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Impact of Plant Nutrition on *Pratylenchus penetrans* Infection of *Prunus avium* Rootstocks[1]

HADDISH MELAKEBERHAN, GEORGE W. BIRD, AND REBECCA GORE[2]

Abstract: A hypothesis that cherry rootstocks grown under optimal nutrient conditions are affected less by *Pratylenchus penetrans* infection than those grown under deficient nutrient conditions was tested by growing four *Prunus avium* L. rootstocks ('Mazzard', 'Mahaleb', 'GI148-1', and 'GI148-8') at a soil pH of 7.0 over a period of 3 months under greenhouse conditions (25 ± 2 °C). *Pratylenchus penetrans* was inoculated at 0 (control) or 1,500 nematodes per g fresh root weight for a total of 3,600, 4,200, 10,500, and 11,400 per plant on Mazzard, Mahaleb, GI148-1, and GI148-8, respectively, with nutrients (commercial fertilizer) applied once at planting (deficient) or twice weekly (optimal). The experiment was repeated once. The optimum nutrient regime resulted in greater soil nutrient levels and plant growth; higher leaf concentrations of N, P, K, and Mg; and fewer *P. penetrans* than under the deficient nutrient regime. The addition of fertilizer either may increase nematode mortality in the soil or improve rootstock resistance to nematode infection. Increases in Ca in leaves from the nutrient-deficient and nematode-infected treatments suggested the plants were physiologically stressed. The Pf/Pi ratios indicated that these rootstocks may have had resistance to *P. penetrans;* however, because of the dominant role of nutrition in the experimental design, the question of resistance could not be properly addressed.

Key words: Cherry, fertilizer, lesion nematode, nematode, nutrition, *Pratylenchus penetrans, Prunus avium,* resistance, rootstock.

Stone fruit decline is a complex problem that involves a range of interacting pathogenic (Lownsbery et al., 1977; Teliz et al., 1967; Underwood et al., 1994) and nonpathogenic factors (Melakeberhan et al., 1993, 1995). In Michigan, low soil pH and high *Pratylenchus penetrans* population densities were the most commonly observed factors in declining sweet cherry orchards (Melakeberhan et al., 1993). Nutritional imbalances (Brady, 1974; Kirkpatrick et al., 1975; Melakeberhan et al., 1995), deficiencies, toxicities, physiological disturbances and early senescence (Foy, 1974; Jones and Jones, 1974; Neilson et al., 1990), and predisposition to infectious diseases and various environmental stresses (Weaver and Wehunt, 1975) are common in soils with low pH (Marschner, 1993). Nutrient deficiency, however, can be present at both optimum or below-optimum pH levels. Hence, there may be a requirement for supplemental nutrients. Plant-parasitic nematodes can affect their plant hosts by impeding the uptake of nutrients or altering nutrient metabolism (Kirkpatrick et al., 1964; Mai and Parker, 1967, 1972). Little is known of the role of nematodes in predisposing sweet cherry trees to nutrient deficiency or increasing host sensitivity in nutrient-deficient soil systems.

Pratylenchus penetrans is the most widespread plant-parasitic nematode on cherry in Michigan (Melakeberhan et al., 1993), but pathogenicity has not been firmly established. Population densities of 123 to 486 *P. penetrans* per g fresh root plus 100 cm^3 soil had little effect on the growth of several cherry rootstocks (Melakeberhan et al., 1994), whereas similar numbers of *P. penetrans* were associated with sweet cherry (Mai and Parker, 1967, 1972) and peach tree (Mountain and Patrick, 1959) replant problems. The conflicting results suggest that either the cherry rootstocks may be tolerant to *P. penetrans* or the nematode may not have a noticeable effect unless other stress factors also are present.

To understand the cause-and-effect relationships, it is important to understand the role of individual and interacting causal factors. If nutritional deficiency or imbalance is a stress-inducing factor, it is logical to hypothesize that the susceptibility of cherry

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[2] Assistant Professor, Professor, and Research Assistant, respectively, Department of Entomology, Michigan State University, East Lansing, MI 48824-1115.

E-mail:melakebe@pilot.msu.edu

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trees to pathogens should be higher under such conditions. If the hypothesis is true, rootstock seedlings planted in nutrient-deficient soil should suffer more from *P. penetrans* infection than those maintained under an optimal soil nutrient condition. The objective of this study was to determine the pathogenicity of *P. penetrans* on four cherry rootstocks under deficient and optimal soil nutrient conditions at a neutral soil pH of 7.0.

Materials and Methods

Experiments, plant material, and nutrients: Two experiments were conducted with 1-year-old 'Mazzard', 'Mahaleb', 'GI148-1', and 'GI148-8' cherry rootstock seedlings under greenhouse conditions at 25 ± 2 °C. Rootstocks were obtained from Meadow Lake Nursery, McMinnville, Oregon, and stored at 4.5 ± 1 °C for approximately 50 days until bud-break occurred. Seedlings were kept for 24 hours under laboratory conditions (20 ± 2 °C), with roots submerged in buckets of tap water. After selection for growth uniformity, individual seedlings were planted in 800 cm^3 (approximately 944 g fresh weight) sandy loam (87% sand, 8% silt, 5% clay) soil contained in 20-cm-deep, 8-cm-diameter black plastic tubes (Melakeberhan et al., 1994).

The factorial experimental design included optimum and deficient nutrient treatments, with and without inoculation with *P. penetrans*. A 20:20:20: N:P:K Peters all-purpose fertilizer mix (Grace Sierra, Milpitas, CA) was used as the source of nutrients. The composition of N consisted of 5.61%, 3.96%, and 10.43% nitrate, ammonia, and urea, respectively. The optimum nutrient treatment consisted of a total of 1.2 mg active ingredient (a.i.) of each of N, P, and K per tube applied at the rate of 40 µg a.i. twice weekly for the duration of the study. Nutrient-deficient treatments received one application of 40 µg a.i. of each of N, P, and K per tube at planting. All seedlings were watered to saturation daily with tap water. Experiment I was initiated on 16 March 1993 and terminated after 110 days on 15 July 1993. Experiment II lasted 109 days (22 April to 30 August 1993).

Inoculation and extraction of Pratylenchus penetrans: Fresh root weights were determined for five seedlings of each rootstock and the mean weights used to determine the inoculum level at the time of planting. Nematode inoculum, obtained from greenhouse pea cultures, was applied at 1,500/g fresh root weight, for a total of 3,600, 4,200, 10,500, and 11,400 nematodes per tube (or 450, 525, 1,250, and 1,300/100 cm^3 soil) in Mahaleb, Mazzard, GI148-1, and GI148-8, respectively. Nematodes were pipetted in 10-ml suspensions into three or four pencil-size holes around each seedling at 9 and 22 days after transplanting in Experiments I and II, respectively. Controls received 10 ml of tap water. At the end of the experiments, nematodes were extracted from 100 cm^3 soil (Jenkins, 1964) and 1.0 g of randomly collected fresh root weight from each treatment (Bird, 1970).

Differences between the combined final root and soil *P. penetrans* population densities extracted from the optimum and deficient soil nutrient treatments were compared with the Student *t*-test (Berry and Lindgren, 1990). The final population comparisons among the four rootstocks were analyzed with standard two-way ANOVA and the Bonferroni multiple-range test (Berry and Lindgren, 1990).

Growth observations and data analysis: At the end of each experiment, shoot and root systems were dried separately and their dry weights recorded. Root, shoot, and total plant growth was calculated as the at-harvest weight minus the mean at-planting weight of the randomly selected seedlings. Differences among the soil nutrient and nematode treatments in root, shoot, and total plant weight were analyzed for each of the rootstocks with a standard two-way ANOVA and the Bonferroni multiple-range test (Berry and Lindgren, 1990). Concentrations of leaf and soil macro nutrients (N, P, K, Mg, and Ca) were determined from three replications for each experiment by the Michigan State University Soil Testing Laboratory (Melakeberhan et al., 1993). Single treatment effects

were analyzed with ANOVA, and means were separated with Tukey's HSD test; interaction effects of *P. penetrans* and fertilizer were analyzed with General Linear Models (SAS Institute, Cary, NC).

Results

Nematode population densities: Final population densities of *P. penetrans* differed among the four rootstocks grown in nutrient-deficient soil in Experiments I ($P \leq 0.001$) and II ($P \leq 0.05$) (Table 1). In Experiment I, population densities of *P. penetrans* extracted from the roots and soil associated with GI148-8 were greater ($P \leq 0.001$) than those extracted from the other three rootstocks. Similar differences in nematode population densities among the four cultivars were not observed when the rootstocks were maintained under optimal soil nutrient conditions (Table 1). Population densities of *P. penetrans* extracted from roots and soil of all *P. avium* rootstocks grown in nutrient-deficient soil in Experiment II, and for Mazzard and GI148-8 in Experiment I, were greater ($P \leq 0.062$) than those extracted from rootstocks maintained under optimal nutrient conditions where soil nutrients were added twice weekly (Table 1).

With the exception of Mazzard growing in nutrient-deficient soil in Experiment II, final *P. penetrans* population densities (Pf) were less ($P \leq 0.05$ to 0.001) than the initial population (Pi) density (Table 2). The Pf/Pi ratios in Mazzard, GI148-1, and GI148-8 under optimal nutrient conditions, however, were less ($P \leq 0.05$) than those under nutrient-deficient conditions. The Pf/Pi ratios from Mahaleb did not respond in this manner, and tended to be higher than those of the other three rootstocks.

Plant growth: Mazzard shoot growth was not affected by *P. penetrans* or nutrient treatments in either experiment (Table 3). However, root weight of the nutrient-deficient treatment was lower ($P \leq 0.05$) than in other treatments in Experiment II (Table 3).

Twice-weekly applications of soil nutrients increased ($P \leq 0.01$) shoot growth of Mahaleb rootstocks, both in the presence and absence of *P. penetrans* in both experiments (Table 3). An increase ($P \leq 0.05$) in total plant growth, however, was observed only in one experiment—in the *P. penetrans* and optimal soil nutrient treatments.

Optimal soil nutrients increased shoot growth of GI148-1 rootstocks ($P < 0.001$) in both the presence and absence of *P. penetrans* in Experiment II (Table 3). Shoot and total plant dry weight, however, were increased ($P \leq 0.05$) by twice-weekly application of soil nutrients in the presence and absence of the nematode.

In Experiment I, twice-weekly applications of soil nutrients resulted in increased ($P \leq 0.05$) shoot growth of GI148-8 rootstocks in the presence of *P. penetrans,* but not in its absence (Table 3). In all cases, root and shoot growth of GI148-8 was the lowest in the presence of *P. penetrans* maintained in a nutrient-deficient soil environment.

Table 1. Population densities of *Pratylenchus penetrans* extracted from roots and soil of four *Prunus avium* rootstocks maintained under optimal and deficient soil nutrient conditions.

	Experiment I[a]			Experiment II[a]		
Rootstocks	Deficient[b]	Optimal[b]	*T*-test	Deficient[b]	Optimal[b]	*T*-test
Mazzard	1,069 a	203	0.006	673 ab	194	0.043
Mahaleb	725 a	440	0.190	389 a	244	0.062
GI 148-1	748 a	442	0.469	1,418 b	324	0.023
GI 148-8	2,307 b	287	0.001	1,040 ab	404	0.046
P	**	ns		*	ns	

Data are means of four replications. Means within each column followed by different letters are significantly different according to Tukey's multiple-range test. Student *t*-test values are comparisons of optimal and deficient nutrient treatments within each experiment and rootstock.

[a] *P. penetrans* per 100 cm^3 soil and 1.0 g root tissue.

[b] 40 µg a.i. N, P, K (each) per tube applied at planting only (deficient) and twice weekly (optimal).

TABLE 2. Final/initial population density ratios of *Pratylenchus penetrans* extracted from roots and soil of four *Prunus avium* rootstocks maintained under optimal and deficient soil nutrient conditions.

	Experiment I[a]			Experiment II[a]		
Rootstocks	Deficient[b]	Optimal[b]	*T*-test	Deficient[b]	Optimal[b]	*T*-test
Mazzard	0.79 abc	0.09 b	0.006	1.25 a	0.29 ab	0.004
Mahaleb	0.86 a	0.48 a	0.136	0.53 b	0.49 a	0.728
GI 148-1	0.13 bc	0.07 b	0.031	0.40 b	0.10 ab	0.012
GI 148-8	0.33 c	0.05 b	0.001	0.15 b	0.05 b	0.001
P	**	***		***	*	

Data are means of four replications. Means within each column followed by different letters are significantly different according to the Bonferroni multiple-range test (Berry and Lindgren, 1990). Student *t*-test values are comparisons of optimal and deficient nutrient treatments within each experiment and rootstock.

[a] *P. penetrans* per 100 cm^3 soil and 1.0 g root tissue.

[b] 40 µg a.i. N, P, K (each) per tube applied at planting only (deficient) and twice weekly (optimal).

Soil nutrients: At the end of both experiments, soil concentrations of P and K in pots of all four rootstocks were lower ($P \leq 0.05$) when nutrients were applied only at planting than when applied twice weekly (Table 4). Soil Ca levels were higher ($P \leq 0.05$) in

TABLE 3. Individual and concomitant influence of *Pratylenchus penetrans* and alternative soil nutrient regimes on root, shoot, or total plant dry weight (g) of Mazzard, Mahaleb, GI148-1, and GI148-8 cherry rootstocks in Experiments I and II.

Treatments					
Nutrient[a]	*P. penetrans*[b]	Expt. I	Expt. II	Expt. I	Expt. II
Mazzard			Roots[c]		Shoots[c]
Deficient	0	1.90	1.74 a	−0.20	0.48
Optimal	0	0.14	2.44 ab	−0.35	1.47
Deficient	450	2.00	7.38 b	−0.17	2.51
Optimal	450	1.01	4.28 ab	0.92	1.87
P		ns	*	ns	ns
Mahaleb			Shoots[c]		Total plant[c]
Deficient	0	1.95 a	3.31 a	4.48 a	8.17 ab
Optimal	0	7.15 b	6.29 b	9.61 ab	9.98 ab
Deficient	525	3.13 a	2.19 a	4.66 ab	5.06 a
Optimal	525	7.23 b	10.00 b	10.41 b	15.98 b
P		***	**	*	*
GI148-1			Shoots[c]		Total plant[c]
Deficient	0	1.81	1.57 a	4.30	4.31 ab
Optimal	0	2.20	5.55 b	2.66	8.91 b
Deficient	1,250	1.09	1.03 a	2.43	3.01 a
Optimal	1,250	2.53	5.32 b	3.32	7.56 b
P		ns	***	ns	*
GI148-8			Roots[c]		Shoots[c]
Deficient	0	0.74	2.53	0.71 ab	1.36
Optimal	0	1.38	1.40	1.77 ab	3.82
Deficient	1,300	0.54	0.65	0.59 a	0.82
Optimal	1,300	1.06	0.73	2.48 b	2.96
P		ns	ns	*	ns

Data are means of four replications. Means within each column followed by different letters are significantly different according to Tukey's multiple-range test.

[a] 40 µg a.i. N, P, K (each) per tube applied at planting only (deficient) and twice weekly (optimal).

[b] *Pratylenchus penetrans* per 100 cm^3 soil.

[c] Mean harvest weight minus mean planting weight of five randomly selected plants.

TABLE 4. Effect of nutrient regime on concentrations (kg/ha) of macronutrient elements in soils in pots planted with four cherry rootstocks.

Nutrient[a]	Experiment I				Experiment II			
	Mazzard	Mahaleb	GI148-1	GI148-8	Mazzard	Mahaleb	GI148-1	GI148-8
				Phosphorus				
Deficient	355 b	333 b	344 b	378 b	200 b	303 b	317 b	—[b]
Optimal	736 a	671 a	771 a	802 a	582 a	701 a	715 a	799
				Potassium				
Deficient	76 b	57 b	61 b	78 b	43 b	47 b	47 b	—
Optimal	286 a	351 a	365 a	258 a	168 a	223 a	194 a	166
				Magnesium				
Deficient	216 a	221 a	212 a	230 a	204 b	244 b	235 b	—
Optimal	228 a	247 a	198 a	198 a	240 a	294 a	281 a	254
				Calcium				
Deficient	1,354 a	1,452 a	1,435 a	1,726 a	1,239 a	1,427 a	1,264 b	—
Optimal	1,318 a	1,318 a	1,141 a	1,021 b	1,128 b	1,418 a	1,402 a	1,288

Data are means of three replications. Means followed by different letters within each column and element are statistically different ($P \leq 0.05$) according a *t*-test.

[a] 40 µg a.i. N, P, K (each) per tube applied at planting only (deficient) and twice weekly (optimal).

[b] — = Missing data.

soils fertilized only at planting for GI148-8 in Experiment I, and for GI148-1 where soil nutrients were applied on a twice-weekly basis in Experiment II. In Experiment II, Mg concentrations in nutrient-deficient soils from Mazzard, Mahaleb, and GI148-1 rootstocks were lower ($P \leq 0.05$) than in those with optimal nutrient conditions.

Leaf tissue nutrients: In the absence of *P. penetrans,* concentrations of N, P, and K in Mazzard, Mahaleb, and GI148-1 leaf tissues grown in optimal nutrients were greater ($P \leq 0.05$) than nutrient levels from leaves grown in a nutrient-deficient soil in Experiment I (Table 5). The concentrations of Mg and Ca in Mazzard and GI148-1 leaves grown under optimum nutrient conditions were less ($P \leq 0.05$) than leaves grown in

TABLE 5. Effect of nutrient regime (optimal or deficient) and *Pratylenchus penetrans* on the concentrations (%) of macronutrient elements in leaves from Mazzard, Mahaleb, and GI148-1 cherry rootstocks in Experiments I.

Treatments		Concentration of nutrient elements (%)				
Nutrient[a]	*P. penetrans*[b]	Nitrogen	Phosphorus	Potassium	Magnesium	Calcium
			Mazzard			
Deficient	0	1.12 a	0.08 a	1.10 a	0.66 a	1.96 a
Optimal	0	2.42 b	0.37 b	2.63 b	0.60 b	1.02 b
Deficient	450	0.96 a	0.09 a	0.77 a	0.75 a	2.24 a
Optimal	450	2.20 b	0.36 b	2.72 b	0.65 a	1.47 a
			Mahaleb			
Deficient	0	0.97 a	0.12 a	0.88 a	0.88 a	1.96 a
Optimal	0	2.49 b	0.38 b	2.07 b	0.83 a	1.81 a
Deficient	525	0.84 a	0.10 a	0.86 a	0.81 a	1.83 a
Optimal	525	2.38 b	0.28 a	1.50 b	0.66 a	1.65 a
			GI148-1			
Deficient	0	0.96 a	0.11 a	1.04 a	0.52 a	1.90 a
Optimal	0	2.61 b	0.28 b	2.37 b	0.36 b	1.18 b
Deficient	1,250	1.02 a	0.10 a	0.84 a	0.56 a	2.03 a
Optimal	1,250	2.62 b	0.25 b	2.44 b	0.35 b	1.15 b

Data are means of three replications. Means followed by different letters within each column of nutrient regime and *P. penetrans* treatment are significantly different according to the Student *t*-test.

[a] 40 µg a.i. N, P, K (each) per tube applied at planting only (deficient) and twice weekly (optimal).

[b] *Pratylenchus penetrans* per 100 cm^3 soil.

nutrient-deficient soils (Table 5). Levels of Mg and Ca in Mahaleb leaves were not affected by nutrient treatment.

In the presence of *P. penetrans,* concentrations of N, P, K in Mazzard and GI148-1, and N and K in Mahaleb leaves from nutrient-deficient soil were less ($P \leq 0.05$) than leaves from twice-weekly fertilized soils (Table 5). Levels of Mg and Ca in Mazzard and Mahaleb, and P in Mahaleb, were not affected by *P. penetrans* in either nutrient regime. Levels of Mg and Ca in GI148-1 leaves from nutrient-deficient soil were higher ($P \leq 0.05$) than in leaves from optimally fertilized soil (Table 5). In Experiment II, the trends in N, P, K, and Ca content in leaves in the absence of *P. penetrans* were similar to Experiment I (data not shown). Nutrient deficiency and *P. penetrans* interactively decreased ($P \leq 0.05$) K only in Mahaleb leaves.

Discussion

Damage thresholds for *P. penetrans* associated with deciduous fruits have been difficult to determine because of the dynamics of tree age and size, cultivar, time of year measurements were taken, soil type and moisture, soil nutrition, climatic factors, and the presence of other plant-parasitic nematodes (Nyczepir et al., 1993). For example, approximately 53 (Mai and Parker, 1967), 80 (Szczygiel and Danek, 1976), and 260 (Kirkpatrick et al., 1964) *P. penetrans* per 100 cm^3 soil have been reported to be injurious to Mahaleb or Mazzard cherry rootstocks. However, similar or higher *P. penetrans* population densities than those reported in the literature showed little effect on growth of the rootstocks (Melakeberhan et al., 1994). It is possible that such contradictory reports may be explained by differences in experimental conditions, which may have included stress factors other than nematodes. In the present study, the number of *P. penetrans* extracted from each rootstock showed variability similar to earlier work (Melakeberhan et al., 1994), suggesting that they differ slightly in their susceptibility to the nematode. The Pf/Pi ratios in the present study, however, suggest that the rootstocks may be resistant to *P. penetrans.* If the rootstocks are resistant to *P. penetrans,* suppression of dry-matter accumulation of Mahaleb, GI148-1, and GI148-8 in the presence of *P. penetrans* under nutrient-deficient conditions indicates the need to account for stress-inducing factors in host response to nematodes. Furthermore, rootstock growth and nematode population densities under optimum and deficient nutrient conditions support the hypothesis that rootstock seedlings planted into nutrient-deficient soil suffer more from *P. penetrans* infection than seedlings planted in optimal soil nutrient conditions.

Differences in the numbers of *P. penetrans* contrasted more between the optimum and nutrient deficient treatments than among rootstocks. The correlation between high numbers of *P. penetrans* and low soil fertility supports earlier work on cherry rootstocks (Kirkpatrick et al., 1964) and on apples (Merwin and Styles, 1989). The smaller numbers extracted from the optimal nutrient treatments compared with the nutrient-deficient treatments suggest that the nutrients may cause changes in soil chemistry that adversely affect nematode mobility, infective behavior, or nematode mortality. Higher Pf/Pi ratios among the four rootstocks in the nutrient-deficient environment, but not in the optimal nutrient environment, suggest that the nutrients may be affecting nematode infective behavior or reproduction. Alternatively, a nutrient-rich environment may improve ability of plants to resist nematode infection or negatively influence nematode reproduction.

The consistent positive correlation between lower amounts of P, K, and Mg in the soil and in leaf tissues in the nutrient-deficient soils shows what could happen if appropriate nutrient management is not followed. Leaf Ca concentrations were greater in nutrient-deficient soil with and without *P. penetrans* than in the optimum nutrient treatment. The increased Ca concentration in tissues of nematode-infected plants, with decreases in other elements, is consistent with earlier reports (Fatemy and Evans, 1986; Melakeberhan et al., 1987; 1988) and

suggests that Ca may be used to enhance repair mechanisms in response to physiological stress (Corden, 1965). These data also suggest that there need not be a statistical difference in nutrient availability to see a significant impact on host physiology (Melakeberhan et al., 1987).

In this study, there was little interaction between nematode and nutrient treatments. However, the concentrations of N, P, and K in leaves from *P. penetrans* treatments were less than in leaves from the controls. Under field conditions, these concentrations would be considered low (Melakeberhan et al., 1993) and possibly conducive to deficiency symptoms. It is possible that the short duration may have been a factor in the lack of deficiency symptoms. The significance of time could be evaluated by measuring the effect on rootstocks when they are maintained under deficient conditions for longer periods than in the present study.

Nutrient regime had a significant influence on *P. penetrans* population dynamics and cherry rootstock growth and response to the nematode. The possibility that unstressed rootstocks express resistance to *P. penetrans* should be tested separately from the influence of soil nutrients. Rootstock response to increases in nutrients with regular fertilizer application demonstrates the need for maintaining appropriate fertilization in orchards. Furthermore, the study suggests that it is beneficial to have nematode, soil, and plant nutrient data when making horticultural recommendations for either nematode or soil nutrient management. This study also illustrates a need for close cooperation among soil scientists, horticulturists, and nematologists to develop optimum orchard management practices.

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