (mid August), and 308 days (early November) in 1998, suggesting that there may be at least four generations per year.

DISCUSSION

Pratylenchus penetrans and *M. hapla* nematodes occupy niches both in soil and in morphologically distinct strawberry roots at different times of the year. The variation in nematode numbers over time reflects changes

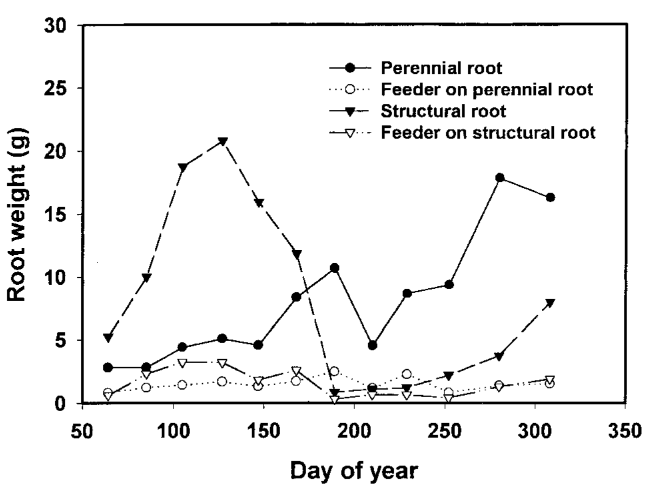

FIG. 1. Strawberry root type and weight over time, Windsor, Connecticut, 1998.

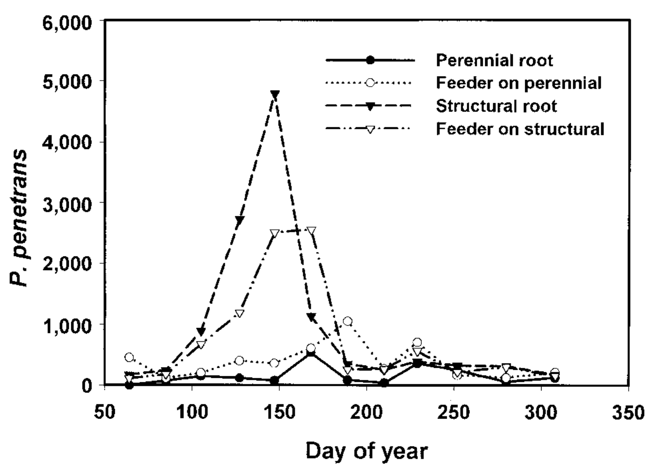

FIG. 2. Total number of *Pratylenchus penetrans* per crown extracted from each strawberry root type over time, Windsor, Connecticut, 1998.

TABLE 4. Numbers of *Meloidogyne hapla* second-stage juveniles (J2) extracted from different morphological root types of 'Honeoye' strawberry and soil in 1998.

		M. hapla per g root			
Day of year	Soil[a]	Perennial roots[b]	Feeder-black	Structural roots	Feeder-structural
64	28	0	310	3	296
85	26	31	9,420	8	5,160
105	21	10	49	5	261
127	3	0	58	0	380
147	11	0	20	0	902
168	0	5	10	3	85
189	13	5	253	25	0
210	19	0	2,703	1,274	3,326
229	8	18	737	575	6,397
252	4	0	182	0	0
280	8	3	73	50	1,133
308	5	3	10	460	1,196
Mean	12	6	1,152	200	1,595

Source (Anova)	$P =$
Root type	0.003
Sample date	0.003
Interaction	0.10
Linear Contrasts	
Feeder vs. structural root	0.05
Perennial vs. structural root	ns
Feeder on perennial vs. feeder on structural	ns

[a] *Meloidogyne hapla* recovery from 50 cm^3 soil by sugar centrifugation.
[b] *M. hapla* per g root in classes: Black suberized perennial roots, white structural roots, and fine feeder roots attached to black suberized perennial roots or white structural roots.

in the distribution of morphological types of strawberry roots that occur over the season. In both 1997 and 1998, *P. penetrans* populations peaked at about day 150 (end of May). The subsequent decline in numbers corresponds to changes in total strawberry root weight and root type distribution. The loss of nematode habitat results both from loss of roots due to disease and also from a natural change in root type from structural root to suberized perennial root.

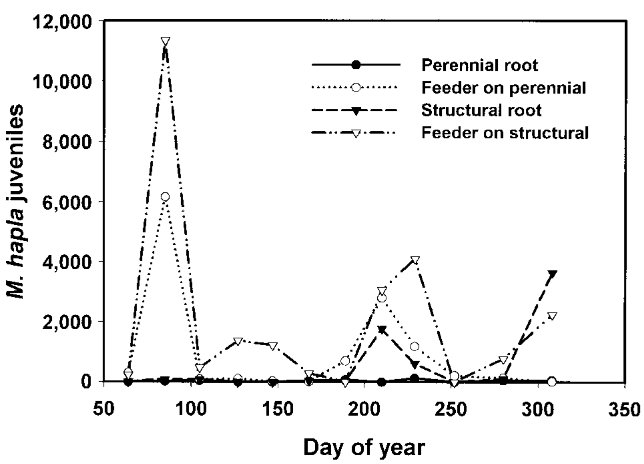

FIG. 3. Total number of *Meloidogyne hapla* second-stage juveniles per crown extracted from each strawberry root type over time, Windsor, Connecticut, 1998.

In the present study, relatively few nematodes were extracted from soil, diseased roots, or suberized roots without associated feeder roots. Previous research in New Jersey (DiEdwardo, 1961) and in Poland (Szczygiel and Hasior, 1972) reported that *Pratylenchus* densities in soil were low and did not exhibit seasonal variation. They reported that numbers extracted from strawberry roots were higher in young roots than in older, heavily symptomatic roots. Lesion nematode numbers peaked in June, and precipitous declines were associated with aging roots (DiEdwardo, 1961) or a drop in the percentage of young white roots (Szczygiel and Hasior, 1972). There were no effects of root age on the ratio of female, male, or juvenile nematodes (DiEdwardo, 1961). The high correlation between percent healthy white roots and lesion nematode numbers by all of these studies underscores the fact that the recovery of these obligate parasites from diseased crowns is unlikely. In Poland, numbers of *M. hapla* J2 in roots had four peaks throughout the year (March–April, June, August–September, and November) (Szczygiel and Hasior, 1972). Our results in Connecticut were remarkably similar; *M. hapla* J2 numbers peaked in April, May, August, and November.

Structural strawberry roots and healthy suberized perennial roots normally produce successive crops of absorptive feeder roots (Wilhelm and Nelson, 1970). During the period of spring fruit production, extensive loss of all root types may occur. Strawberry roots were also reported to decline during fruiting, and lesion nematode populations declined with root growth (DiEdwardo, 1961; Szczygiel and Hasior, 1972). Nematode populations recovered more slowly than roots, perhaps as a dilution effect of slowly increasing nematode numbers in more quickly increasing root biomass. Root growth recovered by fall.

The health, vigor, and productivity of the crown is determined by the extent to which roots are converted from structural to perennial roots and produce successive flushes of feeder roots unimpeded by root pathogens (Wilhelm and Nelson, 1970). Infection of strawberry roots by both *P. penetrans* and *R. fragariae* results in significant and severe root rot (LaMondia and Martin, 1989). We had also reported that black root rot caused by *R. fragariae* reduced healthy structural root length by the development of cortical rot and also reduced feeder root length (LaMondia and Martin, 1989). Strawberry black root rot-affected plants exhibit areas of cortical necrosis, a rat-tail symptom on structural roots, and the collapse of perennial roots. The cortical root rot symptoms are transient, and the loss of root biomass, especially feeder roots, is of primary importance in the decline of the strawberry crown (LaMondia and Martin, 1989). While this disease may increase the inoculum potential of *R. fragariae* over time, populations of *P. penetrans* are already fluctuating with the cycle of root growth, and are further reduced by the destruction of remaining healthy roots and the loss of feeder root production. As a consequence, these nematodes must migrate to adjacent healthy roots to survive. Results of the present study suggest that in order to optimize diagnostic sampling to best determine lesion nematode density and their involvement in black root rot disease, samples should be taken in late May or early June prior to fruiting, or later in the year after mid August. Additionally, crowns exhibiting symptoms of severe black root rot with poor or no healthy roots should not be sampled. Rather, nematodes should be recovered from plants adjacent to diseased areas that still have healthy structural and feeder root tissue.

Literature Cited

Barker, K. R., and T. L. Niblack. 1990. Soil sampling methods and procedures for field diagnosis. Pp. 10–19 *in* B. M. Zuckermann, W. F. Mai, and L. R. Krusberg, eds. Plant nematology laboratory manual. Amherst, MA: University of Massachusetts Agricultural Experiment Station.

Barker, K. R., and J. P. Noe. 1987. Establishing and using threshold levels. Pp. 75–81 *in* J. A. Veech and D. W. Dickson, eds. Vistas on nematology. Hyattsville, MD: Society of Nematologists.

Braun, A. J., and J. A. Keplinger. 1960. THe pathogenicity of meadow nematodes as determined by the growth of plants in a commercial planting. Phytopathology 50:239.

Chen, T. A., and A. E. Rich. 1962. The role of *Pratylenchus penetrans* in the development of strawberry black root rot. Plant Disease Reporter 46:839–843.

DiEdwardo, A. A. 1961. Seasonal population variations of *Pratylenchus penetrans* in and about strawberry roots. Plant Disease Reporter 45:67–71.

Ferris, H. 1981. Dynamic action thresholds for diseases induced by nematodes. Annual Review of Phytopathology 19:427–436.

Ferris, J. M. 1970. Soil temperature effects on onion seedling injury by *Pratylenchus penetrans.* Journal of Nematology 2:248–251.

Goheen, A. C., and J. S. Bailey. 1955. Meadow nematodes in strawberry plantings in Massachusetts. Plant Disease Reporter 39:879–880.

Goheen, A. C., and J. B. Smith. 1956. Effects of inoculation of strawberry roots with meadow nematodes, *Pratylenchus penetrans.* Plant Disease Reporter 40:146–149.

LaMondia, J. A. 1999a. The effects of *Pratylenchus penetrans* on strawberry vigor and yield. Journal of Nematology 31:418–423.

LaMondia, J. A. 1999b. The effects of rotation crops on the strawberry pathogens *Pratylenchus penetrans, Meloidogyne hapla,* and *Rhizoctonia fragariae.* Journal of Nematology 31:650–655.

LaMondia, J. A., and S. B. Martin. 1989. The influence of *Pratylenchus penetrans* and temperature on black root rot of strawberry by binucleate *Rhizoctonia* spp. Plant Disease 73:107–110.

Maas, J. L. 1984. Compendium of strawberry diseases. St. Paul, MN: The American Phytopathological Society.

Plakidas, A. G. 1964. Strawberry diseases. Baton Rouge: Louisiana State University Press.

Szczygiel, A., and H. Hasior, 1972. Seasonal variations in population of plant-parasitic nematodes in strawberry plantations. Ekologia Polska 20:1–16.

Townshend, J. L. 1962. The root lesion nematode, *Pratylenchus penetrans* (Cobb 1919) Filip. & Stek., 1941 in strawberry in the Niagara peninsula and Norfolk County of Ontario. Canadian Journal of Plant Science 42:728–736.

Townshend, J. L. 1963. The pathogenicity of *Pratylenchus penetrans* to strawberry. Canadian Journal of Plant Science 43:75–78.

Vrain, T. C., T. A. Forge, and R. DeYoung. 1997. Population dynamics of *Pratylenchus penetrans* parasitizing raspberry. Fundamental and Applied Nematology 20:29–36.

Wilhelm, S., and P. E. Nelson. 1970. A concept of rootlet health of strawberries in pathogen-free soil achieved by fumigation. Pp. 208–215 *in* T. A. Toussoun, R. V. Bega, and P. E. Nelson, eds. Root diseases and soil-borne pathogens. Berkeley: University of California Press.

Winslow, R. D. 1964. Soil nematode population studies. I. The migratory root *Tylenchida* and other nematodes of the Rothamsted and Woburn six-course rotations. Pedobiologia 4:65–76.