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Resistance in Potato to *Pratylenchus penetrans*[1]

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Abstract: Potato clones from five different breeding populations were evaluated for their relative resistance and susceptibility to *Pratylenchus penetrans*. Resistance and susceptibility were distinguished by an index of susceptibility (SI) calculated from the numbers of *P. penetrans* (including eggs) per g of root of individual clones in relation to that of a susceptible control at 30 or 70 days after inoculation. Evaluations were carried out using 7.5-cm clay pots in a growth chamber at 24 C with 15-hour day length. In the initial evaluation, 70 days after inoculation, the SI of individual clones ranged from 0.01 to 0.75. Clones that supported the least *P. penetrans* were from a breeding population derived from *Solanum tuberosum* ssp. *andigena* that was originally selected for its resistance to the potato cyst nematode, *Globodera pallida*. In succeeding tests, these clones had a significantly low SI than did susceptible controls or cultivars that were previously reported to possess resistance to *P. penetrans*, except cv. Hudson. Resistance to *P. penetrans* from the Pallida-resistant breeding population was incorporated into potato germplasm better adapted to North American growing conditions.

Key words: breeding, control, *Globodera pallida*, nematode, race, *Solanum tuberosum*.

Pratylenchus penetrans (Cobb) Filipjev & Schuurmans Stekhoven is a serious pathogen of potatoes throughout the potato-growing regions of the northeastern United States, the St. Lawrence River basin region, and the Maritime Provinces of Canada (17). In most of this area, *P. penetrans* not only causes economic losses to potato when acting alone, but causes even more severe losses by interacting with the fungus *Verticillium dahliae* Kleb., causing a disease known as potato early dying (16).

For the most part, control of *P. penetrans* in potato production has been achieved with chemical nematicides (8). The declining use of these nematicides, particularly in the northeastern United States, has increased the need for nonchemical means of managing *P. penetrans* in potato production.

A number of commercial cultivars of potato have been reported to possess some degree of tolerance to *P. penetrans* (1,10, 14). The cultivar Russet Burbank is relatively tolerant to infection by *P. penetrans*, but it does not resist multiplication of the nematode (1,9,14).

Breeding for host resistance to control *P. penetrans* so far has not been feasible because of the lack of resistant germplasm to incorporate into commercial cultivars. Early studies indicated that the potato cultivars Peconic and Hudson were less suitable for *P. penetrans* reproduction than were others, but these data were inconclusive (6). Hudson was later found to support significantly fewer *P. penetrans* than did the cultivars Chippewa, Katahdin, or Peconic (7). However, in microplot studies Hudson supported a relatively high population of *P. penetrans* (11). Recently, the cultivar Butte was reported to be highly resistant to *P. neglectus* and to possess some resistance to *P. penetrans* (4). Our objective was to search for resistance to *P. penetrans* among diverse potato germplasm and incorporate this resistance into germplasm better adapted to North American growing conditions. A preliminary report has been given (3).

Materials and Methods

The initial evaluation was based on a representative sample of potato clones from five breeding populations from the Cornell University potato breeding program. These breeding populations were as follows: i) advanced *Solanum tuberosum* ssp. *tuberosum* clones from the variety development program that had been bred and selected for resistance to *Globodera rostochiensis*, ii) a neotuberosum population of *S. tu-*

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berosum ssp. *andigena* derivation that had been selected for adaptation to North American growing conditions, iii) a population selected for resistance to *G. pallida* derived from *S. tuberosum* ssp. *andigena* but containing some *S. vernei* and *S. tuberosum* ssp. *tuberosum* germplasm, iv) an insect-resistant population of *S. berthaultii* derivation that had been crossed to *S. tuberosum* spp. *tuberosum,* and v) a population derived from *S. tuberosum* ssp. *andigena* and *S. sparsipilum* that had been selected for heat tolerance. The advanced clone NY85 from the Cornell potato breeding program was used as a susceptible control.

In the initial evaluations, single tubers of each clone were planted in 7.5-cm clay pots containing a 1:1 mixture of sandy loam soil and fine blasting sand and placed in a growth chamber at 24 C with 15-hour day length. Each clone was replicated five times. After plant emergence, a mixture of 3,500 *P. penetrans* adults and juveniles was added to each pot. The *P. penetrans* used in these studies originated from a single female isolated from apple orchard soil and maintained in alfalfa callus culture. The plants were grown in the *P. penetrans*-infested soil for 70 days, after which the nematodes were extracted from roots of each plant. Root systems were washed free of soil, blotted with absorbent paper, and weighed. Afterwards, the roots from individual plants were cut into 1–2 cm lengths, placed into 250-ml flasks, and covered with water. The flasks were placed on a wrist-action shaker for 48 hours. The contents of each flask were then spread evenly over a paper milk filter in a Baermann pie pan (11). Nematodes were collected from the pie pan 48 hours later and counted. The total number of nematodes per root system were determined, from which nematodes per g of root was calculated. The data were then expressed as an index of susceptibility (nematodes per g of root of clone divided by the nematodes per g of root of susceptible control).

The second trial was to confirm the reaction of clones that supported the fewest *P. penetrans* in the initial evaluation. The conditions of this evaluation were the same as those in the initial evaluation, except that each clone was replicated 10 times.

In the third trial, host suitability of the better adapted clones that supported few *P. penetrans* in the first two tests was comparted to that of the commercial cultivars Hudson, Peconic, and Russet Burbank that were previously reported to possess some degree of resistance or tolerance to *P. penetrans*. The cultivar Superior and the advanced clone NY85 from the Cornell potato breeding program were used as susceptible controls, and Saia oats was used as a resistant control. The conditions of the evaluation were similar to previous trials, except that soil in each pot was infested with a mixture of 5,000 *P. penetrans* adults and juveniles and numbers of *P. penetrans* per g of root were determined 30 days after inoculation by staining the roots. After being washed free of soil, blotted dry, and weighed, entire root systems were stained with acid fuchsin in lactoglycerol (2). Root systems were submerged in the stain and heated for 2 minutes in a 600-watt microwave. After staining, the root systems were macerated for three 10-second intervals in a blender. The macerated root suspension was poured onto a 250-μm screen and rinsed into a beaker, and the volume was brought to 200 ml. The number of eggs and vermiform nematodes were counted in three 1-ml aliquots of the suspension from each root system and the counts were averaged.

In the fourth trial, host suitability to *P. penetrans* of L118-2, the clone that supported the fewest nematodes in previous experiments, was compared to that of the cultivar Hudson. The advanced clone E74-7, which supported large numbers of *P. penetrans* in the second trial, served as the susceptible control, and Saia oats was the resistant control. Conditions of this trial were the same as in trial 3, except that each clone or cultivar was replicated 10 times and each pot was inoculated with 5,000 *P. penetrans* adults. Numbers of nematodes and eggs per g of root were determined 30 days after inoculation using the procedure described above.

The fifth trial was conducted to identify

resistance to *P. penetrans* in progenies of backcross generations resulting from crosses of the cultivars Atlantic and Steuben with bulk pollen from 21 clones of the Pallida-resistant breeding population, including the six clones that supported few *P. penetrans*. Backcross progenies were evaluated for resistance to *P. penetrans,* as previously described. Each plant was inoculated with a mixture of 5,000 *P. penetrans* adults and juveniles and grown in a growth chamber at 24 C with 15 hour day length. The numbers of *P. penetrans* per g of root were determined 30 days after inoculation. The entire root system of each plant was stained with acid fuchsin in lactoglycerol, macerated in a blender, and examined for numbers of *P. penetrans* eggs and vermiform nematodes, as described.

The data were subjected to a one-factor ANOVA. Significant differences between clones were determined by Fisher's PLSD test.

Results

In the initial evaluation, nine clones had an index of susceptibility (SI) of 0.10 or less 70 days after inoculation (Table 1). Clones with a SI ≤0.10 were from three of the five breeding populations tested; seven clones were from the Pallida-resistant populations, and one clone each was from the tuberosum and heat-tolerant breeding populations.

In the second trial, all of the clones, except one, that performed well in the first test had a significantly lower ($P < 0.05$) SI than did the susceptible control 70 days after inoculation (Table 1). The clone E74-7 from the neotuberosum breeding population that supported few *P. penetrans* (SI = 0.13) in the first trial supported a large number of *P. penetrans* (SI = 1.63) in this trial. Consequently, this clone was used as a susceptible control in later trials. The SI of seven of the nine clones that exhibited some resistance to *P. penetrans* did not differ significantly from that of the resistant control, Saia oats. Three of the seven clones were selected for further evaluation.

Table 1. Index of susceptibility of potato clones from different breeding populations 70 days after inoculation with *Pratylenchus penetrans*.

Breeding population and clone	Index of susceptibility† Trial 1	Trial 2
Tuberosum (*Solanum tuberosum* ssp. *tuberosum*)		
NY-85 (susceptible control)	1.00 a	1.00 b
E57-23	0.75 b	—‡
E55-27	0.56 bcd	—
E11-45	0.50 cde	—
F24-12	0.48 cdef	—
NY-78	0.40 defg	—
F100-1	0.34 defgh	—
E55-35	0.30 efghi	—
NY-84	0.21 ghijkl	—
E55-44	0.20 ghijkl	—
F66-15	0.20 ghijkl	—
F143-1	0.05 kl	0.41 c
Neotuberosum (*S. tuberosum* ssp. *andigena*)		
H383-6	0.69 bc	—
H349-6	0.39 defg	—
Purple 5	0.30 efghi	—
H322-5	0.17 hijkl	—
H350-4	0.16 hijkl	—
A149-4	0.14 hijkl	—
E74-7	0.13 hijkl	1.64 a
Pallida resistant (*S. tuberosum* ssp. *andigena, S. vernei*)		
L127-2	0.10 ijkl	0.20 cde
L112-1	0.08 jkl	0.21 cde
L118-1	0.08 jkl	0.14 de
L117-2	0.06 kl	0.11 de
L116-1	0.30 kl	0.30 cd
L118-2	0.03 l	0.11 de
L116-2	0.01 l	0.19 cde
Insect resistance (*S. berthaultii* × *S. tuberosum*)		
L227-5	0.25 ghijk	—
L317-2	0.20 ghijkl	—
Heat tolerant (*S. tuberosum* ssp. *andigena*)		
L510-3	0.28 efghij	—
L503-10	0.28 fghij	—
L511-1	0.21 ghijkl	—
L503-5	0.21 ghijkl	—
L511-2	0.15 hijkl	—
L503-3	0.15 hijkl	—
L105-13	0.08 jkl	0.18 cde
Saia oats (resistant control)	—	0.02 e

Trial 1 means of 5 replicates and trial 2 means of 10 replicates. Means in each column not followed by the same letter are significantly different ($P < 0.05$) according to Fisher's PLSD test.

† Nematodes per g of root of clone divided by nematodes per g of root of susceptible control.

‡ Not tested in trial 2.

In the third trial, the three selected clones and three potato cultivars that were previously reported to possess some resistance or tolerance to *P. penetrans* were compared. The SI of the cultivars Russet Burbank and Peconic did not differ significantly from that of the susceptible controls, NY85 and Superior (Table 2). The SI of Hudson was significantly less ($P < 0.05$) than that of Russet Burbank and Peconic and the susceptible controls, but did not differ ($P < 0.05$) from that of the three selected clones or the resistant control, Saia oats.

Because resistance to *P. penetrans* in Hudson was questionable in previous studies, the host suitability of Hudson for *P. penetrans* reproduction was compared to that of clone L118-2, which had consistently supported few *P. penetrans*. In this test, the SI of Hudson and clone L118-2 did not differ from each other or from the resistant control but were significantly less ($P < 0.05$) than the SI of the susceptible control (Table 2).

In the first backcross generation, 12 clones were identified as possessing some resistance to *P. penetrans*. Among the progeny of backcrosses to the cultivar Atlantic, 11 of 67 clones evaluated supported significantly ($P < 0.05$) fewer nematodes than did the susceptible control having SIs of 0.20 or less. In the progeny of the backcross to the cultivar Steuben, 1 of 74 clones evaluated supported significantly ($P < 0.05$) fewer nematodes than the susceptible control with a SI of 0.08 (data not presented). These 12 clones will be intercrossed to increase the frequency of resistant genes and used in future backcrosses to adapted cultivars.

TABLE 2. Index of susceptibility of selected potato clones and cultivars 30 days after inoculation with *Pratylenchus penetrans*.

Clone or cultivar	Index of susceptibility†	
	Trial 3	Trial 4
E74-7 (susceptible control)	—	1.0 a
Russet Burbank	1.05 a	—‡
NY-85 (susceptible control)	1.00 a	—
Peconic	0.81 a	—
Superior	0.78 a	—
Saia oats (resistant control)	0.30 b	0.27 b
L116-2	0.29 b	—
Hudson	0.28 b	0.46 b
L117-2	0.21 b	—
L118-2	0.16 b	0.34 b

Data are averages of five replications. Means in each column not followed by the same letter are significantly different ($P < 0.05$) according to Fisher's PLSD test.

† Nematodes per g of root of clone divided by nematodes per g of root of susceptible control.

‡ Not tested in trial 4.

DISCUSSION

This study is the first reported detailed search for resistance to *P. penetrans* among diverse potato germplasm. Previous studies have dealt with evaluating commercial cultivars of potato for their ability to support reproduction of *P. penetrans* (1,4,6, 14). The cultivar Peconic, identified as possessing some resistance to *P. penetrans* in previous studies (6,7) was found to support large numbers of *P. penetrans* in our tests. We also confirmed that Russet Burbank supports a high population of *P. penetrans* (1,9,14), but since we did not measure yields, it was not possible to confirm the ability of Russet Burbank to tolerate infection by *P. penetrans* (1,9).

In previous studies of resistance to *P. penetrans* in certain commercial potato cultivars, the cultivar Hudson was found to be less suitable for *P. penetrans* reproduction than were other cultivars tested (6,7). The population of *P. penetrans* used in these earlier studies originated from apple orchard soil and had been reared on alfalfa callus since 1963 (12). Several pathogenicity studies with this population of *P. penetrans* using inoculum from alfalfa callus showed no evidence of loss of virulence in culture (12). In microplot studies on Long Island, New York, with a population of *P. penetrans* from potato soils, Hudson supported high nematode populations (11). In our tests, host suitability of Hudson for *P. penetrans* did not differ significantly from that of the most highly resistant clone that we identified from our Pallida-resistant breeding population. The *P. penetrans* in-

oculum used in our tests was from the population reared on alfalfa callus that was used originally to identify Hudson as resistant to *P. penetrans*. The ability of Hudson to support reproduction of geographically isolated populations of *P. penetrans* differentially suggests the existence of biological races of this nematode species. The existence of races of *P. penetrans* has been suggested from studies of populations that have different multiplication rates on different species of host crops (13).

We found that differences in the numbers of *P. penetrans* per g of root between resistant and susceptible plants increased with an increase in time after inoculation. Higher SIs were recorded for the resistant potato clones and the resistant control 30 days after inoculation than after 70 days. Such differences suggest a number of factors that could be involved in the mechanism of resistance in potato *P. penetrans*. A decrease in the number of nematodes per g of root with time indicates that population development is suppressed in resistant roots. A suppression in population development could be caused by several factors, including differences in penetration, death rate, egression into the soil, or rate of multiplication. We did not measure any of these factors to determine the mechanism of resistance. However, we observed no differences in penetration among clones, as the numbers in nematodes per g of roots of different clones did not differ 5 days after inoculation (data not presented).

All of the potato clones from the Pallida-resistant breeding population that we evaluated seemed to possess some resistance to *P. penetrans*. Most, but not all, of these clones are also resistant to *Globodera pallida* (P_4A and P_5A) and to *G. rostochiensis* (Ro1). This potato-breeding population was derived from *S. tuberosum* ssp. *andigena* that had been crossed to a *S. tuberosum* ssp. *tuberosum* hybrid that contained some *S. vernei* germplasm. It is not known if the resistance to *P. penetrans* in this breeding population in contributed by *S. tuberosum* ssp. *andigena* or *S. vernei*.

The genetics of resistance to *P. penetrans* is unknown for the resistant clones that we identified in our Pallida-resistant breeding population. The lack of complete resistance and variation in the different levels of resistance exhibited between experiments suggest that this resistance is quantitatively inherited and not controlled by a single major gene. As such, this resistance is subject to genetic or environmental interactions similar to resistance to *G. pallida*, which is also quantitatively inherited (5). Such interaction could account for the relatively large variation in the number of nematodes per g of root of resistant plants in the different tests.

The usefulness of this resistance in managing *P. penetrans* has not been tested. Although the number of nematodes in roots of resistant plants was significantly less than that in susceptible plants, resistant plants did harbor a substantial number of nematodes: six to 42 nematodes/g of root 70 days after inoculation. Population densities of 1,000–2,000 *P. penetrans*/kg of soil are reported to reduce potato yields measurably (15). Resistant plants identified in our study could conceivably support population densities of 1,000–2,000 nematodes/kg of soil. If so, host resistance alone would not adequately manage *P. penetrans*, particularly in the potato early dying syndrome, as yield losses in potato due to potato early dying is reported to be related to the presence or absence of *P. penetrans* and not the preplant population density (18). In such cases, the combination of this resistance with other management tactics such as biological agents or minimal chemical application would be necessary to achieve adequate nematode suppression.

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