

Influence of *Pratylenchus penetrans* on Plant Growth and Water Relations in Potato

J. B. KOTCON AND R. LORIA¹

Abstract: Plants of potato (*Solanum tuberosum*) cultivars Katahdin and Superior were inoculated with 0, 1,500, or 15,000 *Pratylenchus penetrans*. Transpiration, measured in the greenhouse with a porometer after 56 days of growth, was not significantly different among nematode inoculum levels or between cultivars. The rate of xylem exudation from decapitated root systems of Katahdin plants inoculated with 1,500 or 15,000 *P. penetrans* and Superior plants inoculated with 15,000 *P. penetrans* was lower than from noninoculated plants. Root weight of Katahdin and Superior was not affected by *P. penetrans* inoculum level. Transpiration of plants inoculated with 0, 500, 5,000 or 50,000 *P. penetrans* was recorded weekly from 14 to 56 days after planting. No consistent effects of nematode inoculum density on transpiration rate were observed. Root hydraulic conductivity was lower in Katahdin plants inoculated with 266 *P. penetrans* per plant and in Chippewa with 5,081 per plant than in noninoculated plants. Nematodes reduced leaf area of Superior, Chippewa, and Katahdin and root dry weight of Chippewa but had no effect on growth of Hudson, Onaway, or Russet Burbank plants. Assessing nematode effects on root hydraulic conductivity may provide a measure of the tolerance of potato cultivars to nematodes.

Key words: host-parasite relationships, leaf water potential, root lesion nematode, root hydraulic conductivity, *Solanum tuberosum*, potato, transpiration, water relations.

The root lesion nematode *Pratylenchus penetrans* (Cobb, 1917) Filipjev and Schuurmans-Stekhoven, 1941 causes substantial yield reduction of potato (*Solanum tuberosum* L.) in eastern North America (3,18). Compared with other crops, potatoes are relatively shallow rooted (8,13). Kotcon et al. (11) have demonstrated that both the length and volume of potato root systems are reduced significantly in fields infested with *P. penetrans* and other root-infecting pathogens.

P. penetrans invades the cortex of feeder roots causing necrotic lesions and root discoloration. Acedo and Rohde (1) reported that the endodermis and stele are also invaded in some hosts and severe damage to vascular tissues occurs. Whereas morphological and histological changes provide visible evidence of root tissue damage, the effects of these changes on plant growth and yield have not been precisely defined. Root tissue damage is presumed to result in reduced water and nutrient uptake, but few quantitative measurements of altered

root function, resultant effects on host water relations, and subsequent growth retardation and yield loss have been made.

Although resistance to *P. penetrans* is not known to occur in potato, some cultivars have been reported to be relatively tolerant to this nematode. A resistant plant is one on which nematodes reproduce poorly; a tolerant plant is one that shows little injury, even under attack by large population densities of nematodes (19). Bernard and Laughlin (2) showed that Russet Burbank was most tolerant, Katahdin and Kennebec were intermediate, and Superior was least tolerant to *P. penetrans* in a field microplot study.

The basis for tolerance to nematodes has not been identified; therefore, techniques for selecting nematode-tolerant cultivars have been based on yield response under nematode pressure. Tolerance of crops to environmental stresses such as excessively high soil moisture, however, has been related to plant water relations. Tolerance to soil water logging in bean cultivars has been determined by analysis of leaf xylem potential values (16). Leaf diffusive resistance has been used as an indicator of increased root resistance and flooding injury in rabbiteye blueberries (4). Few data are available, however, on the relationship of nematode tolerance and plant water relations.

In this study we evaluated the influence of *P. penetrans* on transpiration and xylem

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¹ Department of Plant Pathology, Cornell University, Long Island Horticultural Research Laboratory, Riverhead, NY 11901. Current address of senior author: Division of Plant and Soil Science, West Virginia University, Morgantown, WV 26506.

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exudation from root systems of the potato cultivars Katahdin and Superior. These two cultivars have been observed to differ in tolerance to this nematode. We also compared the influence of *P. penetrans* on transpiration, root conductivity, and leaf water potential among six potato cultivars commonly grown in the northeastern United States.

MATERIALS AND METHODS

The following procedures were used in all three experiments, unless indicated otherwise. Single-eye seedpieces were sprouted for 2 weeks in the greenhouse in moist vermiculite. Seedpieces with stems approximately 5 cm long were transplanted into plastic pots filled with 2,500 cm³ steamed sand: soil (1:1) mix. Inoculum consisted of a water suspension of mixed age groups of *P. penetrans* which had been extracted from roots of field-grown rye (*Secale cereale* L.). Washed rye roots were incubated at 20–22 C in aerated tap water for 1–3 weeks. The suspension was passed through a 300- μ m-pore sieve to remove the roots, and nematodes were concentrated by settling and decanting. Desired numbers of nematodes were applied with a syringe to the roots of each plant at the time of transplanting. Plants were fertilized once each week for 4 weeks with 250 ml liquid fertilizer solution (15-16-17, Peters Fertilizer Products, Fogelsville, Pennsylvania). Greenhouse temperatures were usually 22 \pm 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. Transpiration was measured in the greenhouse with a steady state porometer (Model LI-1600, LI-COR, Inc., Lincoln, Nebraska). Leaf area was measured at harvest with a leaf area meter (Model 3000, LI-COR, Inc.)

Experiment 1: Plants of Katahdin and Superior were inoculated with 0, 1,500, or 15,000 *P. penetrans* per pot. At 56 days after transplanting, transpiration was measured on three leaflets of the uppermost fully expanded leaf of two plants in each treatment. Transpiration measurements were taken in the greenhouse at 1300 and 1500 hours and again the next day at 0900, 1100, 1300, and 1500 hours. Light intensity, measured with a quantum sensor

(Model LI-1905-1, LI-COR, Inc.), ranged from 200 to 1,100 μ E m⁻² sec⁻¹. The soil in each pot was thoroughly wetted and allowed to drain before measuring transpiration; no additional water was applied until the end of the measurement period by which time the soil moisture in some pots was depleted and plants had begun to wilt. The rate of xylem exudation from the root systems of decapitated plants was measured at harvest (60 days). Pots were watered to saturation and allowed to drain at 20 \pm 2 C for several hours before and during exudation measurements. Stems were cut near the soil line and xylem exudate was collected for 2–4 hours in a pipette attached to the stem with plastic tubing. Root fresh weight was determined at harvest.

This experiment was repeated. This time, however, transpiration was measured on three leaflets on each of four plants per treatment. Readings were taken between 1300 and 1500 hours at 57, 58, and 59 days. Because skies were overcast, light intensity ranged from 120 to 480 μ E m⁻² sec⁻¹, which was lower than in the previous trial. Plants were watered daily, and symptoms of water stress were not observed. Root xylem exudation, leaf area, and root fresh weight were determined at 60 days as described previously.

The transpiration rate of each plant was calculated as the mean of all readings taken on the three leaflets. Data from both experiments were combined and analyzed by two-way analysis of variance assuming a randomized block design with experiments as blocks.

Experiment 2: A second experiment was conducted to evaluate the influence of nematodes on transpiration of Katahdin and Superior throughout plant development. Four replicate plants of each potato cultivar were inoculated with 0, 500, 5,000, or 50,000 *P. penetrans*. Transpiration was measured on the distal leaflet of the uppermost fully expanded leaf of each plant at weekly intervals beginning 28 days after transplanting. Soil moisture was adjusted to field capacity in the late afternoon, and measurements were taken the following day at 0900, 1100, 1300, and 1500 hours. This experiment was repeated with transpiration measurements taken weekly beginning at 14 days after transplanting. Both experiments were terminated at 60 days.

TABLE 1. Leaf area, rate of xylem exudation, and root weight of Katahdin and Superior potato plants inoculated with *Pratylenchus penetrans*.

<i>P. penetrans</i> / plant	Leaf area (cm ² /plant)		Water exuded (ml/hour)		Root fresh weight (g/plant)	
	Katahdin	Superior	Katahdin	Superior	Katahdin	Superior
0	2,013 a	1,573 a	0.495 b	0.380 a	4.66 a	2.76 a
1,500	2,023 a	1,851 a	0.168 a	0.370 a	6.52 a	3.27 a
15,000	1,881 a	1,661 a	0.195 a	0.188 a	6.55 a	3.02 a

Mean of 4–6 plants per treatment. Column means followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's multiple-range test.

Data from both experiments were combined and analyzed as a randomized block design with experiments as blocks. Data from each time and date were analyzed separately by two-way analysis of variance to determine the significance of variety and nematode treatment effects. In addition, an analysis of covariance was conducted using light intensity as a covariate.

Experiment 3: Plants of six cultivars—Chippewa, Hudson, Katahdin, Onaway, Russet Burbank, and Superior—were transplanted into plastic pots (1,000 cm³) containing steamed sand. Soil was infested by adding 0, 1.7, or 17 g of corn roots infected with *P. penetrans* from greenhouse cultures. Pots of control plants were inoculated with 8.5 g of noninfected roots. Initial population densities in soil were determined 2 weeks after transplanting by assaying all of the roots and soil in six pots of each treatment level with Baerman pans using a 10-day incubation period. Transpiration was measured with a porometer on one leaflet per plant of five plants per treatment. Measurements were made twice a day at 25, 26, and 27 days after transplanting. Pots were sealed in polyethylene bags and weighed daily to determine whole plant transpiration. Leaf xylem potential on one leaf per plant was measured using a pressure bomb (Soilmoisture Equipment Corp., Santa Barbara, California) at 30 days after transplanting.

Five plants per treatment were harvested at 30 and 45 days after transplanting. Roots were washed gently and stems were severed 1 cm above the soil line. Hydraulic root conductivity was determined by placing decapitated root systems in a 100-ml beaker which was then filled with water at 20 C. The beaker was placed into a pressure bomb, and the plant stem was inserted through the port in the top of the chamber

and sealed. A 1-ml pipette was attached to the cut end of the stem with rubber tubing, and a small amount of water was added. After a 5-minute equilibration period, the pressure in the chamber was increased to 0.4 bars and xylem exudate was collected for 10 minutes. Root dry weights and leaf areas were also measured. Data were analyzed by three-way analysis-of-variance to determine the significance of data, cultivar, and nematode treatment effects and interactions.

RESULTS

Experiment 1: Transpiration rates were usually greatest between 1100 and 1300 hours and declined as light intensity and soil moisture decreased later in the day. Mean transpiration rates did not differ significantly between nematode inoculum levels in either cultivar. In the first trial, plants were allowed to wilt. The mean transpiration rate of Katahdin plants was 0.816 mmol m⁻² sec⁻¹, significantly ($P = 0.05$) less than that of Superior which was 0.911 mmol m⁻² sec⁻¹. In the second trial, with well-watered plants, the mean transpiration rate of Katahdin, 0.774 mmol m⁻² sec⁻¹, was greater ($P = 0.05$) than that of Superior, 0.589 mmol m⁻² sec⁻¹.

The rate of xylem exudation from root systems of decapitated noninoculated plants was similar for both cultivars in these experiments (Table 1). However, Katahdin plants inoculated with either 1,500 or 15,000 *P. penetrans* per pot exuded less ($P = 0.05$) than did noninoculated plants. The same trend occurred with Superior, although this difference was not statistically significant. Root fresh weight was significantly ($P = 0.001$) greater for Katahdin than for Superior, but it was not significantly different among nematode treatments. Leaf area of Katahdin was signifi-

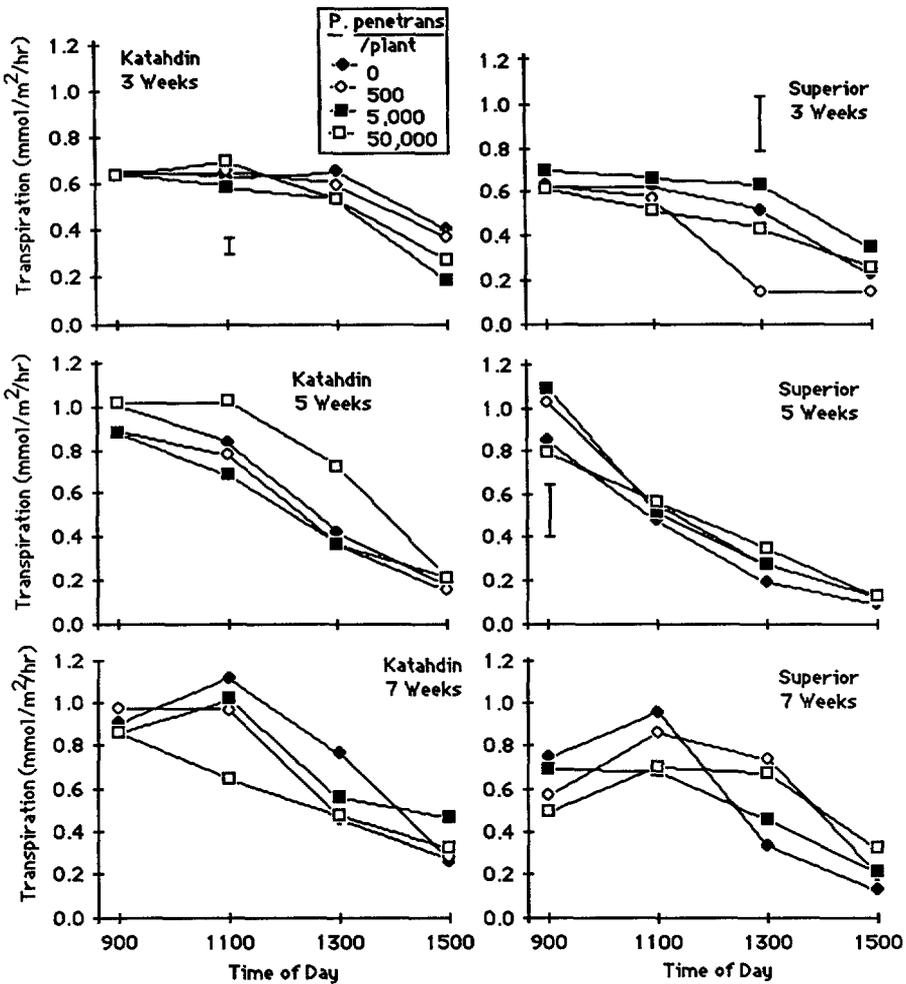


FIG. 1. Influence of *Pratylenchus penetrans* on the transpiration of leaves of Katahdin and Superior potatoes at 3, 5, and 7 weeks after transplanting. Error bars indicate the LSD ($P = 0.05$) for times when analysis of variance indicates a significant effect due to nematode treatment.

cantly ($P = 0.01$) greater than that of Superior. The two-way variety-by-inoculum treatment interaction was not statistically significant for any parameter.

Experiment 2: Mean transpiration rates generally were highest before midday and declined during the afternoon; however, this cycle varied from week to week (Fig. 1). Significant ($P < 0.05$) differences in transpiration rates were associated with cultivars, Katahdin having a greater mean transpiration rate than Superior at 3, 4, 5, 6, and 8 weeks after transplanting. Although statistically significant differences were observed among nematode treatments, these differences were not consistent from week to week or from hour to hour (Fig. 1). Significant ($P = 0.03$) varia-

tion in transpiration was attributed to covariation in light intensity between times of day but not between weeks or within any given time of day.

Experiment 3: Mean initial population densities of *P. penetrans* were 1, 266, and 5,081 per pot. Low population densities of nematodes were found in plants inoculated with corn roots assumed to be noninfected, but differences between treatment means were significant ($P = 0.01$). The average transpiration rate during days 25–27 after transplanting differed significantly ($P = 0.05$) among cultivars. Average leaf transpiration rates for Chippewa, Hudson, Katahdin, Onaway, Russet Burbank, and Superior were 0.506, 0.526, 0.671, 0.565, 0.269, and 0.706 mmol m⁻² sec⁻¹, respec-

TABLE 2. Influence of *Pratylenchus penetrans* on leaf area, root dry weight, and root system conductivity of six potato cultivars at 30 and 45 days after transplanting.

<i>P. penetrans</i> / plant	Chippewa	Hudson	Katahdin	Onaway	Russet Burbank	Superior
Leaf area (cm ² /plant)—30 days after planting						
1	162 a	256 a	194 b	124 a	147 a	134 b
266	136 a	303 a	126 ab	176 a	97 a	66 a
5,081	136 a	258 a	90 a	157 a	111 a	181 b
Leaf area (cm ² /plant)—45 days after planting						
1	227 ab	246 a	197 a	154 a	202 a	170 a
266	262 b	272 a	199 a	198 a	218 a	232 a
5,081	169 a	271 a	183 a	186 a	231 a	193 a
Root dry weight (g/plant)						
1	0.49 b	0.73 a	0.62 a	0.37 a	0.37 a	0.28 a
266	0.45 ab	0.77 a	0.54 a	0.43 a	0.36 a	0.25 a
5,081	0.36 a	0.79 a	0.50 a	0.37 a	0.42 a	0.42 a
Hydraulic conductivity (ml H ₂ O/plant/hour/bar)						
1	2.53 b	3.22 a	2.37 b	2.13 a	1.90 a	1.78 a
266	2.46 b	4.06 a	1.31 a	2.30 a	2.01 a	2.11 a
5,081	1.33 a	2.86 a	1.22 a	2.08 a	2.07 a	1.84 a

Leaf area data are means of five replicates per treatment at each date. Root dry weight and hydraulic conductivity data are means of 10 replicates per treatment, five at 30 days after planting and five at 45 days after planting. Column means followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's multiple-range test.

tively (standard error of the difference [SED] = 0.070); and average whole plant transpiration rates were 12, 23, 9, 13, 8, and 12 grams per day, respectively (SED = 3.3). No significant differences in leaf transpiration or whole plant transpiration were attributed to nematode effects. Leaf xylem potential did not differ significantly among cultivars or nematode inoculum densities.

Leaf area was significantly ($P = 0.05$) reduced by nematodes in the cultivar Katahdin at 30 days after transplanting and in Chippewa at 45 days after transplanting (Table 2). *P. penetrans* initial population densities had no significant effect on leaf area of Hudson, Onaway, or Russet Burbank. The two-way date-by-cultivar interaction was significant ($P = 0.05$); leaf area of Superior at 30 days after transplanting was lower in plants inoculated with 266 *P. penetrans* per pot than in the other two treatments; however, this trend was reversed at 45 days.

Root dry weight of all cultivars was significantly ($P = 0.05$) greater at 45 than at 30 days. Effects of nematodes on root dry weight were not different at the two harvest dates; therefore, results were combined (Table 2). Root dry weight of Chippewa was significantly lower in plants inoculated with 5,081 *P. penetrans* per pot

than in plants inoculated with a single *P. penetrans* per pot. Katahdin responded similarly, but differences among nematode treatments were not significant. Root dry weights of all other cultivars were not affected by initial nematode population densities.

Hydraulic conductivity of root systems was also significantly ($P = 0.001$) greater at 45 than at 30 days after transplanting in all cultivars. Effects of nematodes on conductivity were not different at the two dates; therefore, results were combined (Table 2). Hydraulic conductivity was significantly ($P = 0.05$) lower in Katahdin plants inoculated with 266 *P. penetrans* per pot and in Chippewa and Katahdin plants inoculated with 5,081 per pot than in plants inoculated with one nematode per pot. Hydraulic conductivity of Hudson, Onaway, Russet Burbank, and Superior did not differ among nematode treatments. When hydraulic conductivity was expressed per gram of root, rather than per root system, trends were similar but differences due to nematode effects were not significant.

DISCUSSION

Initial population density of *P. penetrans* had no consistent effect on transpiration rates in any potato cultivar tested in three

experiments. Although fluctuations in soil water potential in drying pots may have masked small changes in transpiration rates, the data indicate that the water status of the plants was not reduced sufficiently by nematode parasitism to stimulate measurable stomatal closure.

Other research indicates that nematode parasitism can, but does not always, result in stomatal closure and, hence, reduced transpiration. Kaplan et al. (9) reported that *P. penetrans* had no significant effect on leaf diffusive resistance of sunflower during daylight periods. However, diffusive resistance of infected plants was greater than that of noninfected plants at night. Meon et al. (15) reported increased diffusive resistance in tomatoes inoculated with 6,000 *Meloidogyne javanica* juveniles, but their study did not detect significant differences in total transpiration between infected and noninfected plants at a lower (1,000/plant) inoculum level. These data are also consistent with greenhouse studies on snap beans infected with *M. hapla* in which transpiration rates were not affected by nematodes at initial population densities of up to 18,000 second-stage juveniles per plant (23).

Xylem exudation from decapitated root systems was reduced by nematode infection in Katahdin but not in Superior plants in experiment 1. In decapitated root systems not under pressure, as in experiment 1, water enters roots entirely by osmosis. In this case, the driving force for root exudation is the active accumulation of solutes, chiefly minerals, in the root xylem (12). Nematode effects on the rate of xylem exudation in Katahdin could be due to either reduced root hydraulic conductivity or reduced solute uptake or both.

In experiment 3, nematode infection reduced xylem exudation from root systems of Katahdin and Chippewa but not Hudson, Onaway, Russet Burbank, or Superior. In transpiring plants or when root systems are under pressure, as in experiment 3, the pressure potential is the dominant force and root hydraulic conductivity becomes important (12). Therefore, low water flow through nematode-infected Katahdin and Chippewa roots was due to reduced hydraulic conductivity in the roots.

Other researchers have found nematode infection to affect water flow through roots.

Kimpinski (10) showed that *P. penetrans*, but not *P. crenatus*, reduced the uptake of tritium-labelled water in infected potato plants. In tomato, root resistance was also positively correlated with *M. hapla* population density, but only at low soil moisture (15). Increased root resistance observed in *Meloidogyne*-infected plants is assumed to be due to the formation of giant cells in the stele, resulting in disruption of the xylem (5,15). Histological studies of roots infected with *P. penetrans* indicate that xylem plugging with pectic materials occurs even if nematodes are restricted to cortical cells (21). Similar plugging of xylem has been suggested to explain transient decreases in hydraulic conductivity of maize roots infected with *Fusarium moniliforme* (20). *P. penetrans* infection of roots also causes phenol accumulation, cell wall thickening in cortical cells, and granulation of the endodermis (1). Such alterations in root anatomy and physiology could be expected to cause changes in cell permeability and, thus, root hydraulic resistance.

Plant growth was not significantly affected by nematodes in experiments 1 and 2. Leaf area of Katahdin was reduced by *P. penetrans* at 30 days but not at 45 days in experiment 3. Root dry weight of Chippewa was also reduced. Plant growth of the other cultivars was not affected by initial nematode population density, except that at 30 days leaf area of Superior plants inoculated with 266 *P. penetrans* was less than that of plants with either a lower or a higher initial inoculum density. The high final population densities of *P. penetrans* in the inoculated treatments indicated that successful inoculation and invasion of roots was obtained in these experiments (unpubl.). Plant growth in the greenhouse may have been limited by cultural and environmental conditions, thus preventing the full expression of nematode-induced damage. Other studies have shown that Superior is relatively intolerant of *P. penetrans* (2,3,18) and that significant yield losses to several cultivars occur under field conditions. Yield responses in field studies, however, are inconsistent from one year to the next (17,18). In addition, interactions with other pathogens affect the amount of yield loss under field conditions (14).

Neither transpiration nor leaf xylem potential was affected by initial nematode

population density in our experiments. However, *P. penetrans* reduced root hydraulic conductivity in those cultivars that also exhibited reductions in plant growth in the presence of this nematode. Our data show that measurements of hydraulic root conductivity provide a sensitive parameter to evaluate the tolerance of potato cultivars to *P. penetrans* under greenhouse conditions. However, significant effects of initial nematode population density on plant growth or water relations were not observed in Superior, contrary to previous reports of intolerance in this cultivar under field conditions (2,3,18).

Effects of nematodes on plant water relations have been correlated with effects on plant growth in other studies. Evans et al. (7) demonstrated a significant correlation between reduced root system size in potato plants heavily infected with potato cyst nematodes (*Globodera rostochiensis* and *G. pallida*) and reductions in water and nutrient uptake and subsequent yields of potato cyst nematode-intolerant cultivars. Their study concluded that potatoes attacked by cyst nematodes were stressed for water and nutrients, even in well-irrigated plots, resulting in premature senescence of foliage and, therefore, reduced yield. Increased diffusive resistance in potato plants infected with potato cyst nematodes was observed under controlled conditions with intolerant but not with tolerant cultivars (22). However, differences between tolerant and intolerant cultivars were not observed under field conditions (6). Wilcox and Loria (23) found that root conductivity, leaf xylem potential, growth, and yield were reduced more by *M. hapla* in one snap bean cultivar than in another.

This study has demonstrated that root xylem exudation is reduced by *P. penetrans* infection in some, but not all, potato cultivars under greenhouse conditions. Although nematode effects on root function appeared to be correlated to nematode intolerance, cultivar responses in the greenhouse were not always consistent with reported field observations. Environmental stresses may play an important role in the expression of nematode-induced changes in plant water relations and subsequent yield losses. Further research is needed to evaluate the relationship between tolerance to nematodes and plant water rela-

tions and to assess how environmental factors affect this relationship.

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