Journal of Nematology 19(2):164–171. 1987.

Anhydrobiosis in *Pratylenchus penetrans* and *Tylenchorhynchus* n. sp. in Cultivated Soils Cropped to Winter Rye

J. L. Townshend[1]

Abstract: Anhydrobiotes of *Pratylenchus penetrans* were found in two cultivated soils sown to rye in southern Ontario during the growing season. Anhydrobiotes at the 0–2.5-cm depth were recovered from 9 and 6 of 11 samplings, respectively, of a Vineland silt loam and a Fox loamy sand during the dry summer of 1983. At the 2.5–15.0-cm depth, anhydrobiotes were recovered less frequently. In the summer of 1984, anhydrobiotes of *P. penetrans* were recovered once and anhydrobiotes of *Tylenchorhynchus* n. sp. twice in 11 samplings. The percentages of *P. penetrans* populations that were anhydrobiotes in 1983 and 1984 were closely related to soil moisture content and corresponding moisture tensions. Populations of *P. penetrans* were greatest in October in the lower soil depth, 2.5–15.0 cm; those of *Tylenchorhynchus* n. sp. were greater in the surface layer of soil, 0–2.5 cm, and peaked in August.

Key words: root-lesion nematode, stunt nematode, soil population, anhydrobiotes, soil moisture.

Studies on anhydrobiosis (life without moisture) in the genera *Pratylenchus* and *Tylenchorhynchus* have been primarily laboratory investigations. *Pratylenchus brachyurus* Godfrey survived 21 months in fallow greenhouse soil (4), *P. crenatus* Loof 21 months in bagged soil (7), and *P. penetrans* Cobb 11 months in one greenhouse study (9) and 24 months in a second greenhouse study when soils were slow dried (13). Over 90% of a *T. dubius* Butschli population survived 3 weeks in greenhouse soil with a 1% moisture content (16). In the field, anhydrobiosis was noted in several genera in desert soil (5). In the northern Negev region of Israel, *P. thornei* Sher & Allen was able to survive the dry summer after a winter wheat harvest when all plants had become desiccated (6). In cultivated soils in southern Ontario, soil populations of *P. penetrans* under tobacco and rye decrease in summer under low soil moisture and increase when soil moisture is high (8). These dry summer soils have not been examined previously for the occurrence of anhydrobiosis. This study demonstrates that anhydrobiosis does occur in populations of *P. penetrans* and *Tylenchorhynchus* n. sp. during the dry summer season in cultivated soils planted to rye in southern Ontario.

Materials and Methods

Two field sites (7 × 12 m) were selected for the anhydrobiosis study: a plot of Fox loamy sand (85% sand, 10% silt, 5% clay; field capacity 8%) on Agriculture Canada's Tobacco Research Station, Delhi, Ontario; and a rye plot of Vineland silt loam (61% sand, 28% silt, 11% clay; field capacity 23%) on the farm of Agriculture Canada's Research Station, Vineland Station, in the Niagara Peninsula, Ontario. The two sites were sown to winter rye in 1982. Particle size analyses and moisture characteristic curves of the two soils were illustrated in an earlier paper (13).

Both sites were sampled every 3 weeks from early May until early December 1983 and 1984. In July of each year, the winter rye was plowed down and the crop allowed to reestablish itself. A zig-zag pattern was used at each sampling (1). Eight soil samples were taken with a trowel from the surface, 0–2.5 cm, and with a 2.0-cm-d core sampler from a lower depth, 2.5–15.0 cm. Each sample weighed approximately 500 g. Soil samples in plastic bags were stored in a styrofoam box so that condensation did not form. Soil temperatures were determined at both levels at four randomly selected sites with a bimetallic probe immediately after sampling. Processing of soil

Received for publication 26 February 1986.
[1] Research Station, Agriculture Canada, Vineland Station, Ontario, Canada L0R 2E0.
The author thanks Diane Beaulieu-Aruvee for technical assistance.

TABLE 1. Development of anhydrobiotes in *Pratylenchus penetrans* at two soil depths* in a cultivated Vineland silt loam planted to rye.

Sampling date	Living† (no./50 g soil)			Anhydrobiotes (%)			Soil moisture (%)	
	Upper	Lower	$LSD_{10\%}$	Upper	Lower	$LSD_{10\%}$	Upper	Lower
1983								
10 May	37	135	19	25	15	ns	15.2	18.8
31 May	33	225	22	34	19	ns	13.5	21.3
21 June	18	50	13	94	27	25	3.6	10.2
13 July	7	112	24	100	34	11	3.4	8.0
4 August	18	68	10	13	6	ns	25.4	19.1
25 August	64	96	ns	20	3	ns	10.0	11.5
13 September	81	155	34	66	45	17	7.6	8.4
4 October	159	298	60	16	19	ns	12.1	11.4
25 October	110	199	52	3	3	ns	26.4	22.3
15 November	60	118	34	0	0		29.7	22.6
6 December	45	214	29	0	0		24.1	38.4
$LSD_{10\%}$	29	35		19	14			
1984								
8 May	10	108	31	0	0		27.6	23.4
29 May	21	135	41	0	0		28.6	21.3
19 June	5	104	22	0	0		28.0	25.3
10 July	9	70	30	0	0		15.4	16.5
31 July	11	51	18	94	75	ns	2.8	8.4
21 August	25	136	35	0	0		10.2	12.2
12 September	13	15	ns	0	0		26.3	21.8
2 October	41	190	37	0	0		25.3	21.5
21 October	89	190	39	0	0		22.6	20.7
13 November	58	88	28	0	0		39.2	33.0
4 December	45	89	25	0	0		28.8	23.1
$LSD_{10\%}$	19	36						

* Upper, 0–2.5 cm; lower, 2.5–15 cm.
† As determined by the pan method.

samples for anhydrobiotes commenced 10 minutes after the final cores were taken.

Anhydrobiotes and non-anhydrobiotes of *P. penetrans* and *Tylenchorhynchus* n. sp. were extracted from soil as follows (4): Each 500-g sample was passed through a 4-mm-pore sieve to remove root debris, and a 50-g subsample was poured slowly into 200 ml hot 4% formaldehyde solution (40–50 C) in a 250-ml centrifuge bottle. All subsamples were processed in hot formaldehyde before centrifugation. Four subsamples per run were shaken and centrifuged for 5 minutes at 1,100 *g*. Each supernatant was discarded, the pellets resuspended in 200 ml sucrose solution (sp. gr. 1.18–1.20), and centrifuged once more. The supernatants were poured three times through a 38-μm-pore sieve to catch the nematode anhydrobiotes. The sieve was back flushed after each passage. Nematodes were concentrated on a millipore filter, and coiled and noncoiled nematodes were counted under a stereo microscope. The proportion of coiled *P. penetrans* and *Tylenchorhynchus* n. sp. to the total number of each species extracted determined the percentage of anhydrobiotes (12).

To extract living nematodes, equal numbers of 50-g soil subsamples were processed for 7 days by the pan method (10). Also, four soil subsamples from each sampling level were processed to determine moisture content by the gravimetric method (3).

Data on the development of anhydrobiosis in *P. penetrans* were gathered in 1983 and 1984, whereas data on *Tylenchorhynchus* n. sp. were gathered only in 1984 from the Vineland Station site. Meteorological data were obtained from records compiled at the Delhi Tobacco Research Station and

TABLE 2. Development of anhydrobiotes in *Pratylenchus penetrans* at two soil depths* in a cultivated Fox loamy sand planted to rye.

Sampling date	Living† (no./50 g soil)			Anhydrobiotes (%)			Soil moisture (%)	
	Upper	Lower	$LSD_{10\%}$	Upper	Lower	$LSD_{10\%}$	Upper	Lower
1983								
5 May	7	13	5	0	0		9.5	9.6
26 May	75	122	19	0	0		11.3	11.2
15 June	61	78	ns	56	3	15	2.3	3.9
7 July	55	220	38	19	4	ns	6.6	7.9
28 July	102	151	ns	39	0		2.3	6.0
19 August	63	43	31	39	0		2.2	5.6
9 September	18	116	64	87	1	11	1.3	5.0
30 September	18	201	78	6	3	ns	3.7	5.0
21 October	163	359	26	0	0		7.5	8.8
10 November	25	129	89	0	0		7.9	8.9
2 December	93	273	91	0	0		18.4	9.3
$LSD_{10\%}$	22	22		22	ns			
1984								
3 May	5	100	22	10	0		1.8	5.9
24 May	8	55	14	0	0		8.3	17.9
14 June	11	92	16	0	0		10.2	8.0
5 July	71	67	ns	0	0		16.2	16.2
26 July	74	101	11	0	0		9.2	8.6
16 August	99	131	ns	27	0		2.5	7.8
5 September	14	128	20	0	0		7.4	9.4
24 September	7	135	29	0	0		8.4	7.2
18 October	34	147	26	0	0		7.9	8.2
8 November	44	120	37	0	0		20.0	19.0
29 November	76	185	57	0	0		10.9	10.0
$LSD_{10\%}$	19	35						

* Upper, 0–2.5 cm; lower, 2.5–15 cm.
† As determined by the pan method.

at the Ontario Ministry of Agriculture and Foods, Horticultural Research Institute of Ontario, Vineland Station.

RESULTS

In Vineland silt loam, the mean numbers of *P. penetrans*/50 g soil at the upper depth were greater in 1983 than in 1984, 57 vs. 30—$LSD_{10\%}$ 11, and the numbers at the lower depth were also greater in 1983 than in 1984, 152 vs. 107—$LSD_{10\%}$ 19. The mean numbers of *P. penetrans*/50 g soil were greater at the lower depth than at the upper in both years, $LSD_{10\%}$ 17 and 13, respectively. The same pattern occurred in Fox loamy sand. The mean numbers of *P. penetrans*/50 g soil at the upper depth was greater in 1983 than in 1984, 62 vs. 40—$LSD_{10\%}$ 11, and the mean numbers at the lower depth were also greater in 1983 than 1984, 151 vs. 115—$LSD_{10\%}$ 23. Again, the mean numbers of *P. penetrans*/50 g soil were greater at the lower depth than at the upper in both years, $LSD_{10\%}$ 23 and 12, respectively. In 11 samplings of the two soils, the number of *P. penetrans*/50 g of soil peaked in October of each year (Tables 1, 2).

The occurrence of anhydrobiotes of *P. penetrans* in cultivated soils at Delhi and Vineland Station in 1983 contrasted greatly with that in 1984 (Tables 1, 2). In Vineland silt loam in 1983 at the upper and lower depths (Table 1), anhydrobiotes of *P. penetrans* were recorded in 9 of 11 samplings (May through September) and in Fox loamy sand at Delhi in 6 of 11 samplings (June through September) at the upper depth (Table 2) and in 4 of 11 samplings (June, July, September) at the lower depth (Table 2). In 1984, anhydrobiotes of *P. penetrans* were noted only once in 11 sam-

TABLE 3. Development of anhydrobiotes in *Tylenchorhynchus* n. sp. at two soil depths* in a cultivated Vineland silt loam planted to rye.

Sampling date	Living† (no./50 g soil)			Anhydrobiotes (%)		
	Upper	Lower	$LSD_{10\%}$	Upper	Lower	$LSD_{10\%}$
1984						
8 May	40	3	15	0	0	
29 May	6	1	4	0	0	
19 June	30	8	11	0	0	
10 July	150	9	28	0	0	
31 July	350	40	40	93	67	8
21 August	540	18	20	14	7	ns
12 September	180	10	40	0	0	
2 October	250	9	60	0	0	
21 October	70	6	20	0	0	
13 November	145	23	40	0	0	
4 December	146	9	20	0	0	
$LSD_{10\%}$	43	9		4	11	

Soil moisture is recorded in 1984 section of Table 1.
* Upper, 0–2.5 cm; lower, 2.5–15 cm.
† As determined by the pan method.

plings at both depths in Vineland silt loam (Table 1) and only once in Fox loamy sand at the upper depth (Table 2).

In the Vineland silt loam during June, July, and September 1983, over 60% of the *P. penetrans* population at the upper level were anhydrobiotes. In July, 100% of the *P. penetrans* population were anhydro-

TABLE 4. Meteorological data for the 5-day period prior to each sampling at Vineland Station, Ontario.

Sampling date	Soil temperature* (C)		Accumulated rainfall (mm)	Mean max. temperature (C)	Total sunshine (hours)	Accumulated wind run (km)
	Upper†	Lower†				
1983						
10 May	21.6	13.8	14.0	14.1	35.1	1,493
31 May	24.3	17.4	17.8	16.7	27.1	908
21 June	30.2	21.7	0	24.7	51.4	531
13 July	30.3	22.8	0	27.0	58.1	1,126
4 August	26.1	23.2	19.2	27.5	36.1	707
25 August	23.0	21.0	2.6	24.3	49.1	685
13 September	17.5	19.4	0.4	26.8	43.1	951
4 October	19.6	17.6	2.8	21.5	31.4	727
25 October	9.8	9.5	22.4	10.8	20.9	990
15 November	2.3	3.1	22.4	4.3	12.0	1,171
6 December	3.1	2.7	0	0	5.0	1,421
1984						
8 May	8.7	8.4	26.6	12.3	15.3	996
29 May	11.5	10.8	10.8	18.1	37.9	1,197
19 June	27.6	20.5	125.6	20.7	43.5	860
10 July	19.5	19.6	9.4	22.9	32.2	885
31 July	29.6	20.9	0	23.4	47.1	446
21 August	27.6	21.4	7.0	23.8	38.3	886
12 September	19.8	17.1	57.0	22.6	29.8	988
2 October			26.0	13.2	17.7	597
23 October	12.6	11.3	9.6	17.4	21.4	701
13 November	6.2	6.2	26.8	10.3	0.4	1,257
4 December	0.1	5.5	6.4	6.0	9.4	1,176

* Soil temperature taken day of sampling.
† Upper, 0–2.5 cm; lower, 2.5–15 cm.

TABLE 5. Meteorological data for the 5-day period prior to each sampling at Delhi, Ontario.

Sampling date	Soil temperature* (C)		Accumulated rainfall (mm)	Mean max. temperature (C)	Total sunshine (hours)	Accumulated wind run (km)
	Upper†	Lower†				
1983						
5 May	15.5	13.3	57.9	14.9	18.1	865
26 May	19.0	17.0	15.4	19.9	27.6	815
15 June	32.5	22.3	0	29.8	57.9	421
7 July	24.5	19.0	6.6	26.7	45.5	820
28 July	36.5	23.5	0	27.8	52.5	529
19 August	35.0	24.4	0	26.9	44.0	369
9 September	34.6	20.8	0	27.1	46.0	644
30 September	21.6	14.5	0	21.3	28.2	426
21 October	12.1	8.0	1.2	12.3	24.5	499
10 November	10.8	6.9	11.6	8.5	2.0	514
12 December	−0.8	0.6	21.6	3.8	23.3	843
1984						
3 May	17.8	11.9	2.2	17.2	43.8	976
24 May	24.0	16.4	49.8	21.3	38.6	643
14 June	24.0	23.2	17.0	28.5	60.5	707
5 July	24.9	22.1	20.0	27.2	44.3	524
26 July	23.5	19.8	2.8	28.3	57.1	630
16 August	34.4	25.9	0.2	27.5	37.8	477
5 September	22.0	16.9	25.6	20.9	32.7	545
24 September	21.1	18.8	31.8	20.6	16.8	754
18 October	15.8	12.1	2.0	18.0	18.1	330
8 November	5.4	3.7	33.0	8.9	16.4	757
29 November	2.6	2.8	3.0	12.7	23.6	642

* Soil temperature taken day of sampling.
† Upper, 0–2.5 cm; lower, 2.5–15 cm.

biotes. At the lower depth, anhydrobiosis was greatest in *P. penetrans* in July and September when 34% and 45% of the population, respectively, were anhydrobiotes (Table 1).

In Fox loamy sand at the upper depth, anhydrobiosis was greatest in June and September 1983 when 56% and 88% of the population, respectively, were anhydrobiotes (Table 2). At the lower depth, anhydrobiosis was much less, with only 4% of the *P. penetrans* population being anhydrobiotes in July and September (Table 2).

In 1984, anhydrobiotes of *P. penetrans* were recovered only once from Vineland silt loam and twice from Fox loamy sand (Tables 1, 2). In Vineland silt loam in August, 94% and 75% of the *P. penetrans* population were anhydrobiotes at the upper and lower depths, respectively, whereas in Fox loamy sand, 10% and 27% of the *P. penetrans* population were anhydrobiotes in May and August, respectively, and only at the upper depth (Table 2).

The mean numbers of *Tylenchorhynchus* n. sp. in Vineland silt loam, monitored only in 1984, were greater at the upper depth than at the lower, 173 vs. 12—$LSD_{10\%}$ 28. Depending on the sampling time, the number of *Tylenchorhynchus* n. sp. at the upper depth exceeded the number at the lower depth by 27 times; the numbers peaked in August (Table 3). Anhydrobiotes of *Tylenchorhynchus* n. sp. were recovered at both depths in 2 of 11 samplings (Table 3). At the upper depth, 93% and 14% of the population were anhydrobiotes in early and late August; at the lower depth, 67% and 7% were anhydrobiotes at the respective sampling times.

Soil moisture in Vineland silt loam was lower at both levels of soil from spring until autumn in 1983 than in 1984 (Table 1). Also soil temperature was higher in spring and early summer 1983 than in 1984 (Ta-

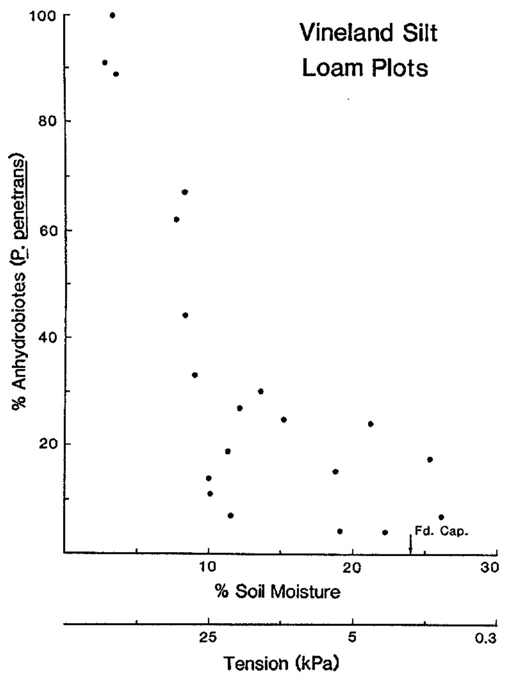

FIG. 1. Relationship between percentage of *Pratylenchus penetrans* anhydrobiotes and soil moisture content–moisture tension in a Vineland silt loam.

ble 4). Soil moisture in Fox loamy sand was also lower at both soil depths in June through November in 1983 than in 1984 (Table 2). However, soil temperatures in both years and at both soil depths were similar (Table 5).

Meteorological data compiled 5 days (a sufficient time for wetting or drying) before each sampling revealed a great contrast in the amount of accumulated rainfall between 1983 and 1984 (Tables 4, 5). In Delhi, there was no rainfall in 5 of the 11 periods before sampling in 1983 (Table 5), whereas in 1984 there was considerable rainfall in these periods; in July and August, the accumulated rainfall was minimal in the periods before sampling. At Vineland in 1983, there was no rainfall in 2 of the 11 periods before sampling and minimal rainfall in 3 of the periods (August, September, October) (Table 4). In 1984, there was no rainfall in one period before sampling (31 July), but there was rainfall in the others (Table 4). Mean maximum air temperatures, total hours of sunshine, and total accumulated wind runs in the 5-day periods before sampling were similar both years at the respective plot sites (Tables 4, 5).

Anhydrobiotes of *P. penetrans* in the upper depth of Vineland silt loam increased as soil moisture and rainfall decreased and as soil and air temperatures and sunshine increased (Fig. 1, Table 6). The same correlations were noted, except for rainfall, in Fox loamy sand (Fig. 2, Table 6). Anhydrobiotes of *P. penetrans* were correlated negatively with only soil moisture in Vineland silt loam at the lower depth and with none of the soil and aerial meteorological data in Fox loamy sand (Table 6).

The percentage of soil moisture at both depths of Fox loamy sand decreased as sunshine, wind, and soil and air temperatures increased and increased with increasing rainfall (Table 6). The same correlations, except for wind, were obtained in Vineland silt loam (Table 6).

DISCUSSION

Anhydrobiosis occurs in nematodes in agricultural soils during the growing season in southern Ontario. Anhydrobiotes of *P. penetrans* were recovered from a cultivated Fox loamy sand and a Vineland silt loam, both sown to rye, when the soil moisture declined to field capacity. Apparently micro-pockets of soil particles exist where soil moisture tension is sufficiently great to reduce moisture to 6–9 monomolecular layers that induce anhydrobiosis in nematodes (2). The number of anhydrobiotes increases greatly as soil moisture is depleted and soil moisture tension increases. The occurrence of anhydrobiotes of *P. penetrans* is greater in the surface layer of soil, where soil moisture tension is greater, than in the lower layers, where soil moisture tension is lower. In another study, *P. thornei* survived the dry summer in an anhydrobiotic state after a winter wheat harvest in the Negev region of Israel (6).

Development of anhydrobiosis in *P. penetrans* may be one reason this nematode is less destructive in tobacco in warm, dry growing seasons than in wet, cool growing seasons (14,15). In warm, dry growing sea-

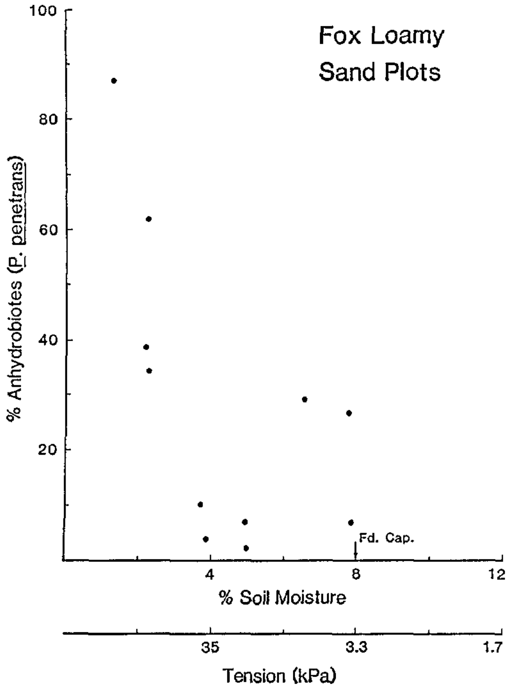

FIG. 2. Relationship between percentage of *Pratylenchus penetrans* anhydrobiotes and soil moisture content–moisture tension in a Fox loamy sand.

sons, soil moisture tension increases, mobility of *P. penetrans* is reduced (11), less root penetration occurs (12), and anhydrobiosis develops which allows *P. penetrans* to survive the low levels of soil moisture.

In this study, the percentage of anhydrobiotes recorded may be skewed because eggs of *P. penetrans* passed through the finest screen in the extraction procedure. It is possible, however, that eggs, particularly those containing juveniles, could be in an anhydrobiotic state as well during dry periods. Second- and third-stage juveniles were found in an anhydrobiotic state in a previous study (13).

The preferred habitat of *Tylenchorhynchus* n. sp. is in the upper 2.5 cm of soil. Its confinement to the surface layer is not due entirely to the shallow root growth of winter rye, as Wyss (16) noted that *T. dubius* also preferred the surface layer of soil in a greenhouse study with strawberry, a deep-rooted crop. Although not studied in the dry 1983 growing season, *Tylenchorhynchus* n. sp. may be a more successful anhydrobiote than *P. penetrans* because of its capacity to survive the far greater extremes of temperature and moisture that occur in the surface soil layers.

LITERATURE CITED

1. Barker, K., J. L. Townshend, G. W. Bird, I. J. Thomason, and D. W. Dickson. 1978. Determining nematode population responses to control agents. Pp. 114–125 *in* Zehr, ed. Methods for evaluating plant fungicides, nematicides, and bactericides. St. Paul, Minnesota: American Phytopathological Society.

2. Demeure, Y., D. W. Freckman, and S. D. Van Gundy. 1979. Anhydrobiotic coiling of nematodes in soil. Journal of Nematology 11:189–195.

3. Donahue, R. L. 1965. Soils: An introduction to

TABLE 6. Correlation of percentage of *P. penetrans* anhydrobiotes and percentage of soil moisture with meteorological data (soil and aerial) at two depths.*

	Correlation coefficients			
	Vineland silt loam		Fox loamy sand	
Variables	Upper	Lower	Upper	Lower
Anhydrobiotes (%) × Soil moisture	−0.8444	−0.6313	−0.7078	−0.4639
Soil temperature	0.7094	0.5240	0.7910	0.2508
Accumulated rainfall	−0.7382	−0.5952	−0.4839	−0.3218
Mean max. air temperature	0.6269	0.4957	0.7570	0.4372
Total sunshine	0.7900	0.4701	0.7824	0.3440
Accumulated wind run	0.1494	0.1355	0.3088	0.1038
Soil moisture (%) × Soil temperature	−0.7499	−0.8013	−0.8967	−0.6059
Accumulated rainfall	0.9165	0.9835	0.5628	0.6051
Mean max. air temperature	−0.6855	−0.7821	−0.8255	−0.6906
Total sunshine	−0.8552	−0.8530	−0.6053	−0.6939
Accumulated wind run	0.2466	0.3499	0.6941	0.6991

Aerial meteorological data was compiled 5 days before each sampling.
Correlation coefficient r (0.05) = 0.6021.
* Upper, 0–2.5 cm; lower, 2.5–15 cm.

soils and plant growth, 2nd ed. New York: Prentice-Hall.

4. Feldmesser, J., W. A. Feder, R. V. Rebois, and P. C. Hutchins. 1960. Longevity of *Radopholus similis* and *Pratylenchus brachyurus* in fallow soil in the greenhouse. Anatomical Record 137:355.

5. Freckman, D. W., D. T. Kaplan, and S. D. Van Gundy. 1977. A comparison of techniques for extraction and study of anhydrobiotic nematodes from dry soils. Journal of Nematology 9:176–181.

6. Glazer, I., and D. Orion. 1983. Studies on anhydrobiosis of *Pratylenchus thornei*. Journal of Nematology 15:333–338.

7. Harrison, B. D., and D. J. Hooper. 1963. Longevity of *Longidorus elongatus* (de Man) and other nematodes in soil kept in polyethylene bags. Nematologica 9:158–160.

8. Olthof, Th. H. A. 1971. Seasonal fluctuations in population densities of *Pratylenchus penetrans* under a rye–tobacco rotation in Ontario. Nematologica 17: 453–459.

9. Rossner, J. 1971. Einfluss der austrocknung des Bodens auf wandernde Wurzelnematoden. Nematologica 17:127–144.

10. Townshend, J. L. 1963. A modification and evaluation of the apparatus for the Oostenbrink direct cotton–wool filter extraction method. Nematologica 9:106–110.

11. Townshend, J. L. 1971. Movement of *Pratylenchus penetrans* and the moisture characteristics of three Ontario soils. Nematologica 17:47–57.

12. Townshend, J. L. 1972. Influence of edaphic factors on penetration of corn roots by *Pratylenchus penetrans* and *P. minyus* in three Ontario soils. Nematologica 18:201–212.

13. Townshend, J. L. 1984. Anhydrobiosis in *Pratylenchus penetrans.* Journal of Nematology 16:282–289.

14. Townshend, J. L., and C. F. Marks. 1976. Available soil moisture and the expression of damage caused by *Pratylenchus penetrans* in flue-cured tobacco. Nematologica 22:65–70.

15. Townshend, J. L., and C. F. Marks. 1977. Temperature and the expression of damage caused by *Pratylenchus penetrans* in flue-cured tobacco. Nematologica 23:29–32.

16. Wyss, U. 1970. Zur toleranz wandernder Wurzelnematoden gegenuber zunehmender austrocknung des Bodens und hohen osmotischen drucken. Nematologica 16:16–73.