Journal of Nematology 25(4):659–665. 1993.

Dynamics of Concomitant Populations of *Meloidogyne incognita* and *Criconemella xenoplax* on Peach

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Abstract: The interaction between *Meloidogyne incognita* and *Criconemella xenoplax* on nematode reproduction and growth of Lovell peach was studied in field microlots and the greenhouse. *Meloidogyne incognita* suppressed reproduction of *C. xenoplax* in both field and greenhouse experiments. Tree growth, as measured by trunk diameter, was reduced ($P \leq 0.05$) in the presence of *M. incognita* as compared with *C. xenoplax* of the uninoculated control trees 26 months following inoculation. A similar response regarding dry root weight was also detected in greenhouse-grown seedlings after 5 months. The presence of *C. xenoplax* did not affect Lovell tree growth. A synergistic effect causing a reduction ($P \leq 0.05$) in tree growth was recorded 26 and 38 months following inoculation. The presence of *M. incognita* increased levels of malonyl-1-aminocyclopropane-1-carboxylic acid content in leaves of trees grown in field microplots 19 months after inoculation. *Meloidogyne incognita* appears to be a more dominant parasite than *C. xenoplax* on Lovell peach.

Key words: concomitant infection, *Criconemella xenoplax*, interaction, *Meloidogyne incognita*, nematode, population dynamics, peach, *Prunus persica*, ring nematode, root-knot nematode, synergism.

Plant-parasitic nematodes considered to be major pests on peach (*Prunus persica* L. Batsch) in the Southeast are the ring (*Criconemella xenoplax* (Raski) Luc & Raski = *Mesocriconema xenoplax* (Raski) Loof & de Grisse) and root-knot (*Meloidogyne* spp.) nematodes. The ring nematode predisposes peach trees to bacterial canker (*Pseudomonas syringae* pv. *syringae* van Hall) and (or) cold injury. Cold injury and bacterial canker are responsible for the sudden collapse of peach trees associated with the peach tree short life (PTSL) syndrome in the southeastern United States (19,22). Trees are generally most susceptible to PTSL when they are 3–6 years of age. In contrast, trees parasitized by root-knot nematodes are often stunted during the first 2 years and show signs of reduced vigor, growth and yield, early defoliation, and occasionally death. Root-knot nematodes have not been implicated in the PTSL complex.

In nature, cohabitation of different plant-parasitic nematodes in peach orchards is common. In a survey of PTSL orchards in Georgia and South Carolina in 1985, *C. xenoplax* was detected in 100% of the orchards sampled (15). *Meloidogyne* spp. were found in 56% of the orchards sampled in Georgia and in 70% of those sampled in South Carolina. In PTSL sites, it is recommended that growers plant trees budded to Lovell rootstock, because such trees survive better than trees budded on Nemaguard rootstock. Lovell is susceptible to ring nematode attack; however, trees on Lovell rootstock can die from PTSL. Unlike Nemaguard, Lovell is also a good host for root-knot nematode.

Interactions between ecto- and sedentary endoparasitic nematodes vary depending on the species involved (5). A combination of *M. hapla* Chitwood and *C. xenoplax* on grape resulted in suppressed reproduction of *M. hapla* but increased reproduction of *C. xenoplax* (20). In comparison, *M. incognita* (Kofoid & White) Chitwood suppressed *Scutellonema brachyurum* (Steiner) Andrássy on cotton after 60 days in the greenhouse, whereas populations of *S. brachyurum* increased in the presence of *Hoplolaimus columbus* Sher (13).

The impact of combined parasitism by a migratory ecto- and a sedentary endoparasitic nematode on growth and stress physiology of peach is unknown. The objective of this study was to determine the effect of the interactions between *M. incog-*

Received for publication 12 April 1993.

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The authors thank R. Adams and L. Daniely for technical assistance.

nita and *C. xenoplax* on peach tree growth, stress physiology, and nematode reproduction.

Materials and Methods

Nematodes: The *C. xenoplax,* which originated from a PTSL orchard in Byron, Georgia was cultured on Nemaguard peach seedlings; and *M. incognita,* which originated from peach in Warner Robins, Georgia, was cultured on tomato (*Lycopersicon esculentum* Mill. cv. Rutgers) in the greenhouse. Root-knot nematode eggs were extracted from tomato roots using the method described by Hussey and Barker (10), whereas *C. xenoplax* was extracted from the culture medium using centrifugation (12). Nematode inocula consisted of 25 ml total solution added to four furrows (20.3 cm long × 10.2 cm wide × 7.6 cm deep) around each seedling. Control plots were inoculated with a nematode-free extract solution obtained from the nematode cultures used to inoculate the other three test treatments.

Microplot: Twenty-four closed-end field microplots (1.2-m-d × 1.2-m deep) containing loamy sand soil (82% sand, 13% silt, 5% clay; 1.2% organic matter; pH 5.1) were preplant fumigated with 681 g methyl bromide (98% methyl bromide, 2% chloropicrin) per plot in April 1989 (18). In August, 2-month-old greenhouse rooted Lovell seedlings and associated pasteurized soil were transplanted into the microplots (one per plot). In November, 3 months after seedling survival was evident, the following nematode treatments were added per microplot: i) 10,000 *C. xenoplax* adults and juveniles (Cx); ii) 10,000 *M. incognita* eggs (Mi); iii) 10,000 *C. xenoplax* adults and juveniles + 10,000 *M. incognita* eggs (Cx + Mi); and iv) an untreated control. Ten thousand each of *C. xenoplax* adults and juveniles or *M. incognita* eggs is equivalent to a Pi of ca. 1 nematode/100 cm^3 soil. Dolomitic limestone was added (907.2 kg/0.4 ha) to each microplot in December 1989 to increase the soil pH to 6.0. The experimental design was a randomized complete block composed of a 2 × 2 factorial with six single tree replications per treatment. Nematode population densities were monitored biannually in March and December, beginning March 1991 after trees and nematodes were established. Four soil cores (2.5-cm-d × 30-cm deep) were collected under the canopy of each tree. Nematodes were counted following extraction from a 100-cm^3 subsample with the use of an elutriation (3) and centrifugation (12) technique. Trees were pruned every December beginning in 1991, as a means to enhance the onset of PTSL (22). Tree-trunk diameters were measured 20.3 cm above the soil line in May 1991 and January 1992 and 1993. All trees received annual applications of fertilizer as recommended by the Georgia Cooperative Extension Service, and water was applied by trickle irrigation as needed.

Microplot leaf assays: Ethylene was monitored by measuring the leaf content of malonyl-1-aminocyclopropane-1-carboxylic acid (MACC) (9). One hundred leaves (25 per tree quadrant) were randomly collected from each tree (at least six nodes below the terminal leaf) in June 1991 and 1992. Leaves were placed in plastic bags and stored in an ice chest containing dry ice for transport to a storage freezer maintained at −16 C. Pesticide grade methanol:water (4:1 v/v) was mixed with leaf tissue (5 ml/g fresh weight) and homogenized 60 seconds (Brinkman Polytron equipped with PT 20ST probe). Samples were centrifuged (17,000 *g,* Sorvall RC2-B refrigerated centrifuge), and the supernatant containing MACC was collected. MACC was converted to 1-aminocyclopropane-1-carboxylic acid (ACC) by drying 0.75 ml of supernatant under a nitrogen stream, resuspending in 6 N HCl (0.75 ml), boiling for 1 hour, and drying again under a nitrogen stream. Finally, the sample was resuspended in 80% methanol.

ACC was converted to ethylene using a procedure modified for peach tissue (14). Samples (0.6 ml) were combined with 20 mM mercuric chloride (0.2 ml) and oxidizer (0.3 ml, 2:1 v/v 5% NaOC1:10N

NaOH) in a microreaction vial sealed with a teflon-faced septum and screw cap. After adding the oxidizer, samples were placed on ice for 1 hour, and 1 ml was removed from the headspace for ethylene analysis.

Ethylene concentration in samples was determined using a Varian 3400 gas chromatograph equipped with a flame ionization detector and a Vista 600 chromatography data system. The detector and injector were maintained at 250 C and 150 C, respectively. The column was activated alumina (2 m × 2 mm id, 60/80 mesh) maintained isothermally at 90 C. Nitrogen carrier gas flow rate was 30 ml/minute. Air flow and hydrogen rates were 300 ml/minute and 30 ml/minute, respectively. Ethylene standards (Scott Specialty Gases, Plumsteadville, PA) were used to standardize equipment, and ACC standards (Sigma Chemical Co., St. Louis, MO) were used for determination of MACC concentrations in peach leaves.

Greenhouse: Two-week-old Lovell peach seedlings were planted in 15-cm-d plastic pots containing approximately 1,500 cm^3 loamy sand (84% sand, 7.6% silt, 8.4% clay; 0.54% organic matter; pH 6.1). One week later, seedlings were inoculated with either 2,000 *C. xenoplax* adults and juveniles, 2,000 *M. incognita* eggs, 2,000 *C. xenoplax* adults and juveniles + 2,000 *M. incognita* eggs/1,500-cm^3 soil, or nematode-free solution obtained from the extraction procedure. Two thousand *C. xenoplax* adults and juveniles or 2,000 *M. incognita* eggs is equivalent to a Pi of ca. 133 nematodes/100 cm^3 soil. The nematode isolates and extraction procedures used were as described in the microplot study, whereas the inoculation procedure was as previously described by Nyczepir et al. (17). Treatments were replicated 10 times. The experimental design was a randomized-complete block composed of a 2 × 2 factorial on benches in an air-conditioned greenhouse (25 ± 5 C). Seedlings were watered daily and fertilized every 2 weeks (16). After approximately 5 months, the study was terminated and the following data were collected: dry root weight (dried at ca. 70 C in aluminum foil until no additional loss in weight occurred) and final population density (Pf) of *C. xenoplax* and *M. incognita* second-stage juveniles (J2). *Meloidogyne incognita* eggs were also extracted as described for the microplot study and counted before drying the roots. Root systems were also rated for galling (21). The gall index consisted of a 0–5 scale, with 0 = no galling, 1 = 1–2 galls, 2 = 3–10 galls, 3 = 11–30 galls, 4 = 31–100 galls, and 5 = >100 galls.

Statistics: All data were subjected to a general linear model analysis. An analysis of variance was performed on the Pf density of *C. xenoplax* in the two treatments that initially received *C. xenoplax* and *C. xenoplax* + *M. incognita.* A similar analysis was also performed on the Pf density of *M. incognita.* Field and greenhouse nematode data were transformed using $\log_{10}(x + 1)$. Actual data were used for table presentation. Additionally, an ANOVA using a factorial design was performed to determine main nematode effects and interactions for trunk diameter, MACC leaf content, and dry root weight. Only significant ($P \leq 0.05$) data will be discussed, unless stated otherwise.

Results

Microplot: The presence of *M. incognita* suppressed the reproduction of *C. xenoplax* 16 and 37 months after inoculation on Lovell peach (Table 1). A similar trend was detected 25 ($P \leq 0.10$) and 29 months after inoculation, but differences were not significant. The presence of *C. xenoplax* did not affect the reproductive potential of *M. incognita* 3 years (37 months) after inoculation.

Differences in Lovell tree growth as related to nematode treatment were not detected until the trees were 26 months of age (Table 2). Main nematode treatment effects indicated that the presence of *M. incognita,* alone or in combination with *C. xenoplax,* reduced mean trunk diameter as compared with *C. xenoplax* and the uninoc-

TABLE 1. Population densities (per 100 cm^3 soil) of *Criconemella xenoplax* (all vermiform stages) and *Meloidogyne incognita* (second-stage juveniles) alone and combined on Lovell peach in field microplots on four sampling dates.

Treatment†	1991 March	1991 December	1992 April	1992 December
		C. xenoplax		
C. xenoplax (Cx)	1,745**	4,539$^+$	3,680 NS	5,851*
Cx + Mi	228	1,043	859	3,312
		M. incognita		
M. incognita (Mi)	245 NS	736 NS	883 NS	522 NS
Cx + Mi	630	1,043	767	557

Data are means of six replications, except for *M. incognita* (December 1991 and December 1992) and *C. xenoplax* (December 1992), which had five replications each.

† Initial population density of *C. xenoplax* = 1 juvenile or adult/100 cm^3 soil, *M. incognita* = 1 egg/100 cm^3 soil, and Cx + Mi = 1 Cx + 1 Mi/100cm^3 soil inoculated in November 1989.

$^+$ = $P \leq 0.10$, * = $P \leq 0.05$, ** = $P \leq 0.01$, and NS = no significant difference according to ANOVA.

ulated control (Table 2). The presence of *C. xenoplax* had no effect on tree growth. The interaction between *C. xenoplax* and *M. incognita* was also significant 26 and 38 months after inoculation. The presence of the two nematode species together caused a greater reduction in tree growth as compared with either species alone.

Nematode effect on MACC content in leaves was detected only during one of the two sampling dates (Table 3). Increased

TABLE 2. Mean trunk diameter (mm) of Lovell peach trees grown in field microplots and sampled 18, 26, and 38 months after inoculation with *Criconemella xenoplax* and *Meloidogyne incognita* alone and combined.

Treatment† (overall mean)	May 1991	January 1992	January 1993
Control	48.9	66.4	79.5
C. xenoplax (Cx)‡	48.8	66.7	81.1
M. incognita (Mi)‡	48.2	57.9	71.0
Cx + Mi‡	40.5	47.0	58.1
Effect mean†			
Mi (main) −	48.9	66.6	80.3
+	44.3	52.4	64.6
Cx (main) −	48.6	62.1	75.3
+	44.6	56.8	69.6
Significance			
Cx (+) vs. Cx (−)	NS	NS	NS
Mi (+) vs. Mi (−)	NS	**	**
Cx × Mi	NS	*	*

Data are means of six replications, except for *M. incognita* (January 1992 and 1993), which had five replications.

† Represents composite means that are an arithmetic function of (M, A, B, A × B), where M = overall mean; A = effect mean for Cx, B = effect mean for Mi, and A × B = effect mean for interaction.

‡ Initial population density of *C. xenoplax* = 1 juvenile or adult/100 cm^3 soil, *M. incognita* = 1 egg/100 cm^3 soil, and Cx + Mi = 1 Cx + 1 Mi/100 cm^3 soil inoculated in November 1989.

* = $P \leq 0.05$, ** = $P \leq 0.01$, and NS = no significant difference according to ANOVA.

TABLE 3. Mean leaf content of malonyl 1-aminocyclopropane-1-carboxylic acid (MACC) in Lovell peach leaves grown in field microplots and sampled 19 and 31 months after inoculation with *Criconemella xenoplax* and *Meloidogyne incognita* alone and in combination.

Treatment† (overall mean)	nMoles MACC/g fresh weight tissue: June 1991	June 1992
Control	9.21	7.70
C. xenoplax (Cx)‡	10.30	7.79
M. incognita (Mi)‡	11.01	8.93
Cx + Mi‡	13.64	8.26
Effect mean†		
Mi (main) −	9.76	7.74
+	12.33	8.59
Cx (main) −	10.11	8.31
+	11.97	8.02
Significance for:		
Cx (+) vs. Cx (−)	NS	NS
Mi (+) vs. Mi (−)	*	NS
Cx × Mi	NS	NS

Data are means of six replications, except for *M. incognita* (June 1992), which had five replications.

† Represents composite means that are an arithmetic function of (M, A, B, A × B) where M = overall mean; A = effect mean for Cx, B = effect mean for Mi, and A × B = effect mean for interaction.

‡ Initial population density of *C. xenoplax* = 1 juvenile or adult/100 cm^3 soil, *M. incognita* = 1 egg/100 cm^3 soil, and Cx + Mi = 1 Cx + 1 Mi/100 cm^3 soil inoculated in November 1989.

* Indicates $P \leq 0.05$ and NS = no significant difference according to ANOVA.

levels of MACC were detected in leaves of trees growing only in soil infested with *M. incognita* 19 months following inoculation (Table 3). *Criconemella xenoplax* had no effect on MACC content in leaves on either sampling date.

In December 1991 and 1992, one tree each was lost from the *M. incognita* and *C. xenoplax* treatments, respectively. The tree inoculated with *M. incognita* died from a possible root rot of unknown origin, whereas the tree inoculated with *C. xenoplax* died from waterlogging caused by defective drainage. Both trees were removed from the test. As of this writing, the remaining 22 trees have not exhibited any typical symptoms associated with PTSL. The only typical nematode-associated symptom observed to date is that of stunting, which was most obvious with trees growing in soil infested with *C. xenoplax* + *M. incognita*. Soil pHs were 6.4 (*C. xenoplax* + *M. incognita*), 6.4 (*C. xenoplax*), 6.2 (uninoculated control), and 6.2 (*M. incognita*) 37 months following inoculation. These soil pH values are in the acceptable range for tree growth as recommended by the University of Georgia Cooperative Extension Service.

Greenhouse: The presence of *M. incognita* suppressed the reproduction of *C. xenoplax* 5 months after inoculation on Lovell peach seedlings (Table 4), which is supportive of our field microplot observations. The presence of *C. xenoplax* had no effect on numbers of *M. incognita* J2 or eggs. The amount of root galling was similar on Lovell seedlings grown in soil infested with *M. incognita* and *M. incognita* + *C. xenoplax* (Table 4).

Differences in root growth, as related to nematode treatment, were detected in the main treatment effects (Table 5). Results indicate that the presence of *M. incognita,* whether alone or in combination with *C. xenoplax,* reduced root growth as compared with *C. xenoplax* and the uninoculated control (Table 5). The presence of *C. xenoplax* had no effect on root biomass. The interaction between the two nematode species was not significant.

TABLE 4. Population densities (per 100 cm^3) of *Criconemella xenoplax* (all vermiform stages) and *Meloidogyne incognita* and root galling after inoculation alone and in combination on Lovell peach seedlings grown in the greenhouse after 5 months.

Treatment†	*C. xenoplax*	*M. incognita*	Root gall rating‡
C. xenoplax (Cx)	8,335*		
Cx + Mi	2,284		
M. incognita J2 (Mi)		87 NS	
Cx + Mi		309	
	Eggs/root system		
Mi		45,050 NS	4.2 NS
Cx + Mi		44,660	4.6

Data are means of 10 replications, except for six replications for *M. incognita* and five replications for Cx + Mi.

† Initial population density of *C. xenoplax* = 133 juveniles and adults/100 cm^3 soil, *M. incognita* = 133 eggs/100 cm^3 soil, and Cx + Mi = 133 Cx + 133 Mi/100^3 soil.

‡ Rated on a scale of 1–5 where 0 = no galls; 1 = 1–2 galls; 2 = 3–10 galls; 3 = 11–30 galls; 4 = 31–100 galls; and 5 = >100 galls per root system.

* Indicates $P \leq 0.05$ and NS = no significant difference according to ANOVA.

DISCUSSION

Meloidogyne incognita and *C. xenoplax* occur together frequently in peach orchards

TABLE 5. Mean dry root weight of Lovell peach seedlings grown in the greenhouse for 5 months following inoculation with *Criconemella xenoplax* and *Meloidogyne incognita* alone and in combination.

Treatment† (overall mean)	Dry root weight (g)
Control	8.91
C. xenoplax (Cx)‡	7.01
M. incognita (Mi)‡	2.21
Cx + Mi‡	2.05
Effect mean†	
Mi (main) −	7.96
+	1.57
Cx (main) −	5.59
+	3.94
Significance for:	
Cx (+) vs. Cx (−)	NS
Mi (+) vs. Mi (−)	**
Cx × Mi	NS

Data are means of 10 replications, except for six replications for *M. incognita* and five replicates for Cx + Mi.

† Represents composite means that are an arithmetic function of (M, A, B, A × B) where M = overall mean; A = effect mean for Cx; B = effect mean for Mi; and A × B = effect mean for interaction.

‡ Initial population density of *C. xenoplax* = 133 juveniles and adults/100 cm^3 soil, *M. incognita* = 133 eggs/100 cm^3 soil, and Cx + Mi = 133 Cx + 133 Mi per 100 cm^3 soil.

** Indicates $P \leq 0.01$ and NS = no significant difference according to ANOVA.

throughout the southeastern United States (15). Yet PTSL is associated with *C. xenoplax* only. Symptoms include the sudden collapse of 3- to 6-year-old trees in the spring that have a sour-sap odor (19). If 1- to 3-year-old trees appear stunted and symptoms of root galling are present, then *Meloidogyne* spp. are considered the causal agent (1). Our results, however, indicated that a reduction in tree growth of a suitable host for both nematodes was more severe with trees growing in the presence of the two nematode species. This is the first evidence of a synergistic interaction between a migratory ecto- and a sedentary endoparasitic nematode on peach. The severe above-ground stunting of trees growing in soil infested with *M. incognita* + *C. xenoplax* is usually observed in peach orchards throughout the Southeast. Reduction ($P \leq 0.05$) in growth was also detected in trees growing in *M. incognita*-infested soil 26 months following inoculation. Tree growth suppression was not as visually apparent as compared with trees growing in soil infested with *M. incognita* + *C. xenoplax*, or with trees growing in the uninoculated and *C. xenoplax*-infested soil. Furthermore, the nematode interactions were dependent on population density. A Pi of only one *C. xenoplax* + one *M. incognita* egg/100-cm^3 soil caused severe stunting 26 months following inoculation.

The feeding sites on roots by migratory ectoparasitic and sedentary endoparasitic nematodes differ. *Criconemella xenoplax* prefers cortical cells further back on the root (11), whereas *Meloidogyne* spp. penetrate at the root tip, establish themselves, and feed in the vascular cylinder region (4). As a result of direct or indirect competition for feeding sites, the more dominant nematode may influence reproduction of the cohabiting nematode. On concord grape, *C. xenoplax* suppressed reproduction of *M. hapla* Chitwood (20), whereas *M. incognita* suppressed reproduction of *Pratylenchus brachyurus* (Godfrey) Filipjev & Schuurmans Stekhoven on soybean (8). Our results indicate that *M. incognita* suppressed the reproduction of *C. xenoplax* on peach in both field and greenhouse tests. The mechanism(s) by which this occurs was not addressed, but *Meloidogyne* spp. creates a source–sink feeding situation with their host by the induction of giant cells. As a result, the nematode remains sedentary, feeding from these modified host cells for the remainder of its life. *Criconemella xenoplax*, on the other hand, forms modified cortical food cells (11). Females were reported feeding from one cortical cell for up to 8 days, with ingestion ceasing when females became gravid (23). It appears that *M. incognita* is the more dominant nematode species in this interaction and is a stronger competitor than *C. xenoplax* for food on Lovell peach.

Meloidogyne incognita was more pathogenic on Lovell peach than was *C. xenoplax* under these test conditions. The presence of *M. incognita* (main effect) caused a greater reduction in seedling dry-root weight and tree-trunk diameter than did *C. xenoplax*. Increased levels of MACC content in leaves were also detected only in trees growing in *M. incognita*-infested soil. Generally, increased ethylene production in plants has been associated with response to stress factors, including many plant–pathogen interactions (2). Our results, showing an increase in MACC content in leaves, are in agreement with increased ACC (ethylene precursor) levels found in tomato leaves infected with *M. javanica* (Treub) Chitwood (7). Increased ethylene production in tomato roots infected with *M. javanica* has been associated with gall formation (6). Ethylene appears to enhance the growth of the cortical hypertrophied parenchymatous tissue in the gall, in addition to playing a major role in the pathological effects of the nematode on the entire host plant.

Because cohabitation of plant-parasitic nematodes in peach orchards is common in nature, interactions among nematodes most likely influence the severity of a disease, as demonstrated in this study. It is, therefore, essential that preplant nematode samples be obtained before orchard

establishment. Such a basic but important practice will allow growers to make the right nematode management decision(s) as to whether or not they should select another site or use a preplant nematicide with an appropriate rootstock to establish the orchard. This approach, as compared to randomly planting trees on a new site without taking soil samples for nematode assay, will prevent unnecessary nematode management costs for the grower.

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