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Impact of *Meloidogyne incognita* on the Incidence of Peach Tree Short Life in the Presence of *Criconemella xenoplax*

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Abstract: The relationship between *Criconemella xenoplax* alone and in combination with *Meloidogyne incognita* on the incidence of peach tree short life disease was studied in field microplots during 1989–96. The presence of *M. incognita* suppressed the population density of *C. xenoplax* on Lovell peach. Tree trunk diameter was significantly reduced in the presence of both nematode species prior to 1993. Soil pH was lowest in the co-infection treatment as compared with the uninoculated control on three of the four sampling dates. In 1994, 80% of the trees growing in soil infested with *C. xenoplax* alone developed typical disease symptoms and died. The remaining tree died in 1995. No trees died in the *M. incognita* alone, *C. xenoplax* + *M. incognita*, or uninoculated control treatments. Parasitism by *C. xenoplax*, but not by *M. incognita*, made Lovell peach trees more susceptible to the disease. These findings were confirmed in an orchard site naturally infested with both *C. xenoplax* and *M. incognita* where Redhaven trees budded to Lovell rootstock exhibited a reduction of 1.6 years in average tree life for every centimeter increase in trunk diameter.

Key words: concomitance, *Criconemella xenoplax*, disease complex, host-parasite relationship, interaction, *Meloidogyne incognita*, nematode, peach, peach tree short life, *Prunus persica*, ring nematode, root-knot nematode.

Information on interactions between ectoparasitic and sedentary endoparasitic nematodes in peach (*Prunus persica* (L.) Batsch) is limited. Research has focused on a single nematode species and its role in association with the peach disease under study. Information on interactions between different plant-parasitic nematodes coinhabiting the same orchard is essential to understanding their combined impact on disease so that an appropriate management strategy can be implemented.

Criconemella xenoplax (Raski) Luc & Raski and *Meloidogyne* spp. have been reported coinhabiting unthrifty or peach tree short life-diseased orchards. In South Africa, peach shoot die-back, premature leaf drop, and a reduction in root system were associated with the presence of both *M. javanica* and *C. xenoplax* (Hugo and Meyer, 1995). In the southeastern United States, *Meloidogyne* spp. and *C. xenoplax* were detected in more than 50% of peach orchards having a history of peach tree short life (Nyczepir et al., 1985). *Criconemella xenoplax* is associated with the predisposition of peach trees to cold injury and (or) bacterial canker (*Pseudomonas syringae* pv. *syringae* van Hall), two factors directly identified with tree death in this disease complex (Nyczepir et al., 1983). It has also been established that peach trees grown in less acidic soils (pH > 6.1) are not as susceptible to *P. syringae* pv. *syringae* infection (Weaver and Wehunt, 1975). In a 13-year survey (1980–1992), the total loss in potential income to growers from tree death associated with this disease was estimated at more than $6 million per year in South Carolina (Miller, 1994). *Meloidogyne* spp. are associated with reduced growth, loss of vigor, an early defoliation of trees during the first 2 years after planting (Nyczepir et al., 1993). In a field microplot study, the interaction between *C. xenoplax* and *M. incognita* caused a greater reduction in Lovell tree growth as compared to either nematode alone 26 months after inoculation. Stunting symptoms were similar to those observed in commercial orchards, but none of the trees developed typical peach tree short life symptoms during that 2-year test (Nyczepir et al., 1993).

Some field observations indicate that peach trees stunted by *Meloidogyne* spp. do

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not succumb to the disease within the first few years after planting, whereas nearby trees not obviously affected by this nematode die from peach tree short life while young (E. Zehr, pers. comm.). Both *C. xenoplax* and *Meloidogyne* spp. were present in these orchards. Since the impact of concomitant populations of *C. xenoplax* and *M. incognita* has not been examined critically, we evaluated the effects of these nematodes in combination on peach tree growth and on the occurrence of peach tree short life.

MATERIALS AND METHODS

Microplots: An experiment was initiated in November 1989 at the USDA, ARS Southeastern Fruit and Tree Nut Research Laboratory in Byron, Georgia, and divided into two experimental phases. The dynamics of concomitant populations of *C. xenoplax* and *M. incognita* on early tree growth of Lovell peach seedling trees were investigated in the first phase from 1989–93. Detailed information on microplot dimensions, soil characteristics, nematode inoculum preparation, and management practices employed have been described (Nyczepir et al., 1993). The test period for the second experimental phase utilizing the same treatment trees was from 1993–96. The nematode treatments per microplot in 1989 were i) 10,000 *C. xenoplax* adults and juveniles, ii) 10,000 *M. incognita* eggs, iii) 10,000 *C. xenoplax* + 10,000 *M. incognita,* and iv) an uninoculated control. The experimental design was a randomized complete block composed of a 2-×-2 factorial with six single-tree replications per treatment. However, one tree each was lost from the *C. xenoplax* and *M. incognita* treatments in December 1991 and 1992, respectively, as previously reported (Nyczepir et al., 1993). Beginning in 1993, nematode population densities were monitored in March or April. Four soil cores (2.5-cm diam. × 30 cm deep) were collected under the canopy of each tree and thoroughly mixed. Nematodes were extracted from a 100-cm^3 subsample by elutriation (Byrd et al., 1976) and centrifugation (Jenkins, 1964), and counted. Soil samples were analyzed 40, 49, 64, and 76 months after inoculation for pH with a standard glass electrode in a 1:1 soil:water solution. Beginning in 1991, trees were pruned in December each year to enhance the onset of peach tree short life (Weaver et al., 1974). Trunk diameters were measured 20 cm above the soil line in March 1994 and 1995, and February 1996. Fertility rates for peach trees were according to the schedule outlined for bearing trees with 10-10-10, 34-0-0, and 14-0-45 (Ferree and Myers, 1989). Weeds in microplots were controlled with glyphosphate (4.49 kg a.i./ha) as necessary. Water was applied by trickle irrigation as needed. The occurrence of peach tree short life symptoms and tree death was recorded over time.

Symptoms used to estimate disease progress were i) cambial browning in the scaffold limbs, ii) cambial browning in the trunk that extends to and stops at the soil line, iii) sucker development from the primary root system, and iv) a sour-sap odor due to the fermentation of carbohydrates released into the intercellular spaces of injured tissues. In addition, light-brown cankers sometimes were observed on twigs due to infection by *Pseudomonas syringae* pv. *syringae* (Brittain and Miller, 1978).

Orchard: Virus-free Redhaven and Springcrest peach cultivars were budded to virus-free Lovell seedling rootstock in June 1988 to determine if incidence of peach tree short life was related to tree growth under orchard conditions in the presence of *M. incognita* and *C. xenoplax.* Lovell rootstock is a susceptible host for both *Meloidogyne* spp. and *C. xenoplax.* The experimental design was completely randomized and consisted of single-tree plots. Twenty Redhaven and 15 Springcrest trees on Lovell rootstock were planted on 17 January 1989 in a Lakeland sand (89% sand, 6% silt, 5% clay; <1% organic matter; thermic, coated Typic Quartzipsamments) at the Sandhill Research and Education Center near Pontiac, South Carolina. At planting in 1989, trees were visually selected for uniformity and then randomly distributed throughout the orchard site. The site, which had a long history of peach tree short life disease, was infested with both

C. xenoplax and *M. incognita*. The trees were planted in the same rows where a peach orchard had been removed in 1988. The soil was not fumigated or limed before planting. No supplemental irrigation was provided after planting. One soil core (2.5-cm diam. × 15 cm deep) per tree quadrant was obtained from within the drip line in February 1989 and March 1991, and six soil cores per tree were taken in April 1995. Samples were thoroughly mixed, and nematodes were extracted as described above.

Trunk diameters were measured at 5 cm above the soil surface on 2 January 1990, 6 October 1992, 28 September 1993, 31 January 1995, and 5 January 1996. Tree mortality as a result of bacterial canker infection or cold injury was recorded on 2 May 1991, 22 April 1992, 22 April 1993, 10 May 1994, and 2 April 1995. Average tree life was calculated by summing individual tree longevity in years (maximum = 6 years; 1990–95) within a size class and dividing by the initial number of trees in that class. For this calculation, size classes were determined by taking the observed range of trunk diameters (1.5 to 4.0 cm) in 1990 and dividing it into five equal classes in 0.5-cm-width increments. Trees were assigned to classes based on 2 January 1990 diameter measurements because obvious differences in tree size had developed by this recording date.

Statistics: Analysis of variance was performed on the final population density (Pf) of *C. xenoplax* in the treatments that received *C. xenoplax* and *C. xenoplax* + *M. incognita*, and on the Pf density of *M. incognita* in the treatments that received *M. incognita* and *M. incognita* + *C. xenoplax*. This was to determine whether the presence of one nematode species influenced the population density of the other. Nematode data were transformed to $\log_{10}(x + 1)$ values before analysis. An analysis of variance was performed to determine treatment effect on trunk diameter and soil pH. Means were separated with Fisher's least significant difference test. The occurrence of peach tree short life tree death among nematode treatments was analyzed for each sampling date with Fisher's Exact Test. In the orchard experiment, average tree life was regressed on the center point of each diameter size class. Only significant differences ($P \leq 0.05$) are discussed unless stated otherwise.

RESULTS

Microplot: The presence of *M. incognita* suppressed the population density of *C. xenoplax* 40 and 52 months after inoculation on Lovell peach in 1993 and 1994, respectively (Table 1). The presence of *C. xenoplax* did not affect the population density of *M. incognita* second-stage juveniles (J2) on any sampling date. The occurrence of typical peach tree short life disease symptoms was first detected in March 1994. Four of five

TABLE 1. Population densities (per 100 cm^3 soil) of *Criconemella xenoplax* (Cx) and *Meloidogyne incognita* (Mi) alone and combined and development of peach tree short life (PTSL) on Lovell peach in field microplots, 1993–96.

	C. xenoplax		*M. incognita*		Incidence of PTSL			
Year	Cx[a]	Cx + Mi[a]	Mi[a]	Cx + Mi	Cx	Mi	Cx + Mi	Check
1993	4,821*	1,932	429	429	0[b] (5[c])	0 (5)	0 (6)	0 (6)
1994	5,674*	643	279	218	4 (5)*	0 (5)	0 (6)	0 (6)
1995	—[d]	258	117	50	5 (5)*	0 (5)	0 (6)	0 (6)
1996	—[d]	148	72	98	5 (5)*	0 (5)	0 (6)	0 (6)

Data are means of six replicates except for *C. xenoplax* and *M. incognita*, which had five replicates.

[a] Initial population density of *C. xenoplax* = 1 juvenile or adult/100 cm^3 soil, *M. incognita* = 1 egg/100 cm^3 soil, and co-infection = 1 *C. xenoplax* + 1 *M. incognita*/100 cm^3 soil inoculated November 1989. Significant differences ($P \leq 0.05$) are for differences between treatments for a given nematode species in a particular year. Actual data are presented, but data were transformed by $\log_{10}(x + 1)$ before analysis.

[b] Cumulative number of dead trees from PTSL.

[c] Total number of trees per treatment. * = $P \leq 0.05$ among treatments on a particular date according to Fisher's Exact Test.

[d] Value missing due to 100% tree loss.

trees growing in soil infested with *C. xenoplax* died from the disease in April 1994, 53 months after inoculation. Three of the four scaffold limbs of the remaining tree in the *C. xenoplax* plot became infected with bacterial canker in 1994, and the tree died in April 1995. No trees in the other treatments died during the first 77 months after inoculation.

Evidence of nematode stress on the growth of Lovell trees was first detected 26 months after inoculation and continued to be observed on all latter sampling dates (Table 2). Trunk diameter was reduced in the presence of *C. xenoplax* + *M. incognita* as compared with the other treatments 52 months after inoculation. No differences in trunk diameter were detected among the *C. xenoplax, M. incognita,* and uninoculated control treatments on this sampling date. The presence of *C. xenoplax* + *M. incognita* continued to cause a greater reduction in tree growth as compared with the uninoculated control 64 and 75 months after inoculation. Furthermore, tree growth was greatest in the uninoculated control plots, intermediate in the *M. incognita* plots, and smallest in the *C. xenoplax* + *M. incognita* plots 75 months after inoculation.

No differences in soil pH were detected among the four nematode treatments 40 months after inoculation (Table 2). In December 1993 (49 months after inoculation) and prior to the occurrence of tree death in spring 1994, soil pH in the *C. xenoplax* + *M. incognita* treatment was lower than in the *C. xenoplax* treatment and in the uninoculated control. No differences in soil pH were detected between *C. xenoplax* + *M. incognita* and *M. incognita* treatments or among treatments of *C. xenoplax, M. incognita,* and the uninoculated control. Soil pH was lower in the *M. incognita* + *C. xenoplax* treatment as compared with the uninoculated control 64 and 76 months after inoculation. Soil pH in the *M. incognita* treatment was greater than in the *M. incognita* + *C. xenoplax* treatment 64 months after inoculation, but not after 76 months. No differences in soil pH were detected between the *M. incognita* treatment and the uninoculated control on either sampling date.

Orchard: The presence of *C. xenoplax* and *M. incognita* was verified in 1989, with soil population densities averaging 10 and 5 nematodes/100 cm^3 soil, respectively. Numbers of *C. xenoplax* adults and juveniles increased to 71 and 51 nematodes/100 cm^3 soil in 1991 and 1995, respectively. In 1990, the presence of *M. incognita* also was evident because some of the trees exhibited a reduction in tree growth, as measured by trunk diameter. The reduction in growth was more severe on some trees than others. Severely stunted trees were initially thought to be affected by crown gall, but further examination of the root systems revealed typical galling caused by *M. incognita.*

Trees of both Redhaven and Springcrest developed typical peach tree short life symptoms and died during the experiment. The number of Redhaven trees that died each year from 1991 through 1995 was 5 (25%), 2

TABLE 2. Soil pH and mean trunk diameter of Lovell peach trees grown in field microplots after infestation with *Criconemella xenoplax* and *Meloidogyne incognita* alone and combined.

	Months after infestation						
	Trunk diameter (mm)			Soil pH			
Treatment	52	64	75	40	49	64	76
Control	83.5 a	90.8 a	94.8 a	6.3 a	5.7 a	6.3 a	6.0 a
C. xenoplax[a]	83.6 a	—[b]	—	6.2 a	5.6 a	—	—
M. incognita[a]	75.6 a	82.4 ab	85.6 b	6.1 a	5.5 ab	6.2 a	5.9 ab
Cx + Mi[a]	62.7 b	71.0 b	73.7 c	6.1 a	5.3 b	5.8 b	5.5 b

Data are means of six replicates except for *C. xenoplax* and *M. incognita,* which had five replicates. Means within a column followed by the same letter are not different ($P \leq 0.05$) according to LSD.

[a] Initial population density of *C. xenoplax* (Cx) = 1 juvenile or adult/100 cm^3 soil, *M. incognita* (Mi) = 1 egg/100 cm^3 soil, and co-infection = 1 *C. xenoplax* + 1 *M. incognita*/100 cm^3 soil inoculated November 1989.

[b] Value missing due to 100% tree loss from peach tree short life.

(10%), 6 (30%), 1 (5%), and 4 (20%) trees, respectively. The number of Springcrest trees that died over the same time period was 3 (20%), 2 (13%), 7 (47%), 0, and 2 (13%), respectively. All Redhaven (40%) and Springcrest (40%) trees with trunk diameters between 3.1 and 4.0 cm in 1990 died by 1993. The only trees that remained alive in 1993 were those that had smaller trunk diameters measuring 1.5 to 3.0 cm in 1990. In 1995, four of the remaining six Redhaven and two of the remaining three Springcrest trees stunted by *M. incognita* died. The average tree life for Redhaven peach was reduced 1.6 years for every centimeter increase in trunk diameter (Fig. 1). A similar trend occurred in Springcrest peach, but the relationship was not significant.

DISCUSSION

Lovell has been the recommended peach rootstock since 1973 for growers who plant trees on orchard sites having a history of peach tree short life in the southeastern United States (Spivey and McGlohon, 1973). All trees budded to Lovell rootstock eventually die from this disease, but they usually live longer than those budded to Nemaguard rootstock, which is resistant to some *Meloidogyne* spp. (Sharpe et al., 1989). Our results show that concomitant inoculations with *C. xenoplax* and *M. incognita* did not enhance the incidence of disease symptoms and death in Lovell after 7 years under field microplot conditions. Only trees planted in soil infested with *C. xenoplax* alone developed symptoms and died. These results were unexpected because Lovell rootstock is a host to both nematode species.

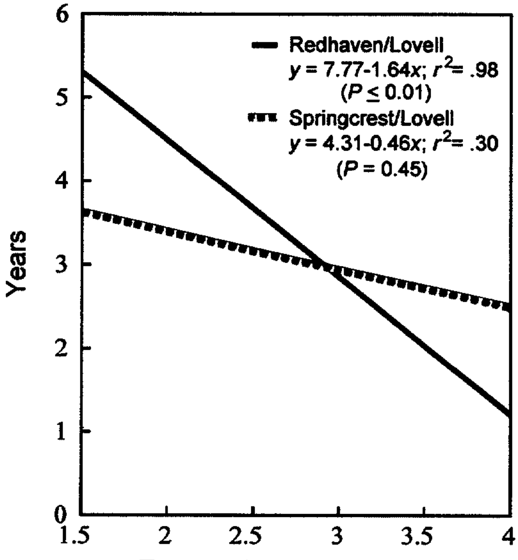

FIG. 1. Average tree life of Redhaven and Springcrest peach budded to Lovell rootstock regressed on the center point of the trunk diameter size class. Size classes were determined by taking the observed range of trunk diameters (1.5 to 4.0 cm) in 1990 and dividing into five equal classes in 0.5-cm-width increments.

Tree stress resulting from parasitism of both nematodes was initially thought to be the reason that Lovell trees eventually died from peach tree short life under orchard conditions. However, the opposite occurred, and the only visible impact that the concomitant inoculation had on Lovell was a reduction in tree-trunk diameter that was first observed and recorded within the first 2 years of the experiment (Nyczepir et al., 1993). Reduction in trunk diameter also occurred in the presence of *M. incognita* alone, but was not as great as that of trees growing in the presence of both nematode species. Lovell trees growing in the presence of *M. incognita* were generally under more stress than those growing in the presence of *C. xenoplax* (Nyczepir et al., 1993).

Further evidence indicating that *M. incognita* is not involved in this disease complex is that no trees died in the presence of *C. xenoplax* + *M. incognita* or *M. incognita* alone, even though soil pH was lowest in *C. xenoplax* + *M. incognita* plots. However, low soil pH in the *C. xenoplax* + *M. incognita* plots probably contributed to the severe reduction in tree growth that was observed.

Low soil pH is known to affect the availability and uptake of nutrient elements (Foy, 1974). In addition, low soil pH (<6.4) is known to be associated with increased incidence of tree death from *P. syringae* pv. *syringae* in the southeastern United States (Weaver and Wehunt, 1975). Moreover, the presence of *C. xenoplax* is required for the disease to occur (Nyczepir, 1990).

One explanation for no tree death in the

C. xenoplax + *M. incognita* treatment is that antagonism between the two nematode species appeared to occur throughout the experiment. The presence of *M. incognita* suppressed the population densities of *C. xenoplax* from 1991 (Nyczepir et al., 1993) until the termination of this study in 1996 (7 years).

The suppression of *C. xenoplax* populations by *M. incognita* may be part of the reason that trees growing in the presence of both nematodes did not develop disease symptoms and die. However, in the orchard experiment some stunted trees eventually developed symptoms and died. This may be the result of a shift in nematode soil population density around individual trees over time that favored *C. xenoplax* and the occurrence of the disease.

Additionally, carbohydrate partitioning may explain why average tree life of Lovell trees decreased with an increase in trunk diameter. Olien et al. (1995) demonstrated that Nemaguard peach (susceptible to *C. xenoplax* and peach tree short life) was more sensitive to *C. xenoplax* feeding than BY520-9 (= Guardian; tolerant to *C. xenoplax* and peach tree short life) because it permits more carbohydrate reserves to be transferred from shoot to root in response to *C. xenoplax* parasitism. However, when the population density of *C. xenoplax* is suppressed in the presence of *M. incognita* and Lovell trees are severely stunted, carbohydrate partitioning is shifted in favor of *M. incognita*, since *M. incognita* is more virulent on Lovell peach than *C. xenoplax* (Nyczepir et al., 1993). Moreover, carbohydrate partitioning in unstunted Lovell trees (microplot study) may be shifted in favor of *C. xenoplax* feeding and then predisposition to the disease. The results of this study substantiate the importance of *C. xenoplax*—and not *M. incognita*—as the primary biotic factor responsible for conditioning Lovell trees to death by *P. syringae* pv. *syringae* infection and (or) cold injury.

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