Journal of Nematology 19(3):361–368. 1987.

Pratylenchus penetrans Population Dynamics on Three Potato Cultivars[1]

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Abstract: Reproduction of *Pratylenchus penetrans* on the potato cultivars Hudson, Katahdin, and Superior was determined in greenhouse and field microplot experiments. Although all three cultivars were good hosts for *P. penetrans*, differences in reproductive rate were found. In one greenhouse experiment, Katahdin plants inoculated with 1,500 or 15,000 *P. penetrans* per pot had larger population densities at harvest than did Superior; however differences between these cultivars were not significant in three other greenhouse experiments. In another experiment, population densities of *P. penetrans* on Hudson did not differ from those on Katahdin and Superior when inoculated with 270 and 5,080 nematodes per pot after 45 days in the greenhouse. However, population densities were usually higher on Hudson and Katahdin than on Superior in field microplots at four initial population densities during two seasons. Higher population densities on Hudson were detectable 304 days after planting in one of the two microplot studies. The juvenile : female and the male : female ratios were sometimes larger on Katahdin than on Superior, but differences were inconsistent. There was no evidence of resistance in the three cultivars evaluated, but reproduction was generally highest on Hudson and lowest on Superior.

Key words: extraction efficiency, fecundity, host suitability, potato, *Pratylenchus penetrans*, resistance, root-lesion nematode, *Solanum tuberosum*, survival.

The root-lesion nematode, *Pratylenchus penetrans* (Cobb, 1917) Filipjev and Schuurmans-Stekhoven, 1941, is the most important *Pratylenchus* sp. affecting potato in the Northeastern United States (13). Although potato cultivars differ in their ability to support nematode reproduction, none are known to be completely resistant to *P. penetrans* (4).

The potato cultivars Superior and Katahdin are widely grown in the Northeastern United States. The cultivar Hudson is resistant to the potato cyst nematode, *Globodera rostochiensis* (12), and has been reported to be more resistant to *P. penetrans* than other potato cultivars (4; Dunn, pers. comm.). Commercially acceptable cultivars with useful levels of resistance to *P. penetrans* would provide a valuable tool for nematode management, particularly in potato production areas where nematicides are unavailable. The objective of the experiments described here was to assess reproduction of *P. penetrans* on the cultivars Hudson, Katahdin, and Superior. A preliminary report of a portion of this data has been published (8).

Received for publication 23 October 1986.

[1] This research was supported in part by a grant from the Northeast Pesticide Impact Assessment Program (subcontract USDA-TPSU-CU-2057-336).

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We thank B. A. Kempter and G. Vassilev for technical assistance. We also thank Drs. B. B. Brodie, W. F. Mai, and R. L. Millar for critical review of the manuscript.

MATERIALS AND METHODS

Greenhouse experiments: The following procedures were used in all experiments except where indicated. Single-eye seed pieces taken from certified seed tubers of potato (*Solanum tuberosum* L. cv. Katahdin and Superior) were sprouted for 2 weeks in the greenhouse in moist vermiculite. Seed pieces with stems approximately 5 cm long were transplanted into 18-cm-d plastic pots containing 2,500 cm^3 steamed sand : soil (1:1). The soil in each pot was infested by adding a water suspension of mixed age groups of *P. penetrans* which had been extracted from roots of field-grown rye (*Secale cereale* L.). Plants were grown for an additional 60 days. Greenhouse temperatures were usually 22 ± 2 C but occasionally reached 30–35 C. High-pressure sodium-vapor lamps were used to provide supplemental lighting to maintain at least a 12-hour photoperiod.

In Experiment 1, eight replicate plants of Katahdin and Superior were inoculated with 0, 1,500, or 15,000 *P. penetrans* and

fertilizer was not applied. In Experiment 2, four replicate plants of Katahdin and Superior were inoculated with 0, 150, 500, 1,500, 5,000, 15,000, 50,000, or 100,000 *P. penetrans*. Plants in this experiment were fertilized with 250 ml liquid fertilizer (15-16-17, Peters Fertilizer Products, Fogelsville, Pennsylvania) at weekly intervals for 4 weeks. Experiment 3 was identical to Experiment 2 except the 100,000 nematode level was omitted. A randomized complete block design was used for all three experiments.

Fresh roots were weighed at harvest, and *P. penetrans* were extracted from roots by incubating a 1-g sample with 50 ml water in a 250-ml flask on a wrist-action shaker for 10 days. Nematodes were extracted from 100-cm^3 soil for 10 days by the Baermann pan method. Four nematode life stages—females, males, juveniles < 0.3 mm long (primarily second-stage juveniles), and juveniles > 0.3 mm long (primarily third-stage and fourth-stage juveniles)—were counted in each soil and root sample. Stage-specific extraction efficiencies of both methods were estimated as follows: Representative soil and root samples were incubated continuously, and the number of nematodes recovered was determined at 3–5-day intervals. Recovery was assumed to be complete when the number of nematodes recovered each day had decreased to less than 2% of the recovery rate (nematodes per day) after the first 3 days incubation. The total incubation period was approximately 4 weeks. Extraction efficiency of each stage was calculated as the number of that stage extracted at 10 days divided by the total number of that stage recovered after 4 weeks, at which time recovery was assumed to be complete. The population density of each stage in each sample was estimated by dividing the number of that stage recovered after 10 days by the extraction efficiency for that stage. The total number of nematodes from each plant was calculated using the root fresh weight and the soil volume in each pot. The male: female ratio and the ratio of total juveniles per female were also calculated.

Reproduction of *P. penetrans* on Hudson, Katahdin, and Superior was evaluated in a fourth greenhouse experiment. Sprouted single-eye seed pieces were transplanted into 12-cm-d pots containing 1,200 g steamed sand. Pots were infested with 0, 1.7, or 17.0 g maize roots, from greenhouse cultures, which were infected with *P. penetrans*. Sand in uninfested pots was mixed with 8.5 g uninfected maize roots. Five replicate pots of each cultivar at each inoculum level were arranged in a randomized complete block design. Pots were watered as needed, and 50 ml Hoagland's nutrient solution was added to each pot twice each week. Initial population densities were determined by assaying six additional pots of each treatment level using Baermann pans. Root fresh weight was determined at 45 days after transplanting. Nematodes were extracted from a 1-g root sample for 5 days as previously described. Nematodes were extracted from sand by suspending the entire pot of sand in 3 liters of water and pouring the supernatant through a 38-μm-pore sieve. The material on the sieve was washed onto a Baermann pan, and the number of nematodes recovered was determined after a 5-day incubation. Extraction efficiencies from sand were assumed to be similar to those from the sand and soil mix used in Experiments 1, 2 and 3; therefore, data were corrected for extraction efficiency.

Nematode populations (P) from all greenhouse experiments were transformed ($\log_{10}P + 1$) and then analyzed using analysis of variance. Data from Experiments 2 and 3 were combined for analysis.

Microplot experiments: Field microplots were established on Riverhead sandy loam (coarse-loamy, mixed, mesic, typic, Dystrochrepts; 67% sand, 29% silt, 4% clay, 2% organic matter; pH 5.2) at the Long Island Horticultural Research Laboratory in 1984. Soil was excavated from 45-cm-d holes with a tractor-mounted auger. The holes were lined with a fiberglass sheet, 40 cm wide, and refilled with soil. The microplots were fumigated with methyl bromide plus 2% chloropicrin at 458 kg/ha to re-

TABLE 1. Efficiency (%) of extraction of *Pratylenchus penetrans* from roots and soil after incubation for 5 or 10 days.

Lifestage	Roots		Soil	
	5 days	10 days	5 days	10 days
Females	58 (9)	88 (6)	34 (5)	63 (3)
Males	61 (6)	86 (2)	44 (6)	72 (6)
Small juveniles†	50 (5)	82 (2)	23 (3)	54 (8)
Large juveniles‡	63 (3)	89 (2)	41 (6)	67 (8)

Number extracted after 5 or 10 days/number extracted after 4 weeks × 100. Roots (1 g) incubated in 50 ml tap water on a wrist-action shaker at 22 ± 4 C. Soil samples (100 cm^3) incubated in Baermann pans at 22 ± 4 C. Data are means and standard errors of seven samples.

† Less than 0.3 mm in length (primarily second-stage juveniles).

‡ Greater than 0.3 mm in length (primarily third-stage and fourth-stage juveniles).

TABLE 2. Population changes and sex and age class ratios of *Pratylenchus penetrans* on Katahdin and Superior potatoes 60 days after planting in greenhouse Experiment 1.

Inoculum level† and cultivar	Nematodes per plant		Male : female	Juvenile : female
	P_i	P_f		
Control				
Katahdin	0	0		
Superior	0	0		
Low				
Katahdin	1,500	2,449 b	0.81 b	8.57 b
Superior	1,500	550 a	0.34 a	2.19 a
High				
Katahdin	15,000	16,032 b	1.05 a	9.14 b
Superior	15,000	4,688 a	0.80 a	3.16 a

Geometric means of eight replicates per treatment. Data adjusted for stage-specific extraction efficiency. Column means within an initial population level followed by the same letter do not differ according to Duncan's multiple-range test ($P < 0.05$).

† Low = 1,500 nematodes per plant; high = 15,000 nematodes per plant.

duce populations of indigenous pathogens. At planting, the microplots received 0, 3, 30, or 300 grams of *P. penetrans*-infected rye roots from greenhouse cultures and 30, 27, 0, or 0 g of noninfected roots, respectively. Ten replicate microplots of each inoculum level were planted 11 May 1984 with a 'B' sized whole seed tuber of Hudson, Katahdin, or Superior potato using a randomized complete block design. Superior potato tubers were planted between microplots to achieve a uniform canopy similar to that in commercial fields. Irrigation needs were determined by soil tensiometers installed in the microplots. Fertilizer and pesticide applications were made according to standard commercial recommendations, but no nematicidal materials were applied to the soil or foliage. Plots were harvested 118 days after planting and were replanted with rye, a common winter cover crop in the Northeastern United States. Population densities of the four nematode life stages were determined from samples of soil and roots collected by removing six cores, 2.5 cm d by 15 cm deep, from each microplot 14, 75, 118, and 304 days after planting potatoes. Cores from each plot were thoroughly mixed, and nematodes were extracted from a 100-cm^3 subsample by incubating on Baermann pans for 10 days.

Microplots were replanted to potato in 1985 with the three cultivars randomized within treatments and blocks. The rye cover crop was turned under and seed pieces were planted 25 April 1985. The procedure was the same as in 1984, except that soil and root samples were collected 12, 70, 119, and 328 days after planting. Population densities were corrected for extraction efficiency using the calculated stage-specific efficiency of extraction from Baermann pans. Population data were transformed ($\log_{10}P + 1$) and subjected to analysis of variance. Means were separated using the least significant ratio test.

RESULTS

Greenhouse experiments: Nematode extraction efficiency varied with the life-stage of the nematode (size), duration of incubation period, and medium (soil vs. roots) from which the nematodes were extracted (Table 1). Average recovery was lower for small juveniles (< 0.3 mm) than for other life-stages. Recovery from roots was greater than from soil, and 10-day incubation resulted in greater nematode recovery than did incubation for 5 days.

Nematode reproduction on Katahdin plants inoculated with 1,500 and 15,000 *P. penetrans* per plant was significantly ($P <$

0.01) greater than on Superior in Experiment 1 (Table 2). The male : female ratio of nematodes recovered from Katahdin was greater than that from Superior, and significantly more juveniles per female were recovered from Katahdin than from Superior (Table 2). There were no significant interactions between cultivar and inoculum level.

Nematode reproduction at comparable inoculum levels was much greater in Experiments 2 and 3 than in Experiment 1. Final populations, averaged for the two cultivars in Experiments 2 and 3, were 8, 300, 2,390, 6,890, 25,800, 60,100, 132,000, and 92,000 per pot for inoculum levels of 0, 150, 500, 1,500, 5,000, 15,000, 50,000, and 100,000 *P. penetrans*/pot, respectively. Final population densities differed significantly ($P < 0.01$) between inoculum levels but not between cultivars. Mean male : female ratios and juvenile : female ratios were 0.35 and 6.21, respectively, and did not differ significantly among cultivars or inoculum levels. Plant growth in these experiments was much greater than in Experiment 1 (data not included), probably due to the application of fertilizer.

Initial populations of *P. penetrans* in Experiment 4 were 1, 270, and 5,080 per pot infested with 0, 1.7, and 17.0 g infected maize roots, respectively. Differences among inoculum levels were significant ($P < 0.01$). Final populations at these inoculum levels were 71, 2,280, and 12,700 per pot and were also significantly different ($P < 0.01$). Nematode reproduction, male : female ratios (0.26) or juvenile : female ratios (2.68) were not significantly different among the three potato cultivars. Nematode reproduction at the high inoculum level was less than in comparable inoculum levels in Experiment 2, probably because of the smaller pot size, which restricted root development, and the shorter period of plant growth before harvest (45 days vs. 60 days in Experiments 2 and 3).

Microplot experiments: Mean initial population densities (14 days after planting) in microplots in 1984 were 0, 1, 8, and 139 *P. penetrans* per 100 cm^3 soil for the control, low, medium, and high treatments, respectively (Fig. 1). Initial population densities did not differ among cultivars. Initial densities differed significantly ($P < 0.01$) among the four levels of rye roots added, and differences due to inoculum levels were evident at all sample dates (Fig. 1). Very low levels of infestation were detected in a few control plots beginning 75 days after planting (data not shown).

At 75 days after planting, population densities in Superior microplots were significantly ($P < 0.05$) greater than in Katahdin or Hudson microplots at the low inoculum level and were significantly ($P < 0.05$) greater than in Katahdin but ($P < 0.05$) less than in Hudson at the medium inoculum level (Fig. 1). Reproduction on cultivars at the high inoculum level was not significantly different. Nematode population densities in Hudson microplots at harvest (118 days after planting) were significantly ($P < 0.05$) greater than in Superior microplots at all inoculum levels except the control. Population densities at 118 days, averaged over the four inoculum levels, were significantly ($P < 0.05$) greater on Hudson than on Superior, unlike the results at 75 days.

Nematode population density decreased over winter even though a rye cover crop was established in the microplots immediately after the potatoes were harvested (Fig. 1). At 304 days after planting, population densities in Hudson microplots were greater than in Katahdin or Superior microplots at the medium and high, but not the low, inoculum levels.

Mean Pi in microplots in 1985 were 1, 21, 217, and 1,060 *P. penetrans* per 100 cm^3 soil for the control, low, medium, and high treatments, respectively, at 12 days after planting. Nematode population densities differed significantly ($P < 0.01$) among the four inoculum levels at all sample dates (Fig. 1). Densities did not differ significantly among cultivars at 12 and 70 days after planting; at 119 days, however, nematode densities on Superior, when averaged over all inoculum levels, were significantly ($P < 0.01$) less than on Katahdin

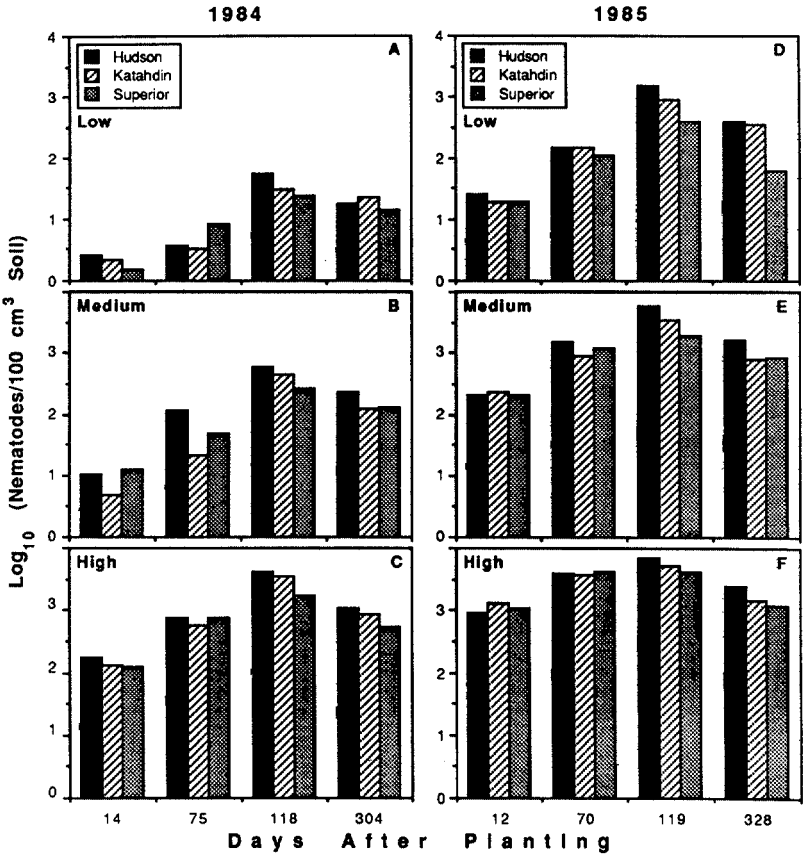

FIG. 1. Population densities of *Pratylenchus penetrans* in field microplots, infested with three initial populations (nematodes/100 cm^3 soil) and planted to three potato cultivars in 1984 (A, B, C) and 1985 (D, E, F). A) Low inoculum level, Pi = 1. B) Medium inoculum level, Pi = 8. C) High inoculum level, Pi = 139. D) Low inoculum level, Pi = 21. E) Medium inoculum level, Pi = 217. F) High inoculum level, Pi = 1,062.

or Hudson. Population densities on Hudson were significantly ($P < 0.01$) greater than on Katahdin or Superior at the low and medium inoculum levels and significantly ($P < 0.01$) greater than on Superior at the high inoculum level. At 328 days after potato planting, population densities in Superior microplots were significantly ($P < 0.01$) lower than in Hudson or Katahdin microplots at the lower inoculum level only.

The mean male : female ratio declined significantly through the 1984 season but did not change greatly over winter (Table 3). This ratio also declined as initial inoculum density increased; however, this trend may be an artifact attributed to a number of zero counts in the control and low initial inoculum treatments. No significant effects were attributed to cultivars and inoculum level interactions in 1984. The mean male : female ratio was 0.36 in 1985 and did not differ significantly among sample dates or cultivars (data not shown).

The mean number of juveniles per female in 1984 was significantly ($P < 0.01$) greater at 118 days after planting than at 14 or 75 days after planting, but then declined ($P < 0.01$) over winter (Table 4). This ratio also increased as inoculum density increased; again, however, zero counts may introduce this trend as an artifact of the analysis. No significant effects were attributed to cultivars and inoculum level interactions. The mean number of juveniles per female in 1985 was 2.78. Differences among cultivars or sample dates were not significant in 1985 (data not shown).

TABLE 3. Male : female ratio of *Pratylenchus penetrans* on Hudson, Katahdin, and Superior potatoes 14, 75, 118, and 304 days after planting in microplots, 1984.

Inoculum level† and cultivar	Male : female			
	14	75	118	304
Control				
Hudson	0.00	0.87	0.83	0.00
Katahdin	0.00	0.00	0.00	0.91
Superior	0.91	0.00	0.83	0.00
Low				
Hudson	0.89	0.56	0.30	0.34
Katahdin	0.72	0.82	0.72	0.44
Superior	0.99	0.49	0.51	0.45
Medium				
Hudson	0.42	0.27	0.32	0.45
Katahdin	0.67	0.30	0.34	0.35
Superior	0.60	0.34	0.58	0.29
High				
Hudson	0.33	0.37	0.39	0.38
Katahdin	0.32	0.20	0.27	0.36
Superior	0.57	0.34	0.25	0.36

Geometric means of 10 replicates per treatment. Data adjusted for stage-specific extraction efficiency. Analysis of variance indicated a significant difference between control and inoculated treatments, and between day 14 and the next three dates. Standard error of the difference of means = 1.44.

† Low = 1, medium = 8, and high = 139 nematodes per 100 cm^3 soil.

TABLE 4. Juvenile : female ratio of *Pratylenchus penetrans* on Hudson, Katahdin, and Superior potatoes at 14, 75, 118, and 304 days after planting in microplots, 1984.

Inoculum level† and cultivar	Juvenile : female			
	14	75	118	304
Control				
Hudson	1.11	1.07	0.83	1.17
Katahdin	1.00	1.00	1.23	0.91
Superior	0.91	1.00	1.11	1.20
Low				
Hudson	1.47	1.14	2.32	1.45
Katahdin	1.36	1.96	3.90	2.31
Superior	1.18	1.64	2.17	1.18
Medium				
Hudson	2.19	2.71	3.72	1.72
Katahdin	1.82	2.52	3.98	1.66
Superior	2.47	2.66	4.98	2.33
High				
Hudson	7.31	3.48	5.27	1.81
Katahdin	3.39	2.29	4.23	1.60
Superior	4.70	2.91	3.99	1.91

Geometric means of 10 replicates per treatment. Data adjusted for stage-specific extraction efficiency. Analysis of variance indicated significant differences occurred among dates and treatments. Standard error of the difference of means = 1.37.

† Low = 1, medium = 8, and high = 139 nematodes per 100 cm^3 soil.

DISCUSSION

All cultivars tested were good hosts for *P. penetrans.* Final population densities were greater than initial densities for all cultivars in all experiments except for Superior in Experiment 1, where lack of nutrients limited plant growth. Hudson, however, supported higher nematode population densities at harvest than did Katahdin or Superior in microplots, although differences were not significant at all inoculum levels in both years. *P. penetrans* population densities at harvest were up to 1.8 and 2.5 times higher on Hudson than on Katahdin and Superior, respectively, in 1984 and up to 1.7 and 3.8 times higher, respectively, in 1985. The larger population density produced in microplots planted to Hudson resulted in a significantly larger population density in those microplots the following spring.

Host suitability to *P. penetrans* has been related to physiological differences (5,6); however, such differences have not been reported among potato cultivars. Studies by Dunn (pers. comm.) and Fawole and Mai (4) showed that population density per gram of root was lower for Hudson than for other cultivars, including Katahdin, and suggested that this indicated the existence of resistance in commercially available potato cultivars. Root weights of Hudson are significantly larger than those of Katahdin, which are larger than those of Superior (9). Large nematode populations in previous studies (4) may have been diluted among a larger root mass in the cultivar Hudson. Jaffee (7) reported a negative correlation between root biomass and the number of *P. penetrans* recovered per gram of root. Since we incorporated root system size and soil populations in calculating final nematode population density, a more accurate estimate of population size was obtained.

In microplots, Katahdin appeared to

support higher final population densities than did Superior, although *P. penetrans* population densities were higher on Superior than on Katahdin at 75 days after planting in 1984. Olthof also found mid-season populations on Superior to be high relative to other cultivars (10,11). Reproduction in the greenhouse was also greater on Katahdin than on Superior in one experiment, although no significant differences were observed in other experiments. Bird (3) suggested that the earlier senescence of Superior reduced the number of generations that could be produced, compared with late-maturing cultivars. In this study, the rate of population increase in microplots in the second half of the season was less for Superior than for Hudson or Katahdin in both 1984 and 1985. This effect would not be readily observed in short-term greenhouse experiments. Bernard and Laughlin (1) also found higher population densities of *P. penetrans* in roots of Katahdin than of Superior. Their study, and a study by Olthof (10), showed that the cultivar Russet Burbank was a better host than Superior.

In general, male : female ratios ranged from 0.2 to 0.8, whereas juvenile : female ratios were always greater than 1.1 and usually ranged from 2 to 9. No consistent effect of cultivar on juvenile : female ratios was observed. Such ratios may indicate nematode resistance in potato cultivars; in the case of *P. penetrans,* however, a resistant cultivar may induce a longer life cycle without necessarily altering the juvenile : female ratio of the nematode population. The reduction in juvenile : female ratio over winter could be due to better survival by adults or to maturation of juveniles into adults on the rye cover crop.

Previous studies of host suitability of potato cultivars to *Pratylenchus* spp. have not included an estimate of the extraction efficiency. The extraction efficiency varies greatly with the nematode lifestage (Table 1). Adjusting for extraction efficiency improves estimates of the actual population density, thereby allowing comparisons with results from other experiments or other studies. However, the ability to accurately estimate the extraction efficiency itself may be limited by the extraction procedure involved. Incubating soil and root samples for 4 weeks, as previously described, may allow sufficient time for females to lay eggs and for the eggs to then hatch, effectively increasing the population of small juveniles (< 0.3 mm) in the sample with time. This could explain the low extraction efficiency of this life stage after 5 and 10 days (Table 1), although other factors may also be involved.

The use of *Globodera rostochiensis*-resistant cultivars such as Hudson has been legally mandated in *G. rostochiensis*-infested fields in New York. This study has demonstrated that root-lesion nematode population densities following Hudson may be higher than those following other potato cultivars, particularly at low (< 140 nematodes/100 cm^3 soil) initial population densities. An economic yield loss model for *P. penetrans* on potato has been described (2). Incorporation of the influence of potato cultivars on nematode population dynamics may be useful in such models. Because of constraints on pesticide use, nematode management programs for potato are likely to depend more on manipulation of nematode populations through cultural practices, including cultivar selection.

Successful long-term management depends on understanding the role of host effects on nematode population dynamics. This study showed that potato cultivars differ significantly with respect to the population build-up they will support. We also have concluded that assessment of resistance of potato cultivars to *P. penetrans* should be based on total populations rather than root population densities and that microplot studies are more effective for determining differences among potato cultivars in host suitability than are greenhouse studies.

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