

Nematode Population Fluctuations during Decomposition of Specific Organic Amendments¹

R. McSORLEY AND J. J. FREDERICK²

Abstract: Population densities of nematodes in field soil without plants were monitored for 10 months following application of organic amendments to pots in a greenhouse. The four treatments consisted of three different kinds of organic amendments: homogeneous crop residues of maize (*Zea mays*, C:N = 48.0:1), Texas panicum (*Panicum texanum*, C:N = 32.9:1), or velvetbean (*Mucuna pruriens*, C:N = 18.6:1), plus a control without any amendment. Plant-parasitic nematodes declined in all treatments due to absence of a food source. Bacterivore numbers increased following amendment application and remained greater than initial population levels until 4 months after application. Fungivore numbers were higher than initial levels until 6 months after amendment application and did not decline below the initial numbers during the course of the experiment. On several sampling dates, the bacterivorous genera *Cervoidellus* and *Eucephalobus* were most abundant in pots with maize residues. Among the fungivores, *Aphelenchoides* numbers early in the experiment were greatest in pots amended with velvetbean, whereas numbers of *Aphelenchus*, *Nothotylenchus*, and Tylenchidae (mainly *Filenchus*) were greatest during the latter half of the experiment following the maize amendment. Omnivorous nematodes, particularly *Eudorylaimus*, showed two peaks in abundance during the course of the experiment. Results provided some evidence that population levels of some genera of bacterivores and fungivores may be affected by specific organic amendments.

Key words: bacterivores, fungivores, nematode community, omnivores, plant parasitics, predators, soil ecology, trophic groups.

Soil-inhabiting nematodes are important in the processes of decomposition and nutrient recycling (Anderson et al., 1981; Freckman, 1988; Ingham et al., 1985). However, much less is known about the nematode bacterivores and fungivores involved in decomposition than the plant-parasitic nematodes that inhabit the same environment. The preferences of many kinds of plant-parasitic nematodes for particular plant hosts are well known and used to develop management strategies (Christie, 1959; Evans et al., 1993). It is unclear whether different kinds of organic materials could provide substrates for different bacterial and fungal decomposers, which in turn could provide food sources for different kinds of bacterivorous and fungivorous nematodes. There is evidence that levels of these bacterivores and fungivores fluctuate seasonally and in response to treatment

(Bostrom and Sohlenius, 1986; Freckman and Ettema, 1993; McSorley, 1993; McSorley and Frederick, 1996; Todd, 1996; Yeates, 1982; Yeates and Bird, 1994), which may reflect changes in the type and quality of organic substrate available to decomposer food webs. A succession of nematode bacterivores and fungivores is known to occur as the primary decomposers (bacteria and fungi) and the quality of organic matter change during the decomposition process (Elkins and Whitford, 1982; Wasilewska and Bienkowski, 1985).

The objective of the present study was to determine the effects of different kinds of organic amendments on population levels of nematode genera present during the decomposition process in a sandy field soil.

MATERIALS AND METHODS

A large volume (ca. 100 liters) of soil was collected on 9 December 1993 from an old maize (*Zea mays*) field at the University of Florida agronomy farm in Alachua County, Florida, at approximately 29°40'N and 82°30'W. The soil type was an Arredondo fine sand (89.5% sand, 3.5% silt, 7.0% clay) with 2.3% organic matter and pH 5.9. The soil was transported to Gainesville, Florida,

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mixed in a small cement mixer, and five 100-cm³ samples were removed for extraction of nematodes. The soil was placed into 20 4-liter clay pots (19.5 cm high × 21 cm top diam. × 12.8 cm bottom diam.). Each pot held 3.12 kg soil at an average initial soil moisture of 5.3%.

Crop and weed residues for use as organic amendments were collected in late November. Maize stover (mostly stalks) and top residues of Texas panicum (*Panicum texanum*) were collected separately from the same field in which the soil was obtained. Top residues (mostly leaves) of velvetbean (*Mucuna pruriens*; syn. *M. deeringiana*) were collected from an adjacent field. The three different amendment sources were kept separate, chopped into pieces ≤2 cm in length, and dried in an oven at 80 °C for 1 week. Preliminary tests had established that this drying protocol was necessary to eliminate Rhabditidae persisting in crop residues. Subsamples of each amendment were incubated on Baermann trays (Rodríguez-Kábana and Pope, 1981) for 1 week to verify that they were free of nematodes. Amendment composition (Table 1) was determined by R. N. Gallaher at the University of Florida Agronomy Department by methods described elsewhere (Whitty and Gallaher, 1997).

On 9 December 1993, 20 g of amendment (0.64% by weight) was mixed with the soil from each pot. Four amendment treatments (maize, panicum, velvetbean, non-amended control) were replicated 5 times. Pots were arranged on a greenhouse bench in a randomized complete block design. Pots were observed daily and watered as needed to prevent drying. Weed seedlings were removed immediately.

In addition to the original soil samples

extracted on 9 December 1993, pots were sampled 6 more times between 26 January and 19 October 1994 with a cork borer (11 cm long × 2 cm diam.) used to remove 3 soil cores per pot. The cores from each pot were pooled, and nematodes were extracted from 100 cm³ soil by sieving and centrifugation (Jenkins, 1964). All nematodes from each subsample were identified to genus where possible (exceptions included Rhabditidae, Tylenchidae, and some Neotylenchidae) and counted at ×150 on an inverted microscope equipped such that individual specimens could be examined at higher magnification (×600). Nematodes were assigned to trophic groups based on recent literature (Yeates et al., 1993) with a few exceptions, as described later in this paper.

Within each sampling date, nematode data from the four amendment treatments were compared by analysis of variance followed by mean separation with Duncan's multiple-range test. Nematode population densities on various sampling dates were compared with the population density at the beginning of the experiment by appropriate orthogonal contrasts. MSTAT-C statistical software (Michigan State University, East Lansing, MI) was used for all statistical analyses. Unless noted otherwise, all differences discussed in the text are significant at $P \leq 0.05$.

The experiment was terminated on 19 October 1994. During the course of the experiment, a total of ca. 600 cm³ soil was removed from each pot.

RESULTS AND DISCUSSION

At the end of the experiment, the organic matter levels in pots amended with cornstalk (1.9%), panicum (2.0%), and velvetbean

TABLE 1. Mineral analyses and C:N ratios for organic amendments.

Amendment source	C:N ratio	Grams per kilogram dry weight					Milligrams per kilogram dry weight			
		Ca	Mg	K	P	N	Cu	Fe	Mn	Zn
Velvetbean	18.6:1	6.83	1.82	24.1	3.10	28.0	7	80	51	23
Panicum	32.9:1	4.22	3.05	18.2	1.54	10.5	4	480	170	57
Maize	48.0:1	3.11	1.85	6.8	1.88	10.7	4	1,030	34	38

TABLE 3. Effect of soil amendments on numbers of plant-parasitic nematodes in greenhouse experiment, 1993–1994.

Amendment	Nematodes per 100 cm ³ soil						
	9 Dec.	26 Jan.	10 Mar.	20 Apr.	15 Jun.	11 Aug.	19 Oct.
				<i>Belonolaimus</i>			
Maize	—	1 a ^{*a}	0 a*	0 a*	0 *	0 *	0 *
Panicum	—	4 a*	1 a*	0 a*	0 *	0 *	0 *
Velvetbean	—	3 a*	0 a*	1 a*	0 *	0 *	0 *
None	28 ^b	7 a*	0 a*	1 a*	0 *	0 *	0 *
				<i>Criconebella</i>			
Maize	—	22 b*	18 a*	7 b*	1 b*	1 a*	6 b*
Panicum	—	23 b*	15 a*	8 b*	4 b*	2 a*	7 b*
Velvetbean	—	20 b*	21 a*	9 b*	1 b*	3 a*	4 b*
None	98	75 a*	27 a*	19 a*	9 a*	3 a*	13 a*
				<i>Helicotylenchus</i>			
Maize	—	6 b*	3 a*	1 ab*	1 b*	0 a*	0 a*
Panicum	—	6 b*	3 a*	4 b*	1 b*	0 a*	2 a*
Velvetbean	—	7 b*	4 a*	3 b*	1 b*	0 a*	2 a*
None	18	14 a	5 a*	9 a*	3 a*	2 a*	5 a*
				<i>Meloidogyne</i>			
Maize	—	5 a*	0 a*	0 a*	0 *	0 *	0 b*
Panicum	—	1 a*	0 a*	0 a*	0 *	0 *	0 b*
Velvetbean	—	3 a*	0 a*	0 a*	0 *	0 *	0 b*
None	18	4 a*	1 a*	1 a*	0 *	0 *	4 a*
				<i>Paratrichodorus</i>			
Maize	—	2 b*	0 *	0 b*	0 a*	0 *	0 b*
Panicum	—	1 b*	0 *	0 b*	0 a*	0 *	0 b*
Velvetbean	—	0 b*	0 *	0 b*	0 a*	0 *	0 b*
None	40	6 a*	0 *	2 a*	1 a*	0 *	1 a*
				<i>Pratylenchus</i>			
Maize	—	0 b*	1 a*	0 *	0 *	0 *	0 *
Panicum	—	1 b*	0 a*	0 *	0 *	0 *	0 *
Velvetbean	—	1 b*	1 a*	0 *	0 *	0 *	0 *
None	3	3 a	0 a*	0 *	0 *	0 *	0 *

Data are means of five replications. For each nematode, means in a column followed by the same letter are not different ($P \leq 0.05$), according to Duncan's multiple-range test.

^a Asterisk (*) indicates significant ($P \leq 0.05$) difference from number present on 9 December.

^b Numbers present on 9 December are initial numbers before treatments were imposed.

remained higher than the initial level (85/100 cm³ soil) until 15 June and never declined below the initial level at any time during the experiment. The initial bacterivore: fungivore ratio of 2.34:1 declined to 1.10:1 (averaged over all amended pots) on 20 April, and was <1:1 on all subsequent sampling dates. This succession of bacterivores and fungivores over time and the long persistence of nematode fungivores (and presumably fungal decomposition) have been observed in earlier decomposition studies as well (Elkins and Whitford, 1982; Wasilewska and Bienkowski, 1985). Interestingly, in field soil in Poland, Wasilewska and Bienkowski (1985) observed a peak in activity of fungivorous nematodes at 24 to 32 weeks

after decomposition was initiated, which corresponds to the 15 June sample in this study.

Bacterivores: Fluctuations in total numbers of bacterivores over time in amended pots were determined to a great extent by trends in levels of *Acrobeles* and *Rhabditidae*, both of which were elevated above initial levels until 20 April and declined thereafter (Table 4). *Acrobelloides* numbers declined more quickly, but *Eucephalobus* was more persistent over time. The kind of amendment used did not consistently affect bacterivore numbers; however, *Cervidellus* and *Eucephalobus* were most abundant in pots with maize amendment on several sampling dates. Because the C:N ratio of this amend-

TABLE 4. Effect of soil amendments on numbers of bacterivorous nematodes in greenhouse experiment, 1993–1994.

Amendment	Nematodes per 100 cm ³ soil						
	9 Dec.	26 Jan.	10 Mar.	20 Apr.	15 Jun.	11 Aug.	19 Oct.
				<i>Acrobeles</i>			
Maize	—	79 a**a	153 a*	312 a*	50 a	23 a	41 ab
Panicum	—	67 a	236 a*	92 b*	72 a	30 a	77 a
Velvetbean	—	29 b	70 a*	240 a*	41 a	22 a	38 ab
None	29 ^b	18 b	7 b*	10 c*	5 b*	2 b*	9 b*
				<i>Acrobeloides</i>			
Maize	—	608 a*	86 a	42 a	4 a*	2 a*	2 a*
Panicum	—	275 ab*	57 a	29 a*	30 a*	12 a*	1 a*
Velvetbean	—	166 bc	48 a	26 a	3 a*	6 a*	2 a*
None	56	66 c	7 b*	3 b*	1 a*	0 a*	2 a*
				<i>Cephalobus</i>			
Maize	—	36 a	20 ab	11 a	6 a	4 a*	2 a*
Panicum	—	28 a	16 ab	17 a	7 a*	4 a*	6 a*
Velvetbean	—	53 a*	36 a	19 a	4 a*	4 a*	6 a*
None	15	23 a	9 b	5 a*	2 a*	0 b*	3 a*
				<i>Cervidellus</i>			
Maize	—	63 a*	43 a	34 a	2 a*	3 a*	7 a*
Panicum	—	66 a*	29 ab	11 b	3 a*	0 b*	1 b*
Velvetbean	—	43 ab	19 ab	14 b	2 a*	1 b*	4 ab*
None	19	23 b	5 b*	6 b*	1 a*	0 b*	1 ab*
				<i>Eucephalobus</i>			
Maize	—	119 a*	94 a*	115 a*	23 a*	15 a*	24 a*
Panicum	—	120 a*	142 a*	48 b*	15 a*	3 b	9 b
Velvetbean	—	77 ab*	73 ab*	61 b*	8 ab	4 b	9 b
None	2	22 b*	6 b	13 c*	3 b	2 b	3 b
				<i>Rhabditidae</i>			
Maize	—	535 a*	282 b*	213 a*	27 a*	9 b*	59 ab
Panicum	—	421 a*	209 b*	301 a*	66 a	32 a	108 a
Velvetbean	—	894 a*	594 a*	162 a*	34 a*	17 ab*	40 b
None	75	27 b*	4 c*	7 b*	2 b*	0 c*	1 c*

Data are means of five replications. For each nematode, means in a column followed by the same letter are not different ($P \leq 0.05$), according to Duncan's multiple-range test.

^a Asterisk (*) indicates significant ($P \leq 0.05$) difference from number present on 9 December.

^b Numbers present on 9 December are initial numbers before treatments were imposed.

ment is high, decomposition would be expected to proceed over a longer time period than with the other amendments, apparently providing a food source for some bacterivores for the duration of the experiment. Data for Rhabditidae were variable and difficult to interpret since this taxon likely contained a mixture of several genera and species. Other genera of bacterivores found in low numbers but included in totals (Table 2) were *Alaimus*, *Chiloplacus*, *Monhystera*, *Panagrolaimus*, *Plectus*, *Prismatolaimus*, *Teratocephalus*, *Wilsonema*, and *Zeldia*.

Fungivores: Among the fungivores, numbers of *Aphelenchoides* and Tylenchidae remained higher than their initial numbers (9 December) throughout the experiment

(Table 5). The placement of Tylenchidae (consisting primarily of two *Filenchus* spp. in this study) with the fungivores is controversial. It is not clear whether members of this group feed on root epidermal cells and root material or on fungal hyphae (Bostrom and Sohlenius, 1986; Yeates et al., 1993). Because of this confusion, some authors have included them along with herbivores or plant parasites (Büttner, 1989; Freckman and Ettema, 1993; Sohlenius and Wasilewska, 1984), others have included them with fungivores (Bostrom and Sohlenius, 1986; McSorley, 1993), and some recent authors have separated them from the other trophic groups as "plant associates" (McSorley, 1997; McSorley and Frederick, 1996;

TABLE 5. Effect of soil amendments on numbers of fungivorous nematodes in greenhouse experiment, 1993–1994.

Amendment	Nematodes per 100 cm ³ soil						
	9 Dec.	26 Jan.	10 Mar.	20 Apr.	15 Jun.	11 Aug.	19 Oct.
				<i>Aphelenchoides</i>			
Maize	—	282 a ^{*a}	116 b*	174 a*	33 a*	24 ab*	32 a*
Panicum	—	437 a*	209 ab*	273 a*	74 a*	23 ab	55 a
Velvetbean	—	444 a*	354 a*	299 a*	87 a*	59 a*	39 a*
None	11 ^b	38 b*	12 c	13 b	2 b*	2 b*	1 b*
				<i>Aphelenchus</i>			
Maize	—	135 a*	84 a*	77 a*	22 a	13 a	33 a
Panicum	—	58 a	35 ab	30 b	14 ab*	3 b*	24 ab
Velvetbean	—	87 a	106 a*	31 b	12 ab	5 b*	13 bc
None	30	49 a	19 b	16 b*	7 b*	4 b*	6 c*
				<i>Nothotylenchus</i>			
Maize	—	23 a	35 a*	25 a*	36 a*	24 a	10 a
Panicum	—	18 a	24 a*	25 a*	10 b	5 b	3 b
Velvetbean	—	17 a	40 a*	31 a	25 ab	4 b	2 b
None	9	13 a	6 b	12 a	10 b	3 b*	3 b*
				<i>Tylenchidae</i>			
Maize	—	541 a*	210 a*	227 a*	140 a*	76 a*	133 a*
Panicum	—	539 a*	192 a*	162 a*	70 a*	26 b	57 b
Velvetbean	—	272 a*	137 a*	245 a*	78 a*	52 ab	90 ab*
None	25	36 b	14 b*	27 b	12 b*	4 c*	5 c*
				Fungal-Feeding Dorylaimida			
Maize	—	2 *	2 a*	12 a	4 a*	0 *	15 a
Panicum	—	1 *	0 b*	1 b*	4 a*	0 *	8 a
Velvetbean	—	1	0 b	6 ab	1 a	0	17 a
None	11	0 *	1 ab*	1 b*	0 a*	0 *	2 a*

Data are means of five replications. For each nematode, means in a column followed by the same letter are not different ($P \leq 0.05$), according to Duncan's multiple-range test.

^a Asterisk (*) indicates significant ($P \leq 0.05$) difference from number present on 9 December.

^b Numbers present on 9 December are initial numbers before treatments were imposed.

Todd, 1996). The Tylenchidae are a diverse group containing many different genera and species (Siddiqi, 1985) that are difficult to distinguish, and it is likely that members of this group may differ in their feeding habits (Bostrom and Sohlenius, 1986). In the current study involving fallow soil without host plants, the increase of Tylenchidae (mainly *Filenchus* spp.) in amended pots appeared inconsistent with root feeding or root association. Their population fluctuations during decomposition of the organic amendments were similar to those of *Aphelenchoides*, the other dominant fungivore in the system.

Addition of an organic amendment resulted in increased levels of the common fungivores on most sampling dates (Table 5). The kind of amendment used also affected fungivore numbers. Numbers of *Aph-*

elenchoides were greatest on 10 March following velvetbean, whereas numbers of *Aphelenchus*, *Nothotylenchus*, and Tylenchidae during the latter half of the experiment tended to be greatest following the maize amendment. Possibly the high C:N ratio of this amendment caused extensive fungal decomposition to be delayed. Fungal-feeding Dorylaimida consisted of *Diphtherophora* (>80% of specimens), *Leptonchus*, *Mesodorylaimus*, and *Tylencholaimus*.

Omnivores: Densities of omnivorous nematodes in amended pots exhibited two peaks approximately 6 months apart (Table 2). Among the omnivores, numbers of *Eudorylaimus* particularly were enhanced by amendment application (Table 6), raising the possibility that they could be using the bacterivores or fungivores as food sources. It is not known whether the extreme peaks in

TABLE 6. Effect of soil amendments on numbers of omnivorous (*Aporcelaimellus*, *Eudorylaimus*) and predatory (*Discolaimus*) nematodes in greenhouse experiment, 1993–1994.

Amendment	Nematodes per 100 cm ³ soil						
	9 Dec.	26 Jan.	10 Mar.	20 Apr.	15 Jun.	11 Aug.	19 Oct.
				<i>Aporcelaimellus</i>			
Maize	—	3 a	6 a	15 a ^a	2 a	1 a	3 b
Panicum	—	2 a	5 a	4 b	0 a	1 a	1 b
Velvetbean	—	2 a	4 a	7 ab	1 a	1 a	17 a*
None	1 ^b	1 a	0 b	0 b	0 a	0 a	0 b
				<i>Eudorylaimus</i>			
Maize	—	12 a	29 a*	85 a*	11 a	21 a	76 a*
Panicum	—	14 a	33 a*	36 ab*	13 a	31 a	75 a*
Velvetbean	—	14 a	15 a	77 a*	3 b	10 ab	71 a*
None	9	2 b*	1 b*	5 b	2 b*	4 b	10 b
				<i>Discolaimus</i>			
Maize	—	0	1 a	5 a*	0	0	1 a
Panicum	—	0	1 a	1 b	0	0	1 a
Velvetbean	—	0	0 a	3 ab	0	0	1 a
None	2	0	0 a	1 b	0	0	1 a

Data are means of five replications. For each nematode, means in a column followed by the same letter are not different ($P \leq 0.05$), according to Duncan's multiple-range test.

^a Asterisk (*) indicates significant ($P \leq 0.05$) difference from number present on 9 December.

^b Numbers present on 9 December are initial numbers before treatments were imposed.

Eudorylaimus numbers on 20 April and 19 October might correspond to a generation time for this nematode. The omnivore genera *Ecumenicus* and *Mesodorylaimus* were found in low numbers but not included in Table 6.

Predators: Total numbers of predators (Table 2) included *Discolaimus*, *Mononchus*, *Mylonchulus*, *Nygolaimus*, and *Tripyla*. All were sporadic in their occurrence and found only in low numbers. *Discolaimus* was the most common genus of predators present (Table 6).

Many additional studies would be needed to clarify the trends observed in this study. For example, relatively little is known about the identity, life cycle, and food preferences of the *Eudorylaimus* species observed here. Although the circumstantial evidence presented here is consistent with fungivory, critical studies are needed to clarify the feeding habits of *Filenchus* spp. and other Tylenchidae that are common in most soil ecosystems.

There was evidence that some bacterivores and fungivores were affected by the type of organic amendment used. Elevated population levels of several nematode genera were most persistent during decomposi-

tion of maize stalks, which had the highest C:N ratio of the amendments tested. Perhaps future studies may provide more detail about which specific amendments and which features of amendments (C:N ratio, chemical composition, alkaloid content, etc.) most influence the bacteria and fungi involved in decomposition and the nematode bacterivores and fungivores associated with the decomposition process.

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