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Interaction of Concurrent Populations of *Meloidogyne partityla* and *Mesocriconema xenoplax* on Pecan

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Abstract: The effect of the interaction between *Meloidogyne partityla* and *Mesocriconema xenoplax* on nematode reproduction and vegetative growth of *Carya illinoinensis* 'Desirable' pecan was studied in field microplots. *Meloidogyne partityla* suppressed reproduction of *M. xenoplax*, whereas the presence of *M. xenoplax* did not affect the population density of *M. partityla* second-stage juveniles in soil. Above-ground tree growth, as measured by trunk diameter 32 months following inoculation, was reduced in the presence of *M. partityla* alone or in combination with *M. xenoplax* as compared with the uninoculated control trees. The interaction between *M. partityla* and *M. xenoplax* was significant for dry root weight 37 months after inoculation. Results indicate that the presence of the two nematode species together caused a greater reduction in root growth than *M. xenoplax* alone, but not when compared to *M. partityla* alone. Mouse-ear symptom severity in pecan leaves was increased in the presence of *M. partityla* compared with *M. xenoplax* and the uninoculated control. Infection with *M. partityla* increased severity of mouse-ear symptoms expressed by foliage. The greater negative impact of *M. partityla* on vegetative growth of pecan seedlings in field microplots indicates that it is likely a more detrimental pathogen to pecan than is *M. xenoplax* and is likely an economic pest of pecan.

Key words: Carya illinoinensis, concomitance, host-parasitic relationship, interaction, *Meloidogyne partityla*, *Mesocriconema xenoplax*, mouse-ear, nickel deficiency, pecan, ring nematode, root-knot nematode.

Pecan (*Carya illinoinensis*) is North America's most valuable native tree-nut crop, with worldwide cultivation and substantial production in both the United States and Mexico (Wood et al., 1990; Wood, 1994). United States kernel production alone was approximately 175,000 tonnes in 2007 (Anonymous, 2008). It is increasingly cultivated in Africa (i.e., South Africa), Australia and South America (e.g., Argentina, Brazil, Chile, Paraguay, Peru and Uruguay). Pecan trees are attacked by a wide variety of disease and insect pests that can reduce tree productivity if not properly managed. Cultivated trees are also prone to exhibit certain micronutrient deficiencies (e.g., Zn) when grown in soils substantially different than the hydrophilic oligotrophic soils typical of its habitat along the river bottoms of the central and southern United States.

The "mouse-ear" (ME) or "little leaf" malady of pecan is a nutrient disorder that was first reported in 1918 (Matz, 1918) and then subsequently observed in yard trees growing in specific regions of the Gulf Coast Coastal Plain of the southeastern United States (Demaree, 1926). This nutrient disorder has increasingly manifested itself more recently as an orchard "replant" disorder (Wood et al., 2004a). Both maladies have recently been found to be due to a nickel (Ni) deficiency, with timely foliar application of Ni correcting both disorders (Wood et al., 2004a, 2004b). Nickel-deficient trees sometimes, but not always, exhibited evidence of nematode damage, especially that from *Meloidogyne* sp.

Two root-knot nematode species had been reported to parasitize pecan in Georgia prior to 2002, *Meloidogyne incognita* (Kofoid and White) Chitwood and *M. arenaria* (Neal) Chitwood (Hendrix and Powell, 1968; Carithers, 1978). In 2002, the pecan root-knot nematode, *M. partityla* Kleynhans, was found on pecan in the southeastern United States and was associated with stressed trees exhibiting dead branches in the upper canopy and/or typical ME-associated foliar symptoms (Nyczepir et al., 2002). This was the first report of *M. partityla* on pecan in Georgia and the third report of this nematode outside of South Africa (Kleynhans, 1986), where it was initially found and described. It is noteworthy that the first report of *M. partityla* on pecan within the United States occurred in Texas in 1996 (Starr et al., 1996). In many of these ME orchards sampled in Georgia, *Mesocriconema xenoplax* (Raski) Loof & de Grisse [= *Criconemoides xenoplax* (Raski) Loof and de Grisse] was detected in the same soil as *M. partityla* (A. P. Nyczepir, USDA-ARS, pers. com). A subsequent survey was conducted in the major pecan-growing regions of Georgia to determine the distribution of *M. partityla* and other possible *Meloidogyne* spp. (Nyczepir et al., 2004). Results showed that *M. partityla* and two unknown *Meloidogyne* spp. were the only root-knot nematode species found parasitizing pecan. Neither *M. incognita* nor *M. arenaria* were detected in any of the root samples collected during this survey. *Meloidogyne partityla* was found in a greater number of samples and was the dominant root-knot nematode species parasitizing pecan in Georgia. Further evidence in controlled field microplot studies showed that severity of ME symptoms, and thus Ni deficiency, in pecan trees can be triggered or enhanced by the presence of *M. partityla* (Nyczepir et al., 2006). It appears that *M. xenoplax* parasitism has little influence on ME severity, but additional information to substantiate this initial observation would be beneficial.

The combined impact of parasitism by a sedentary endoparasitic and migratory ectoparasitic nematode on growth of pecan is unknown. This study assesses the effects of the interactions between *M. partityla* and *M. xenoplax* on pecan vegetative growth, nematode reproduction and incidence of ME.

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Materials and Methods

Nematode source and inoculum: Eggs of *M. partityla*, originating from a commercial pecan orchard with ME symptoms in Cobb, GA, were extracted directly from the roots of a single tree. Identification of the root-knot nematode as *M. partityla* was confirmed using the esterase phenotype technique (Esbenshade and Triantaphyllou, 1985). *Meloidogyne partityla* eggs were extracted from pecan roots using the method described by Hussey and Barker (1973). *Mesocriconema xenoplax* originating from a pecan orchard with ME symptoms in Leary, GA, were cultured on 'Desirable' pecan seedlings and extracted from the culture medium using centrifugation (Jenkins, 1964).

Field microplot experiment: Approximately 4-wk-old open-pollinated 'Desirable' pecan seedlings were planted singly in bucket microplots (Barker, 1985) (25-cm diam. × 31-cm deep) containing 15,000 cm^3 of steam-pasteurized soil (86% sand, 10% silt, 4% clay; pH 6.1; 0.54% organic matter) in May 2002. The soil was obtained from a site at the USDA ARS Southeastern Fruit and Tree Nut Research Laboratory, Byron, GA, that had been cleared of peach trees in the late 1970s and had remained fallow since that time. Microplots were established in a shaded area (30% shade) in a different field in Byron, GA.

In July 2002, two mon after seedling survival was evident, the following nematode treatments were added per microplot: i) 4,000 *M. partityla* eggs (Mp); ii) 4,000 *M. xenoplax* adults and juveniles (Mx); iii) 4,000 *M. xenoplax* adults and juveniles + 4,000 *M. partityla* eggs (Mx + Mp); and iv) an untreated control. The initial population density of 4,000 *M. partityla* or 4,000 *M. xenoplax*/microplot is equivalent to 27 *M. partityla* eggs/100 cm^3 soil or 27 *M. xenoplax* juveniles or adults/100 cm^3 soil, respectively. The soil in each microplot was infested with the respective nematode inoculum in 40 ml total solution poured into two furrows (10-cm long × 3-cm wide × 7-cm deep) around each seedling. The soil in the steam-pasteurized nematode-free control microplots was inoculated with an egg/nematode-free soil extract suspension from the same *M. partityla* pecan orchard and *M. xenoplax* culture. The experiment consisted of a 2 × 2 factorial with 10 single tree replications/treatment arranged as a randomized complete block. Tree-trunk diameters were measured 8.0 cm above the soil line in February 2003 and March 2004 and 2005. The study was terminated approximately 37 mon (August 2005) after soil infestation, and nematode population densities in roots and soil were quantified. Nematode population density in soil was determined from five cores (2.5-cm diam. × 30-cm deep) that were collected beneath the canopy of each tree. Nematodes were counted following extraction from a 100 cm^3 subsample with a semi-automatic elutriator (Byrd et al., 1976) and centrifugal-flotation (Jenkins, 1964). *Meloidogyne partityla* eggs in roots were estimated by randomly cutting a 5-gram fresh weight portion of the root system and extracting eggs with a NaOCl solution as mentioned above. After extracting the eggs from the roots, the dry root weight (dried to a constant weight at 70°C in aluminum foil) of each tissue extraction sample was determined. The remaining root systems were dried on greenhouse benches to a constant weight and then combined with the tissue extraction sample weights for total dry weight.

Trees were evaluated for ME severity in April 2003 and May 2004 and 2005. Mouse-ear severity was based on the following scale developed for Ni deficiency symptoms by Wood et al. (2004a, 2004b): 1 = no Ni-associated morphological distortions of leaflets or leaves (i.e., normal); 2 = 1% to 25% of leaflets on the seedling exhibiting Ni-deficient morphological distortions (i.e., slightly blunted); 3 = 26% to 50% of leaflets exhibiting some degree of Ni-associated morphological distortions; 4 = >50% of leaflets exhibiting morphological distortions; 5 = #4, plus leaflet cupping; 6 = #5, plus necrosis of leaflet tips; 7 = #6, plus necrosis of leaflet margins, crinkled leaflets and dwarfed leaflets; 8 = #7, plus dwarfed shoots; 9 = #8, plus rosetting; and 10 = #9, plus tree death.

Plants were watered as needed; however, annual applications of fertilizer were not made because most fertilizers contain Ni as a trace contaminate which could confound the experiment by preventing ME symptoms from developing.

Statistical analysis: All data were subjected to a general linear model analysis. An analysis of variance was performed on the final soil population density (Pf) of *M. xenoplax* in the two treatments that initially received *M. xenoplax* and *M. xenoplax* + *M. partityla*. A similar analysis was also performed on the Pf density of *M. partityla*. Additionally, an ANOVA using a factorial design was performed to determine main nematode effects and interactions for trunk diameter, mouse-ear severity rating and dry root weight. The occurrence of seedling mortality among nematode treatments was analyzed for each sampling date with Fisher's Exact Test. Only significant differences ($P \leq 0.05$) will be discussed unless stated otherwise.

Results and Discussion

The presence of *M. partityla* contributed to the suppression ($P \leq 0.05$) in population density of *M. xenoplax* on 'Desirable' pecan 37 months after inoculation (Table 1), whereas the presence of *M. xenoplax* did not detectably affect the population density of *M. partityla* second-stage juveniles (J2) in soil. Neither did the presence of *M. xenoplax* significantly affect the reproduction potential of *M. partityla* in pecan as measured by number of eggs per plant (i.e., *M. partityla*-alone = 746,971 eggs/plant vs. Mx + Mp = 441,765 eggs/plant;

TABLE 1. Population densities (per 100 cm^3 soil) of *Meloidogyne partityla* (second-stage juveniles) and *Mesocriconema xenoplax* (all vermiform stages) alone and combined on 'Desirable' pecan in field microplots 37 months after soil infestation.

Treatment[a]	Nematode
	M. xenoplax
M. xenoplax (Mx)	324*[b]
Mx + Mp	133
	M. partityla
M. partityla (Mp)	4 ns
Mx + Mp	18

Data are means of 10 replications, except for *M. partityla* which had four replications and nine replications for Mx + Mp.

[a]Initial population density of *M. partityla* = 27 eggs/100 cm^3 soil, *M. xenoplax* = 27 juveniles or adults/100cm^3 soil, and Mx + Mp = 27 Mx + 27 Mp/100 cm^3 soil inoculated in July 2002.

[b]*Significant at $P \leq 0.05$; ns = $P > 0.05$ according to ANOVA.

TABLE 2. Trunk diameter and dry root weight of 'Desirable' pecan seedlings grown in field microplots and sampled seven, 20 and 32 months after inoculation and 37 months after inoculation, respectively, with *Meloidogyne partityla* and *Mesocriconema xenoplax* alone and in combination.

	Trunk diameter (mm)			Dry root weight (g)
		March		
Factors	February 2003	2004	2005	August 2005
Treatment mean				
Control	6.03	8.35	10.51	133.33
M. xenoplax (Mx)[a]	5.70	8.11	8.75	73.50
M. partityla (Mp)[a]	6.19	7.81	8.00	34.03
Mx + Mp[a]	5.89	7.72	8.29	43.28
Main effect mean				
Mp −	5.86	8.23	9.63	101.84
+	6.04	7.76	8.16	38.65
Mx −	6.11	8.08	9.48	102.78
+	5.79	7.91	8.53	64.86
Significance for:				
Mx (+) vs. Mx (−)	ns[b]	ns	ns	*
Mp (+) vs. Mp (−)	ns	ns	*	**
Mx × Mp	ns	ns	ns	**

Data are means of 10 replications, except for *M. partityla* and Mx + Mp in March 2005, which had seven and nine replications, respectively, and for *M. partityla* and Mx + Mp in August 2005, which had three and four replications, respectively.

[a]Initial population density of *M. partityla* = 27 eggs/100 cm^3 soil, *M. xenoplax* = 27 juveniles or adults/100cm^3 soil, and Mx + Mp = 27 Mx + 27 Mp/100 cm^3 soil inoculated in July 2002.

[b]*Significant at $P \leq 0.05$; ** = $P \leq 0.01$; ns = $P > 0.05$ according to ANOVA.

data not presented in Table) or number of eggs per gram dry root (i.e., *M. partityla*-alone = 24,302 eggs/gram dry root vs. Mx + Mp = 11,911 eggs/gram dry root; data not presented in Table).

One explanation for the suppression in nematode reproduction by one nematode species on another may be attributed to a reduction or alteration of suitable feeding sites on the root. Nematode-feeding sites on roots differ between a sedentary endoparasite, such as the root-knot nematode, and a migratory ectoparasite, such as the ring nematode. *Meloidogyne* spp. penetrate at the root tip, establish themselves and feed within the vascular cylinder region for the remainder of their life cycle (de Guiran and Ritter, 1979). The ring nematode feeds from individual cortical cells further back on the root for up to eight days and then moves to a new feeding site along the root (Hussey et al., 1992); these sites are modified into discrete food cells. Apparently, as a result of direct or indirect competition for feeding sites, the more aggressive nematode may influence reproduction of the cohabiting nematode. On soybean and peach, *M. incognita* suppressed reproduction of *Pratylenchus brachyurus* and *M. xenoplax*, respectively (Herman et al., 1988; Nyczepir et al., 1993), whereas *M. xenoplax* suppressed reproduction of *M. hapla* on grape (Santo and Bolander, 1977). Our results showed that *M. partityla* suppressed the reproduction of *M. xenoplax* in pecan and appears to be the more aggressive nematode specie and competitor in this nematode-nematode host-parasite relationship.

Differences in 'Desirable' tree growth as related to nematode treatment were not detected until the trees were 32 months of age (March 2005) (Table 2). Main nematode treatment effects indicated that the presence of *M. partityla* alone or in combination with *M. xenoplax* reduced ($P \leq 0.05$) mean trunk diameter as compared with *M. xenoplax* alone and the uninoculated control. The presence of *M. xenoplax* had no effect on above-ground tree growth, and the interaction between the two nematodes was not significant on any of the three sampling dates. Below-ground differences in pecan root growth as related to nematode treatment were detected 37 months after inoculation (August 2005) (Table 2). Main treatment effects indicate that the presence of *M. partityla* alone or in combination with *M. xenoplax* and *M. xenoplax* alone or in combination with *M. partityla* reduced ($P \leq 0.05$) root growth (Table 2). The interaction between *M. partityla* and *M. xenoplax* was also significant ($P \leq 0.01$) for dry root weight. Although the effect of the combined nematode treatment (Mx + Mp) was less than that of *M. xenoplax* alone, it was not less than *M. partityla* alone, which resulted in a significant interaction for dry root weight. Our results indicate that above-ground tree growth is smaller with trees growing in the presence of *M. partityla* than *M. xenoplax*. This is the first experimental proof of the pathogenicity between *M. partityla* and pecan and may explain the above-ground stunting of pecan observed in commercial orchards in the southeastern United States.

The severity of ME symptoms was related to nematode treatment on all three sampling dates (Table 3). Main nematode treatment effects indicated that the presence of *M. partityla* alone or in combination with *M. xenoplax* increased ($P \leq 0.05$) the severity of ME as compared with *M. xenoplax* and the uninoculated control. The presence of *M. xenoplax* had no effect on ME severity, and the interaction between the two nematodes was not significant on any of the three sampling dates. The occurrence of tree mortality (i.e., ME severity rating =

TABLE 3. Mouse-ear (ME) severity in 'Desirable' pecan seedlings grown in field microplots and evaluated nine, 22 and 34 months after inoculation with *Meloidogyne partityla* or *Mesocriconema xenoplax* alone and in combination.

Factors		April 2003	May 2004	May 2005
Treatment mean				
Control		1.3[a]	1.3	1.1
M. xenoplax (Mx)[b]		1.3	1.6	2.0
M. partityla (Mp)[b]		1.9	5.3	7.9
Mx + Mp[b]		2.7	3.6	7.6
Main effect mean				
Mp	−	1.3	1.5	1.6
	+	2.3	4.5	7.8
Mx	−	1.6	3.3	4.5
	+	2.0	2.5	4.8
Significance for:				
Mx (+) vs. Mx (−)		ns[c]	ns	ns
Mp (+) vs. Mp (−)		*	**	**
Mx × Mp		ns	ns	ns

Data are means of 10 replications.

[a]ME severity was based on the following foliar symptom class scale: 1 = no Ni-associated morphological distortions of leaflets or leaves (i.e., normal); 2 = 1% to 25% of leaflets on the seedling exhibiting Ni-deficient morphological distortions (i.e., slightly blunted); 3 = 26% to 50% of leaflets exhibiting some degree of Ni-associated morphological distort; 4 = >50% of leaflets exhibiting morphological distortion; 5 = #4, plus leaflet cupping; 6 = #5, plus necrosis of leaflet tips; 7 = #6, plus necrosis of leaflet margins, crinkled leaflets and dwarfed leaflets; 8 = #7, plus dwarfed shoots; 9 = #8, plus rosetting; and 10 = #9, plus tree death.

[b]Initial population density of *M. partityla* = 27 eggs/100 cm^3 soil, *M. xenoplax* = 27 juveniles or adults/100cm^3 soil, and Mx + Mp = 27 Mx + 27 Mp/100 cm^3 soil inoculated in July 2002.

[c]*Significant at $P \leq 0.05$; ** = $P \leq 0.01$; ns = $P > 0.05$ according to ANOVA.

#10) was first detected in May 2004 (22 months after inoculation) (Table 4). In May 2005 (34 months after inoculation), a greater ($P \leq 0.05$) number of trees died in the *M. partityla* alone and *M. partityla* in combination with *M. xenoplax* treatments than trees in the *M. xenoplax* alone and control treatments. No trees in the *M. xenoplax* alone and control treatments died during the first 34 months after inoculation. Our findings substantiate that i) the presence of *M. partityla* triggers ME symptoms, and thus Ni deficiency, in pecan trees and ii) the parasitic habit of *M. xenoplax* appears to have little or no influence on ME severity in pecan (Nyczepir et al., 2006).

In summary, *M. partityla* is an economically importance pest to the pecan industry in the southeastern United States, and it is therefore important that preplant nematode samples be collected and analyzed for the presence of this pathogenic nematode prior to orchard establishment. Furthermore, the total economic impact of *M. partityla* on orchard longevity, yield and nut quality is unknown. However, our findings indicate that there is a need for further study of the impact of *M. partityla* on pecan orchard profitability and development of control and of IPM management strategies such as rootstock resistance and biological control.

TABLE 4. Effect of *Meloidogyne partityla* (Mp) or *Mesocriconema xenoplax* (Mx) alone and in combination on development of mortality in 'Desirable' pecan seedlings grown in field microplots, 2003-05.

Year	Mx[a]	Mp[a]	Mx + Mp[a]	Control
2003	0[b](10)[c]	0 (10)	0 (10)	0 (10)
2004	0 (10)	3 (10)	1 (10)	0 (10)
2005	0 (10) b	7 (10) a	6 (10) a	0 (10) b

Data are means of 10 replications. Treatments within a row followed by the same letter on a particular date are not different ($P \leq 0.05$) according to Fisher's Exact Test.

[a]Initial population density of *M. partityla* = 27 eggs/100 cm^3 soil, *M. xenoplax* = 27 juveniles or adults/100cm^3 soil, and Mx + Mp = 27 Mx + 27 Mp/100 cm^3 soil inoculated in July 2002.

[b] Cumulative number of dead trees.

[c] Total number of trees per treatment.

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