

Effect of the Ring Nematode Upon Growth and Physiology of Peach Rootstocks Under Greenhouse Conditions

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ABSTRACT

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Seedlings and herbaceous cuttings of cultivars Lovell and Nemaguard peach were grown for 8-13 mo in soil with or without ring nematodes, *Crictonemella xenoplax* (Cx). In seedlings and rooted herbaceous cuttings, the presence of Cx resulted in reduced root fresh and dry weights and reduced free amino acids of shoots and roots as measured by levels of ninhydrin-reactive compounds. The proportions of specific amino acids

were changed. Molar percentage of proline, glycine, and alanine increased, whereas arginine decreased in roots of both seedlings and herbaceous cuttings in the presence of Cx. Levels of the cyanogenic glucoside prunasin decreased in stem tissue of cuttings and seedlings in the presence of Cx, but levels in the roots were increased.

Additional key words: cyanide, ectoparasite, peach tree short life.

Peach tree short life (PTSL) syndrome continues to limit peach production in the southeastern United States despite more than 30 yr of research on the problem (23). "Predisposing" factors are now thought to include the ring nematode [*Crictonemella xenoplax* (Raski) Luc & Raski], rootstock, cultural practices, and fluctuating winter temperatures (16,17,23,28). Little is known of the physiological and biochemical basis for this predisposition although changes in auxin levels have been suggested (2). Tree death, which is often limited to the aboveground portion, is apparently caused by cold injury or bacterial canker caused by *Pseudomonas syringae* van Hall.

As early as 1949, a ring nematode [*C. simile* (Cobb) Chitwood] (= *C. xenoplax*) was found associated with declining orchards in Maryland and North Carolina (3). Growth reduction of peach by *C. xenoplax* (Cx) was demonstrated only after potted trees were kept in infested soil for 2.3 yr (11). Subsequent research in California indicated 16 mo of exposure to Cx could reduce fresh weight and increase susceptibility to bacterial canker of trees in pots (12). That *C. xenoplax* can produce a heat-labile auxin inactivating enzyme has been reported (24). When 1,2-dibromo-3-chloropropane (DBCP) was available, regular pre- and postplant soil fumigation kept Cx at low levels and prolonged peach tree life in the southeastern United States (23,28). This circumstantial evidence and the results of recent work (17) indicate that Cx plays a key role in tree death. Resistant rootstocks would be an attractive alternative to chemical fumigation, especially since the nematicides currently available are less effective than DBCP.

Lovell and Nemaguard cultivars are the most common rootstocks for peach in the United States. At one time, Lovell was the predominant drying peach in California, so seed was readily available for nursery use. Although trees on Lovell generally outlive those on Nemaguard in the southeastern United States, particularly where Cx is prevalent, all are nonetheless subject to

cold injury and tree death. Nemaguard, which was released by the USDA in 1961, is resistant to root-knot nematode [*Meloidogyne incognita* (Kofoid & White) Chitwood and *M. javanica* (Treub) Chitwood] whereas Lovell is susceptible to root knot. Although Nemaguard was originally developed in Georgia, poor survival limits its use in the southeastern United States.

Although trees on Lovell may be longer-lived than those on Nemaguard, data on the tolerance or resistance of Lovell rootstock to Cx are inconclusive. Apparent differences in rate of population buildup on Lovell as compared to Nemaguard (28) may be more related to the higher growth rate of Nemaguard (27) than to inherent resistance or susceptibility. It is not clear whether the ideal rootstock would i) resist or inhibit buildup of Cx on its roots, ii) tolerate high levels of Cx without growth reduction, iii) simply not predispose a scion to injury from cold or *P. syringae* (unrelated to i, ii, or iv) have some combination of these characteristics. Screening procedures for resistance and tolerance are relatively straightforward and currently underway. Screening for longevity requires an understanding of the physiology of predisposition so that it can be induced and measured under controlled conditions in a reasonable length of time. Although it is difficult to simulate fluctuating weather conditions and field cultural practices under greenhouse conditions, a comparison of Lovell and Nemaguard may provide clues to why Nemaguard is shorter-lived and how to screen for survival potential. One measure of differences in plant metabolism is the level of free amino acids that appear as ninhydrin-reactive compounds (NRC). Both NRC levels and specific amino acids have been related to cold hardiness (4,8,10) and nematode injury (5-7,14,20). Cyanide has been suggested to have a role in replant problems (13,25). This paper describes the effect of Cx on growth parameters, free amino acids, and prunasin in peach. Preliminary work has been reported (19,22).

MATERIALS AND METHODS

Plant materials. Experiment 1 consisted of 1-mo-old seedlings of Lovell and Nemaguard planted in September 1981 and harvested in October 1982. Experiment 2 was initiated in May 1983 and harvested in January 1984. It consisted of 1-mo-old Nemaguard seedlings and herbaceous cuttings of Lovell and Nemaguard seedlings rooted in April 1983 as previously described (18).

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Seedlings and cuttings were transplanted into individual 3-L (experiment 1) or 1.5-L (experiment 2) clay pots containing steam-pasteurized Faceville loam soil from a site planted to peaches from 1970 to 1975, and again in 1981. Half of the trees were infested by adding 2,300 Cx in 500 ml (experiment 1) or 2,000 Cx in 400 ml (experiment 2) of a similar, but infested, soil from greenhouse cultures. Each pot was initially fertilized with 10 g of Osmocote 18-6-12 slow-release fertilizer; after that, Peters 20-20-20 soluble fertilizer was added as needed. Pots were arranged in a split-plot design with cultivars as main plots, and nematode treatments as subplots. There were eight randomized complete blocks for experiment 1, and six blocks for experiment 2 with one pot per treatment per block. All plants were grown in the greenhouse under ambient light at 25 ± 5 C. Stem diameter and root fresh and dry weights were measured. Percent dry matter was calculated as dry weight/fresh weight $\times 100$.

NRC analysis. About 1 g of fibrous roots and a 1- to 2-cm section of the stem 5 cm above the soil line were collected from each plant

and analyzed for NRC by using the technique of Moore and Stein (15). Samples were extracted by autoclaving for 15 min in 10 ml of water and held in a cold room overnight. Duplicate 0.05-ml aliquots of the aqueous extracts were reacted with ninhydrin. Absorption was converted to millimolar glycine equivalents on a root dry weight basis by using a standard curve generated by analyzing known amounts of glycine. After removal of the entire soil mass from the pot, nematodes were extracted from 150 cm³ of soil by centrifugal flotation (9,26) and counted under a dissecting microscope.

Amino acid analysis. Analysis of roots from experiment 2 was conducted as described in Product Data Bulletin 9702-2 (Alltech Associates, Deerfield, IL). Specifically, triplicate samples from each treatment were obtained by combining two replicates of the treatment and pulverizing the entire root systems with a Wiley mill. Pulverized roots were mixed well to ensure uniform sampling and 3-g samples were removed for analysis. Samples were extracted for 24 hr at 60 C in 20 ml of 80%

TABLE 1. Effects of *Criconebella xenoplax* (Cx) on growth and ninhydrin reactive compounds (NRC) of seedlings and rooted cuttings of Lovell and Nemaguard peach rootstocks

Rootstock	Cx ^a	Stem diam. (mm)	Root fresh weight (g)	Root dry weight (g)	Root % dry matter	NRC ^b		Number Cx/150 cm ³ soil
						Shoot	Root	
Experiment 1								
Seedlings								
Lovell	-	8.6	132	46	35	0.53	1.30	0
Lovell	+	7.8	115	34	30	0.33	0.69	1,100
Nemaguard	-	8.8	129	43	33	0.56	1.82	0
Nemaguard	+	8.9	117	40	34	0.29	1.08	1,400
Significant effects								
Cx			+	*		**	**	
Rootstock		*					*	
Experiment 2								
Herbaceous cuttings								
Lovell	-	7.7	24	7.5	31	0.64	1.73	0
Lovell	+	6.6	14	3.3	25	0.64	1.30	6,800
Nemaguard	-	7.5	24	6.7	27	0.58	1.57	0
Nemaguard	+	7.1	17	4.0	23	0.40	1.22	7,900
Seedlings								
Nemaguard	-	7.8	39	14.7	38	0.69	1.20	0
Nemaguard	+	7.9	27	7.7	29	0.44	1.03	18,300
Significant effects ^c								
Cx			**	**	**	**	**	
Rootstock			*	**	**	**	+	**

^a With (+) or without (-) Cx for 13 months (experiment 1) or 8 months (experiment 2).

^b Ninhydrin reactive compounds as mM glycine equivalent/g dry weight.

^c Indicates significance of *F*-test from analysis of variance at the 10% (+), 5% (*), or 1% (**) levels. Means over eight blocks (experiment 1) or six blocks (experiment 2).

TABLE 2. Effect of *Criconebella xenoplax* (Cx) on amino acid composition in roots of Lovell and Nemaguard peach rootstocks after 8 mo

Amino acid	Rootstock/treatment ^a					
	Lovell cutting		Nemaguard cutting		Nemaguard seedling	
	-Cx	+Cx	-Cx	+Cx	-Cx	+Cx
Alanine	6.7 \pm 0.9 ^b	12.7 \pm 0.6	6.6 \pm 1.7	10.3 \pm 1.1	6.8 \pm 1.0	14.3 \pm 3.2
Glycine	0.9 \pm 0.1	1.8 \pm 0.3	1.0 \pm 0.6	1.9 \pm 0.6	0.5 \pm 0.1	2.5 \pm 0.1
Proline	1.5 \pm 0.2	7.4 \pm 2.2	2.0 \pm 0.6	8.3 \pm 1.1	1.7 \pm 0.1	9.5 \pm 5.5
Threonine	1.2 \pm 0.6	2.2 \pm 0.5	1.7 \pm 0.3	3.1 \pm 1.6	2.2 \pm 0.6	2.9
Serine	8.1 \pm 0.3	12.3 \pm 3.6	7.9 \pm 3.2	10.4 \pm 2.5	2.6 \pm 1.1	6.7 \pm 6.5
Aspartic acid	24.6 \pm 3.0	17.4 \pm 0.2	22.9 \pm 5.8	15.1 \pm 7.5	21.3 \pm 4.2	27.9 \pm 11.4
Phenylalanine	3.6 \pm 1.0	7.8 \pm 1.6	6.0 \pm 1.7	6.5 \pm 2.3	4.1 \pm 1.5	6.9 \pm 2.6
Glutamic acid	0.7 \pm 0.2	1.0 \pm 0.1	0.6 \pm 0.1	1.0 \pm 0.4	0.7 \pm 0.9	0.6 \pm 0.2
Tyrosine	0.6 \pm 0.1	2.0 \pm 1.4	0.3 \pm 0.1	0.5 \pm 0.2	1.0 \pm 0.3	2.5 \pm 1.3
Arginine	52.4 \pm 2.3	35.5 \pm 1.6	50.8 \pm 13.8	33.0 \pm 5.6	52.6 \pm 4.5	11.2 \pm 6.0
Total ^c	37.0 \pm 4.3	17.3 \pm 1.7	38.7 \pm 12.1	15.5 \pm 2.3	44.9 \pm 18.4	12.4 \pm 4.1

^a Denotes presence (+Cx) or absence (-Cx) of *C. xenoplax* on seedlings or rooted cuttings.

^b Mean molar percent \pm s.e. of triplicate determinations for each treatment.

^c Total identified as μ moles per gram dry weight of roots.

ethanol. Residue was removed from the ethanol by filtration with Whatman #1 filter paper, washed with an additional 20 ml of 80% ethanol, and refiltered. The combined filtrate containing the amino acids was taken to dryness at 60 C under vacuum. The residue was dissolved in 5 ml of deionized water and adjusted to pH 2.5 with glacial acetic acid. Ten micromoles of norleucine was added as the internal standard and the extract was subjected to ion exchange chromatography and derivatization as described in Product Data Bulletin 9702-2. The *N*-acetyl amino acid *n*-propyl esters were detected and quantitated with gas liquid chromatography (GLC). Amino acid separation was attained with a 0.61 m (2 ft) × 3.2 mm (1/8 in.) stainless steel amino acid analysis column (Alltech Associates, Deerfield, IL); carrier gas, helium, 12 ml/min; injector temperature, 250 C; detector temperature F.I.D., 300 C; oven temperature program 110–182 C at 8 C/min, 182–275 C at 31 C/min.

Prunasin analysis. From plants in experiment 2, 0.5-g samples of fresh root and stem tissue were taken and placed in 80% ethanol and disrupted with a Polytron operated at a control setting of 6 for 15 sec. Samples were then extracted at 75 C for 30 min, filtered through Whatman #1 filter paper, and concentrated to 1–2 ml under a stream of N₂ at 80 C. Concentrated samples were adjusted to 4.0 ml with deionized H₂O and reacted with 1 ml of 1 mg/ml β-glucosidase (Sigma Chemical Co.) for 30 min at 22 C. Benzaldehyde was extracted from the reaction mixture with 2 ml of ethyl acetate. The concentration of prunasin was calculated from the amount of benzaldehyde measured by GLC. A 1.83 m (6 ft) × 3.2 mm (1/8 in.) stainless steel column containing 10% Alltech AT-1000 on 80/100 chromasorb H-AW (Alltech Associates) was used to achieve separation. Chromatography conditions were: oven, 150 C; injector, 225 C; detector F.I.D., 250 C; and carrier gas helium, 20 ml/min. Authentic prunasin (Sigma Chemical Co.) was used as an external standard and processed in the same manner as the experimental tissue.

RESULTS

Experiment 1. Three check pots were contaminated with *C. xenoplax* and were not included in the analysis. The presence of Cx significantly reduced root fresh and dry weight on Lovell and Nemaguard seedlings (Table 1). NRC of roots decreased 47 and 41% while shoot NRC decreased 38 and 48% with nematodes for Lovell and Nemaguard, respectively. Rootstock effect differed only for stem diameter and root NRC (Table 1). No treatment × rootstock effects were significant.

Experiment 2. The presence of Cx on rooted cuttings of Lovell and Nemaguard significantly reduced root fresh and dry weight, and percent dry matter (Table 1). NRC of roots decreased 25 and 23% for Lovell and Nemaguard cuttings, respectively. Shoot NRC remained the same for Lovell but in Nemaguard decreased 31% in the presence of nematodes. Rootstocks differed in root dry weight and dry matter content.

TABLE 3. The effect of 8 mo of exposure to *Criconebella xenoplax* (Cx) on the cyanogenic glucoside prunasin in peach seedlings and rooted herbaceous cuttings

Rootstock	Cx	Prunasin (mg/g dry wt ± S.E.)	
		Stem	Root
Herbaceous cuttings			
Lovell	–	6.7 ± 1.0	21.5 ± 2.7
Lovell	+	6.0 ± 1.0	26.2 ± 1.9
Nemaguard	–	5.2 ± 0.5	16.8 ± 4.0
Nemaguard	+	3.1 ± 0.3	23.8 ± 2.5
Seedlings			
Nemaguard	–	6.4 ± 1.0	15.9 ± 1.5
Nemaguard	+	4.2 ± 0.6	20.4 ± 1.4
Significant effects ^b			
Cx		*	**
Rootstock		*	+

^a Mean of six determinations per treatment.

^b F-test significant at *P* = 0.10 (+), 0.05 (*), or 0.01 (**).

Significant reductions in root fresh and dry weight, and percent dry matter occurred in the presence of Cx on Nemaguard seedlings (Table 1). Nematode effects on growth were greater in this test than in experiment 1. The NRC of shoots decreased 36% and that of roots 14%.

The relative ratios of amino acids as well as the total concentration were altered by Cx in roots of both Lovell and Nemaguard cuttings (Table 2). The presence of Cx increased the molar percent of alanine, glycine, and proline in particular, whereas arginine was decreased. Nemaguard seedlings generally showed the same pattern as cuttings, except for aspartic acid (Table 2). Total free amino acid concentration was reduced 53% in roots of Lovell with Cx, whereas Nemaguard cuttings had total amino acids reduced 60% and Nemaguard seedlings had a 72% reduction in the presence of Cx.

The cyanogenic glucoside prunasin decreased significantly in stem tissue for both Lovell and Nemaguard herbaceous cuttings and Nemaguard seedlings infested with Cx (Table 3). Concentrations decreased less in Lovell stems (10%) than in stems of Nemaguard cuttings (49%) or seedlings (34%), respectively. Prunasin levels of root tissue were, however, significantly increased for all rootstocks in the presence of Cx.

DISCUSSION

Results of this study agree with those of Lownsbery et al (11,12) who showed growth reduction resulting from long-term exposure to Cx by using a larger pot (11.4 L) and longer exposure time (16 mo). Where bacterial canker was not a factor, Nemaguard and Lovell showed similar growth reduction as a result of nematode infestation in both their study and ours. Nematode population increase was also comparable for the two rootstocks, which agrees with the results of Barker and Clayton (1). The poor performance of Nemaguard as a rootstock in the Southeast may not be due to its quality as a host for Cx but to its different physiological response to parasitism. The greater reduction in fresh and dry root weights and the higher nematode counts in experiment 2 compared to experiment 1 are probably due to cooler temperatures preceding harvest of experiment 2.

It is not unexpected that the presence of Cx reduced NRC and total free amino acid levels in the roots of infested plants. When total free amino acid levels are compared, it is obvious that the root chemistry is radically altered. It is not clear whether the nematodes removed NRCs, or whether NRC production was reduced or the compounds redirected. The only report on the physiological effects of a *Criconebella* sp. is that for *C. ornatus* (Raski) Luc & Raski, which caused qualitative, but not quantitative, changes in NRC levels in finger millet (14). Endoparasitic nematodes have been found to increase NRC levels in plant roots, but these nematodes also alter root morphology (6,7). The gall-forming ectoparasite *Longidorus africanus* Merny caused increased free amino acids on roots of bur marigold, a herbaceous plant in which root growth stops when a gall forms. In contrast, free amino acid levels did not increase in grape roots, apparently because the root continued to grow and utilize the amino acids after galls were formed (5). Except for Lovell cuttings, shoot NRC levels in both experiments were also reduced by the presence of Cx, even though the variation was high in experiment 2. These changes in shoot NRC levels indicate a response by the shoot to the presence of an ectoparasitic nematode on the roots.

Changes in individual amino acids have been associated with cold hardiness and dormancy in shoots of peach and apple trees (4,8,10), but data are not available on amino acid levels in the roots of orchard trees. Our results showing changes in relative molar ratios of specific amino acids in the roots of potted trees may provide clues to the predisposition caused by the nematode. Since Cx is implicated in PTSL, it is clear that the nematode-induced changes in root physiology must alter scion physiology to the point that normally nonlethal temperatures can cause tree injury. Additional work is needed to relate these results to field conditions.

The observed changes in prunasin levels in roots correspond to those measured in roots by a completely different method (22),

although absolute levels differ. Mizutani (13) has suggested that breakdown of prunasin to release cyanide may be involved in peach tree decline and PTSL. Prunasin is present in relatively high concentrations in bark and roots of peach trees, and has been found to be a potent inhibitor of nitrate reductase (21) upon breakdown to mandelonitrile and cyanide.

These results demonstrate that an ectoparasitic nematode Cx can cause biochemical changes not only in the roots where they feed, but also in the shoot. Additional work is needed to clarify the nature of the predisposition of peach trees to PTSL, determine the relationship of changes in amino acid and prunasin levels and predisposition, and develop an efficient rootstock screening technique for long-term survival.

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