Influence of Edaphic Factors and Previous Crop on *Pratylenchus* spp. Population Densities in Potato

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Abstract: Root and soil samples from commercial potato fields were assayed for nematodes in 1983 and 1984. Pratylenchus spp. population densities in Suffolk County, New York, were consistently, though not always statistically, higher in potato fields that had been planted to rye or wheat rather than potatoes during the previous growing season. Regardless of the previous crop, population densities in the two potato production areas in Suffolk County differed significantly: population densities on the south fork were 1.9–5.5 times higher than those on the north fork. Species prevalence differed significantly on the two forks but was not related to the previous year's crop. P. penetrans and P. crenatus were found primarily on the north and south forks, respectively. Differences in species distribution were associated with differences in soil types. P. crenatus was usually found on loams and silt loams, but P. penetrans was found more frequently on sandy soils.

Key words: Baermann pie pan, edaphic factor, population density, potato, Pratylenchus crenatus, Pratylenchus penetrans, root lesion nematode, rye, Secale cereale, soil moisture, soil type, Solanum tuberosum, survey, Triticum aestivum, wheat.

Rotation of potato with cereals, particularly rye, is a common practice in Suffolk County, New York. Several species of Pratylenchus Loof which parasitize potato reproduce well on cereals (16,31). Cereal rotations can help control the Colorado potato beetle, Leptinotarsa decemlineata (Say), which limits potato production in the Northeast (40). The effect of rotation on Pratylenchus spp., however, needs to be assessed, especially as greenhouse tests showed that P. penetrans soil population densities under a potato crop were higher following rye than fallow (6). In field experiments in the Netherlands, soil population densities of both P. penetrans and P. *pratensis* Thorne (= P. *crenatus*) (15) were higher following rye than potato (24). The pathogenicity and reproductive potential of different species in this genus vary considerably on different hosts, but most are polyphagous. The identity of Pratylenchus spp. from potato in Suffolk County was not known, although Sher and Allen (29) identified specimens from bean as *P. penetrans* and from an unspecified crop as *P. crenatus*.

Information on the effects of rotation on plant parasitic nematode populations is especially important in Suffolk County. Both fumigant (17) and nonfumigant (18) nematicides have contaminated groundwater here, and resulting regulations have greatly limited options for nematode control. Our objective was to evaluate the influence of 1 year of a cereal rotation on Pratylenchus spp. population densities on potato. The relationship of population densities to edaphic factors likely to be influenced by rotation was also investigated. Potatoes are produced at the eastern end of Suffolk County on two peninsulas, the north fork and the south fork. These two areas were considered separately in this study because of differences in potato production practices, soil types, and climate.

MATERIALS AND METHODS

In 1983 and 1984, respectively, 3 and 14 commercial farms on each of the two forks of Long Island were selected for sampling. A pair of fields, one rotated and one nonrotated, was chosen from each farm to minimize cultural differences between the fields. The rotated field had grown rye, or in one case wheat, during the previous growing season. The nonrotated field had been cropped to potatoes the previous year;

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however, it might have been planted to cereals in other years. The same cultivar was present in the rotated and the nonrotated field on all farms selected in 1983 and on 23 of 28 farms selected in 1984. In 1983, samples were taken from Superior on all three south fork farms, Katahdin on two north fork farms, and Hudson on the third north fork farm. In 1983, fields were sampled twice: once midseason (27 June-19 July) and again late in the growing season (20 July-19 August). In 1984, samples were taken from Superior on 15 south fork and 9 north fork farms, Katahdin on 12 south fork and 14 north fork farms, Hudson on 1 south fork and 2 north fork farms, and Chippewa on 3 north fork farms. Fields were sampled only once early in the growing season (15 May-20 June) in 1984. Fields sampled in 1984 were not the same as those sampled in 1983.

Samples were taken along five diagonal passes across a 1.5-2-ha section of each field. Approximately 1 g lateral roots and 50 cm³ of the soil falling from the roots were collected from each of 10 potato plants along each of the diagonals. Each of the five composite soil samples was sieved through a 6.3-mm-pore screen and mixed thoroughly. Nematodes were then extracted from 50 cm³ of each soil sample for 5 days at 20-25 C using a modification of the Baermann pie pan technique (9). After the nematode suspension had settled overnight at 10 C, its volume was reduced to 50 ml. Nematodes were extracted from a 5-g subsample of root segments randomly chosen from each composite root sample. The root segments were shaken in 100 ml water for 3 days at 20-25 C; the root suspension was then extracted for 24 hours on a Baermann pie pan. Male, female, and juvenile Pratylenchus spp. were counted under a dissecting microscope. Temporary water mounts were made of at least 20 randomly selected Pratylenchus females from one of the five root samples from 48 of the 56 fields surveyed during 1984. These females were identified to species with Nomarski optics. Although we used Corbett's key for species identification (3), we relied less on tail shape than on presence of sperm in spermathecae for differentiating *Pratylenchus penetrans* from *P. crenatus*, as tail shape is variable in both these species (30,36).

Using descriptions from the Suffolk County soil survey (38), we compared soil types found in sampled fields. In addition, representative portions of the soil samples collected for nematode extraction were analyzed for selected soil characteristics. Moisture content at three matric potentials (-10, -30, and -100 kPa) was determined for the 1983 samples with a ceramic plate extractor (Soil Moisture Laboratory, Santa Barbara, Calif.). The pH of samples from 1984 was measured in 0.01 M calcium chloride (7). The Cornell University Soil Testing Laboratory analyzed 1984 samples for organic matter content and 1983 samples for organic matter content, pH in 0.01 M calcium chloride, exchangeable acidity, phosphorus, potassium, magnesium, and calcium (7). The pH values were adjusted to represent pH as measured in water by adding 0.6 pH units.

For data analysis, we assumed that selected farms at the two locations were randomly chosen with respect to within-farm rotational differences and within-field seasonal differences. Linear combinations of the log_e-transformed nematode population density data were analysed by one-way analyses of variance according to repeated measures methods (28). Edaphic factors and species data were evaluated with correlation coefficients, analyses of variance, and chi-square.

RESULTS

In 1983, population densities of *Pratylenchus* spp. did not differ significantly between sampling times (Table 1), although densities were usually higher in late-season than in mid-season samples. Mean population densities in both roots and soil were always higher in rotated than in nonrotated fields. Root population densities were 2-14 times higher (P < 0.10) in rotated than in nonrotated fields. Soil population densities were up to 11 times higher in

Field location	Crop preceding _ potato	Pratylenc	hus/g root	Pratylenchus/100 cm ³ soil		
		Mid season	Late season	Mid season	Late season	
North fork†	Rye Potato	$135 \pm 71 \\ 10 \pm 8$	$292 \pm 260 \\ 34 \pm 34$	$126 \pm 103 \\ 11 \pm 6$	$112 \pm 107 \\ 14 \pm 14$	
South fork	Rye Potato	$993 \pm 25 \\ 546 \pm 285$	$1,524 \pm 33 \\ 856 \pm 330$	513 ± 5 478 ± 308	$723 \pm 126 \\ 400 \pm 201$	

TABLE 1. Influence of previous crop, field location, and sampling time* on *Pratylenchus* spp. population densities collected from potato fields in Suffolk County, New York, in 1983.

Mean population density \pm standard error calculated from three field means (five samples per field).

* Sampling times: mid season = 27 June-19 July; late season = 20 July-19 August.

† Only two of the three farms on the north fork could be sampled during the late season.

rotated than in nonrotated fields, although the differences were not significant. Root and soil samples from the south fork had significantly higher mean population densities than those from the north fork at both sampling times (P < 0.05). Root population densities from nonrotated fields were 25–55 times higher on the south fork than on the north fork. Root population densities from rotated fields were 5–7 times higher on the south fork than on the north fork. Analysis of soil population densities gave similar results. No interactions between sampling time, location, or rotation were evident.

In 1984, population densities in root samples were up to 2 times higher in rotated than in nonrotated fields (Table 2); however, these differences in population densities were not statistically significant. Root population densities from the south fork were 2-4 times higher (P < 0.05) than those from the north fork regardless of rotational history. Analysis of soil population densities gave similar results. No interactions between location or rotation were evident. The conclusions of this experiment were not changed by eliminating from the analysis all farms with different cultivars in rotated and nonrotated fields.

Among the samples collected in 1983 in which female *Pratylenchus* were found, males were present in 81% of 27 north fork samples and in only 67% of 60 south fork samples. In 1984, males were again absent from many south fork samples; among samples in which female *Pratylenchus* were found, males were present in 86% of 125 north fork samples and in only 22% of 134 south fork samples. The relative absence of males in south fork samples suggests that different sex ratios or different species of *Pratylenchus* might occur on the north and south forks.

Only two species of Pratylenchus were found in 1984. On the north fork, P. penetrans was detected in root samples from all of 12 rotated and 10 of 11 nonrotated fields, but P. crenatus was found in only one rotated and two nonrotated fields. On the south fork, P. penetrans was identified in root samples from only 2 of 12 rotated and 4 of 13 nonrotated fields, whereas P. crenatus was found in 11 rotated and 11 nonrotated fields. Mixed populations were detected in three south fork and two north fork fields. The distribution of the two species differed significantly between the two forks ($\chi^2 = 15.48$ for rotated fields, $P < 0.01; \chi^2 = 7.36$ for nonrotated fields, P < 0.01). There was no difference in

TABLE 2. Influence of previous crop and field location on *Pratylenchus* spp. population densities collected from potato fields in Suffolk County, New York, in 1984.

Field location	Crop preceding potato	Pratylenchus per g root	Pratylenchus per 100 cm ³ soil	
North fork	Rye Potato	400 ± 91 206 ± 59	$369 \pm 111 \\ 171 \pm 55$	
South fork	Rye Potato	$779 \pm 209 720 \pm 187$	$1,181 \pm 309 \\944 \pm 191$	

Mean population density \pm standard error calculated from 14 field means (five samples per field) sampled 15 May-20 June.

		OM† (%)	рН	H⁺ (meq)	P (ppm)	K (ppm)	Mg (ppm)	Ca (ppm)	
				Nonrotate	d fields				
1983	Root‡ Soil	$0.522 \\ 0.449$	$0.813* \\ 0.770$	$-0.215 \\ -0.294$	$-0.606 \\ -0.500$	$-0.339 \\ -0.361$	$0.533 \\ 0.494$	$0.343 \\ 0.279$	
1984	Root Soil	$0.397** \\ 0.275$	$\begin{array}{c} 0.128\\ 0.200 \end{array}$						
				Rotated	fields				
1983	Root Soil	$-0.029 \\ 0.062$	$0.687 \\ 0.615$	$-0.119 \\ -0.031$	$0.057 \\ 0.029$	$0.237 \\ 0.323$	$0.236 \\ 0.299$	$0.737 \\ 0.791$	
1984	Root Soil	$\begin{array}{c} 0.255\\ 0.282 \end{array}$	$-0.076 \\ -0.042$						

TABLE 3. Correlation of edaphic factors with *Pratylenchus* spp. population densities from commercial potato fields sampled in 1983 and 1984 in Suffolk County, New York.

Correlation coefficients based on five replicates for 1983 and 28 for 1984. Significant correlations are denoted by * for P < 0.10 and ** for P < 0.05.

 \dagger Organic matter (OM), pH, exchangeable acidity in milliequivalents/100 g soil (H⁺), phosphorus (P), potassium (K), magnesium (Mg), and calcium (Ca) from portions of soil samples collected for nematode extraction.

[‡]Root or soil population densities transformed by natural logarithms. In 1983, one (1) was added to all population densities before transformation.

species distribution between rotated and nonrotated fields within each fork.

The moisture-holding capacity of sample soils at -10 and -30 kPa was not related to rotation or location. Mean soil moistures (\pm standard errors) were 31.7%(± 1.8) and 19.2% (± 1.4), respectively. At -100 kPa, however, repeated measures analysis detected a significant (P < 0.05) interaction between rotation and location in the soil moisture data. On the north fork, rotated fields had higher moistureholding capacities ($14.1\% \pm 1.0$) than nonrotated fields ($10.9\% \pm 1.6$), while the reverse was true for fields on the south fork (rotated = $12.5\% \pm 2.9$; nonrotated = $13.7\% \pm 2.5$).

A similar interaction (P < 0.025) was observed in the organic matter data from 1983. On the north fork, organic matter was higher in rotated (2.24–3.04%) than in nonrotated (1.70–2.30%) fields; but on the south fork, it was lower in rotated (1.64–3.52%) than in nonrotated (2.38– 4.14%) fields. Repeated measures analysis also showed that in 1983 pH was lower (P < 0.025) on the north fork (4.58–4.82) than on the south fork (4.78–5.06).

Exchangeable acidity (9–20 meq/100 g), phosphorus (23–43 μ g/g), potassium (41–132 μ g/g), magnesium (17–90 μ g/g), and

calcium (118–402 μ g/g) were not strongly correlated with root or soil population densities in samples from rotated or nonrotated fields in 1983 (Table 3). In nonrotated fields, pH (4.58–5.06) was positively correlated with population densities in roots (r = 0.813, P < 0.10).

For 1984 samples, only pH and percent organic matter were evaluated (Table 3). Log_e-transformed Pratylenchus spp. root population densities from nonrotated fields were weakly (r = 0.397) but significantly (P < 0.05) correlated with organic matter (1.64-3.96%). Organic matter was positively correlated (r = 0.503, P < 0.10) with log_e-transformed root population densities of P. crenatus in nonrotated fields. No correlation between Pratylenchus spp. population densities and pH (4.1-5.2) was seen in 1984. Even when samples were separated according to species, no correlations were found between pH and log_e-transformed population densities of either species.

DISCUSSION

Pratylenchus spp. population densities in Suffolk County were consistently, though not always statistically, higher in potato fields that had been in rye rather than in potatoes during the previous year. Rye has a dense root system and is known to support high population densities of both P. penetrans and P. crenatus (6,24). In addition, rotation with crops such as rye can modify edaphic factors influencing nematode movement, penetration of host roots, and survival. Although organic residues and amendments have been observed to decrease nematode population densities (8,14), the additional organic matter from rye stubble might also increase nematode population densities indirectly by improving soil tilth and moisture-holding capacity and by promoting increased potato root growth. In our 1984 samples from nonrotated fields, there was a weak but significant positive correlation between organic matter and Pratylenchus spp. root population densities. Although not statistically significant, this correlation was stronger in 1983, reflecting the difference between nonrotated fields on the two forks: nonrotated fields on the south fork had both higher population densities and more organic matter than those on the north fork (data not presented). The amount of organic matter was similar in rotated fields on the two forks, so no correlation with nematode population densities was detected.

Soil texture (10,25,33,34) and soil moisture (9,33,34) affect Pratylenchus spp. population densities. The moisture-holding capacity of some soils is primarily determined by soil texture but is also influenced by the organic matter in those soils. According to the Suffolk County soil survey (38), north fork fields tend to be sandier than south fork fields. Riverhead sandy loam, coarseloamy Dystrochrept, was found in 3% of the south fork fields and in 53% of the north fork fields sampled in this experiment. None of the north fork fields sampled contained Bridgehampton silt loam, a coarse-silty Dystrochrept found in 74% of the south fork fields sampled. Haven loam, a coarse-loamy Dystrochrept, was present in 71% of north fork and 44% of south fork fields. For sandy north fork fields in particular, more organic matter in rotated than in nonrotated fields may have been

responsible for the increased moistureholding capacity in rotated fields, and hence their ability to sustain higher *Pratylenchus* spp. population densities. Both moistureholding capacity and organic matter were slightly higher in nonrotated fields than in rotated fields on the south fork, but in these siltier soils, organic matter and moistureholding capacity had less effect on nematode population densities.

In both 1983 and 1984, Pratylenchus spp. population densities were much higher in south fork than in north fork fields, regardless of the previous year's crop. We do not feel that the differences are primarily related to cultivar. Our samples were collected early in the growing season in 1984 to minimize the effect of cultivar on nematode population density. P. penetrans soil population densities did not increase at different rates on six potato cultivars (22). Bernard and Laughlin (1) reported that P. penetrans reproduces more on Katahdin than on Superior. In microplots in Suffolk County, P. penetrans reproduced most on Hudson, less on Katahdin, and least on Superior (Loria and Kotcon, unpubl.). On the basis of cultivar alone, therefore, we would expect higher population densities to occur on the north fork than on the south fork because more samples were taken from Superior than from Katahdin on the south fork and more samples were taken from Katahdin than from Superior on the north fork. Population densities, however, were higher on the south fork than on the north fork.

Fields from the north and south forks did not differ in exchangeable acidity, potassium, phosphorus, magnesium, or calcium. Soil pH can affect nematode population densities (12,20,39), but the positive correlation of pH with root population densities in 1983 did not adequately explain the observed population density differences on the two forks, as these correlations did not hold in 1984. Although the moisture-holding capacity of north fork soil at -100 kPa was higher in rotated than in nonrotated fields, usually the moistureholding capacity of the soils sampled from each fork varied little. At matric potentials of -10 and -30 kPa, no differences could be detected in the field soils of either location. Evidently, soil porosity and soil structure strongly influence moistureholding capacity at these low matric potentials even in plowed soil (25,37). The edaphic factors measured did not account for the large difference between the north and south population densities.

The difference in Pratylenchus population densities on the two forks of Long Island may be related to the occurrence of different species in these areas. Mixed populations did occur in some fields, but P. penetrans, an amphimictic species (32), was primarily associated with north fork fields while P. crenatus, a species in which males do not occur (16), was associated with south fork fields. The two species are sympatric over much of the northeastern United States and eastern Canada (35), but they also occur alone much of the time (2,5,11,23). Species distribution is certainly influenced by host crop, soil type, pH, temperature, and moisture. Loof (16) reported that potatoes are a poor host for P. crenatus, whereas grains and cereals are very favorable. P. penetrans has a wide host range, including both grains and potatoes. Brown et al. (2) reported a predominance of P. crenatus in wheat-potato rotations. It is possible that more frequent grain (rye, wheat, sorghum-sudangrass) rotations on the south fork have encouraged the buildup of P. crenatus. P. crenatus is reported to occur primarily on light sandy soils in Europe and Wisconsin (5,16). In Suffolk County, as in Ohio (2), this species was associated with loams and silt loams, whereas P. penetrans was more frequently found on sandier soils. Kimpinski and Willis (12) reported that P. penetrans has a higher optimum pH range than P. crenatus on alfalfa, but there was little difference in the reproduction of the two species at pH 5.0, the lowest pH they tested. We found no correlation between pH (4.1-5.2) and population densities of either species on potato in north and south fork fields sampled in 1984. Although the effect of pH on population densities of Pratylenchus spp. varies with the host crop (12), the lack of correlation in our study may be a function of the narrow range of pH detected. A slight temperature difference between the two forks may also be responsible for the distribution of the two species. The 30-year average daily maximum temperatures were 16.0 C on the north fork and 14.7 C on the south fork (21). On alfalfa, P. crenatus reproduces better than P. penetrans at lower temperatures (12). Similarly, on maize, temperatures higher than 15 C are detrimental to P. crenatus (4). Dickerson et al. (5) reported optimum reproduction of P. penetrans at 24 C. The effect of temperature on population densities of Pratylenchus spp., however, is influenced by host crop (5,12) and soil moisture (13). Krause (13)found that P. penetrans reproduces better at 25 C than at 20 C regardless of the soil moisture. P. crenatus, on the other hand, increases more in dry soil than wet soil at 25 C, yet at 20 C the reverse is true. Our data also show P. crenatus populations predominating on the south fork where temperatures are cooler and the moistureholding capacity of the soil is higher than on the north fork.

Proper identification of these two species of *Pratylenchus* is important for growers, as the pathogenicity of these species differs markedly on potato. Microplot data (26) have indicated that *P. crenatus* does not cause yield losses on potato even in association with *Verticillium dahliae*. Dickerson et al. (5) also found that *P. crenatus* does not cause significant yield losses on potato.

P. penetrans, on the other hand, does decrease potato yields (22), especially when the potatoes suffer temperature and moisture stress. P. penetrans also interacts synergistically with V. dahliae, causing yield losses even at low nematode population densities (19,27). Comparative sampling in Suffolk County has indicated that high populations of P. crenatus are often associated with apparently healthy potatoes, while low populations of P. penetrans are associated with poorly growing potatoes (Florini and Loria, unpubl.). Diagnostic services should consider the identity of *Pratylenchus* species as well as population densities when recommending control measures to potato growers. Though they seem to occupy different ecological niches, further study of possible competition between the two species might show whether *P. crenatus* could be limiting *P. penetrans* damage.

LITERATURE CITED

1. Bernard, E. C., and C. W. Laughlin. 1976. Relative susceptibility of selected cultivars of potato to *Pratylenchus penetrans*. Journal of Nematology 8:239– 242.

2. Brown, M. J., R. M. Riedel, and R. C. Rowe. 1980. Species of *Pratylenchus* associated with *Solanum tuberosum* cv. Superior in Ohio. Journal of Nematology 12:189–192.

3. Corbett, D. C. M. 1969. *Pratylenchus pinguicaudatus* n. sp. (Pratylenchinae: Nematoda) with a key to the genus *Pratylenchus*. Nematologica 15:550–556.

4. Dao, F. 1970. Climatic influence on the distribution pattern of plant parasitic and soil inhabiting nematodes. Mededelingen Landbouwhogeschool, Wageningen 70-2.

5. Dickerson, O. J., H. M. Darling, and G. D. Griffin. 1964. Pathogenicity and population trends of *Pratylenchus penetrans* on potato and corn. Phytopathology 54:317-322.

6. Fawole, B., and W. F. Mai. 1975. Population dynamics of *Pratylenchus penetrans* in a potato-rye crop rotation. Proceedings of the American Phytopathological Society 2:97 (Abstr.).

7. Grewling, T., and M. Peech. 1965. Chemical soil tests. Cornell University Agricultural Experiment Station and New York State College of Agriculture Bulletin 960, Ithaca.

8. Johnson, L. F., A. Y. Chambers, and H. E. Reed. 1967. Reduction of root knot of tomatoes with crop residue amendments in field experiments. Plant Disease Reporter 51:219-222.

9. Kable, P. F., and W. F. Mai. 1968. Influence of soil moisture on *Pratylenchus penetrans*. Nematologica 14:101–122.

10. Kable, P. F., and W. F. Mai. 1968. Overwintering of *Pratylenchus penetrans* in a sandy loam and a clay loam soil at Ithaca, New York. Nematologica 14: 150–152.

11. Kimpinski, J. 1979. Root lesion nematodes in potatoes. American Potato Journal 56:79-86.

12. Kimpinski, J., and C. B. Willis. 1981. Influence of soil temperature and pH on *Pratylenchus penetrans* and *Pratylenchus crenatus* in alfalfa and timothy. Journal of Nematology 13:333–338.

13. Krause, W. 1981. Zur Populationsdynamik von Pratylenchus penetrans (Cobb, 1917) Chitwood und Oteifa, 1952 und P. crenatus Loof, 1960 in Abhängigkeit ausgewählter ökologischer Faktoren. (On the population dynamics of Pratylenchus penetrans (Cobb, 1917) Chitwood and Oteifa, 1952 and P. crenatus Loof, 1960, as influenced by select ecological factors. Translated by J. Hamilton and I. Mueller. Archiv für Phytopathologie und Pflanzenschutz 17:379–386.

14. Linford, M. B., F. Yap, and J. M. Oliveira. 1938. Reduction of soil populations of the root-knot nematode during decomposition of organic matter. Soil Science 45:127-141.

15. Loof, P. A. A. 1960. Taxonomic studies on the genus *Pratylenchus* (Nematoda). Tijdschrift over Plantenziekten 66:29-90.

16. Loof, P. A. A. 1978. The genus *Pratylenchus* Filipjev, 1936 (Nematoda: Pratylenchidae): A review of its anatomy, morphology, distribution, systematics and identification. Swedish University of Agricultural Sciences Research Information Centre, Växtskyddraporter. Jordbruck 5. Uppsala, Sweden.

17. Loria, R., R. E. Eplee, J. H. Baier, T. M. Martin, and D. D. Moyer. 1986. Sweep shank fumigation with 1,3-dichloropropene: Efficacy against *Pratylenchus penetrans* and subsequent groundwater contamination. Plant Disease 70:42-45.

18. Marshall, E. 1985. The rise and decline of Temik. Science 229:1369-1371.

19. Martin, M. J., R. M. Riedel, and R. C. Rowe. 1982. Verticillium dahliae and Pratylenchus penetrans: Interactions in the early dying complex of potato in Ohio. Phytopathology 72:640-644.

20. Morgan, G. T., and A. A. MacLean. 1968. Influence of soil pH on an introduced population of *Pratylenchus penetrans*. Nematologica 14:311-312.

21. National Oceanic and Atmospheric Administration. 1982. Monthly normals of temperature, precipitation, and heating and cooling degree days 1951– 1980, New York. Climatology of the United States, Number 81. Asheville, North Carolina: National Oceanic and Atmospheric Administration.

22. Olthof, Th. H. A. 1986. Reaction of six Solanum tuberosum cultivars to Pratylenchus penetrans. Journal of Nematology 18:54–58.

23. Olthof, Th. H. A., R. V. Anderson, and S. Squire. 1982. Plant-parasitic nematodes associated with potatoes (*Solanum tuberosum L.*) in Simcoe County, Ontario. Canadian Journal of Plant Pathology 4: 389-391.

24. Oostenbrink, M. 1956. Over de invloed van verschillende gewassen op de vermeerdering van en de schade door *Pratylenchus pratensis* en *Pratylenchus penetrans* (Vermes, Nematoda), met vermelding van een afwijkend moheidsverschijnsel bij houtige gewassen. (English summary: The influence of different crops on the reproduction of and damage by *Pratylenchus pratensis* and *Pratylenchus penetrans* [Vermes, Nematoda], with a record of an unidentified sickness in woody perennials; English subtitles on tables.) Tijdschrift over Plantenziekten 62:189–203.

25. Prasad, J. S., and Y. S. Rao. 1980. Influence of edaphic factors on the buildup of the root lesion nematode, *Pratylenchus indicus* Das, 1960, in rice: I. Effect of type, texture, porosity, and moisture content of soil. Revue d'Écologie et de Biologie du Sol 17: 173–179.

26. Riedel, R. M., R. C. Rowe, and M. J. Martin. 1985. Differential interactions of *Pratylenchus crena*tus, P. penetrans, and P. scribneri with Verticillium dah*liae* in potato early dying disease. Phytopathology 75: 419-422.

27. Rowe, R. C., R. M. Riedel, and M. J. Martin. 1985. Synergistic interactions between *Verticillium dahliae* and *Pratylenchus penetrans* in potato early dying disease. Phytopathology 75:412-418.

28. Rowell, J. G., and D. E. Walters. 1976. Analysing data with repeated observations on each experimental unit. Journal of Agricultural Science, Cambridge 87:423-432.

29. Sher, S. A., and M. W. Allen. 1953. Revision of the genus *Pratylenchus* (Nematoda: Tylenchidae). University of California Publications in Zoology 57: 441-470.

30. Tarte, R., and W. F. Mai. 1976. Morphological variation in *Pratylenchus penetrans*. Journal of Nematology 8:185–195.

31. Thames, Walter H. 1982. The genus *Pratylenchus*. Pp. 108–126 in R. D. Riggs, ed. Nematology in the southern region of the United States. Southern Cooperative Series Bulletin 276.

32. Thistlewayte, B. 1970. Reproduction of *Pratylenchus penetrans* (Nematoda: Tylenchida). Journal of Nematology 2:101-105.

33. 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.

34. Townshend, J. L. 1973. Survival of *Pratylen*chus penetrans and *P. minyus* in two Ontario soils. Nematologica 19:35-42. 35. Townshend, J. L., J. W. Potter, and C. B. Willis. 1978. Ranges of distribution of species of *Pratylenchus* in northeastern North America. Canadian Plant Disease Survey 58:80-82.

36. Townshend, J. L., R. Tarte, and W. F. Mai. 1978. Growth response of three vegetables to smoothand crenate-tailed females of three species of *Pratylenchus*. Journal of Nematology 10:259–263.

37. Wallace, H. R. 1958. Movement of eelworms. I. The influence of pore size and moisture content of the soil on the migration of larvae of the beet eelworm, *Heterodera schachtii* Schmidt. Annals of Applied Biology 46:74–85.

38. Warner, J. W., Jr., W. E. Hanna, R. J. Landry, J. P. Wulforst, J. A. Neeley, R. L. Holmes, and C. E. Rice. 1975. Soil survey of Suffolk County, New York. United States Department of Agriculture, Soil Conservation Service, in cooperation with Cornell Agricultural Experiment Station. Washington, D.C.: United States Government Printing Office.

39. Willis, C. B. 1972. Effects of soil pH on reproduction of *Pratylenchus penetrans* and forage yield of alfalfa. Journal of Nematology 4:291-295.

40. Wright, R. J. 1984. Evaluation of crop rotation for control of Colorado potato beetles (Coleoptera: Chrysomelidae) in commercial potato fields on Long Island. Journal of Economic Entomology 77: 1254–1259.