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Grazing in a porous environment. 2. Nematode community structure

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Abstract

The influence of soil matric potential on nematode community composition and grazing associations were examined. Undisturbed cores (5 cm diameter, 10 cm depth) were collected in an old field dominated by perennial grasses on a Hinckley sandy loam at Peckham Farm near Kingston, Rhode Island. Ten pairs of cores were incubated at −3, −10, −20 and −50 kPa matric potential after saturation for 21–28 or 42–58 days. Nematodes were extracted using Cobb's decanting and sieving method followed by sucrose centrifugal-flotation and identified to family or genus. Collembola and enchytraeids present were also enumerated because they are grazers that reside in air-filled spaces. Direct counts of bacteria and fungi were made to estimate biovolume using fluorescein isothiocyanate and fluorescein diacetate stains, respectively. Trophic diversity and maturity indices were calculated for nematode communities. Three patterns of matric potential effect were observed for nematode taxa. One, there was a consistent effect of matric potential for all seasons for *Alaimus*, Monhysteridae, *Prismatolaimus*, *Paraxonchium* and *Dorylaimoides*. Two, some effects of matric potential were consistent among seasons and other effects were inconsistent for *Aphelenchoides*, *Aphelenchus*, Cephalobidae, *Coomansus*, *Eudorylaimus*, *Huntaphelenchoides*, Panagrolaimidae, *Paraphelenchus*, *Sectonema*, and *Tripyla*. Third, effects of matric potential were always inconsistent among seasons for *Aphanolaimus*, *Aporcelaimellus*, *Bunonema*, Rhabditidae, and *Tylencholaimus*. As predicted, fungal and bacterial biomass responded oppositely to matric potential. Total bacterial biomass was greater at −3 kPa than −10, −20 and −50 kPa (P=0.0095). Total fungal biomass was greater at −50, −20 and −10 kPa than −3 kPa (P=0.0095). Neither bacterial-feeding, fungal-feeding nor predacious nematodes correlated significantly with bacterial or fungal biomass. Omnivorous and predacious nematodes correlated positively with number of bacterial-feeding nematodes; predacious nematodes also correlated positively with fungal-feeding nematodes. Numbers of Collembola and enchytraeids were more often correlated positively with microbial-grazing nematode numbers in drier than moist soils. From this study, we propose two mechanisms that may explain nematode community structure changes with matric potential: differential anhydrobiosis and/or enclosure hypotheses. The later suggests that drying of soil generates pockets of moisture in aggregates that become isolated from one another enclosing nematodes and their food in relatively high concentrations creating patches of activity separated by larger areas of inactivity.

Introduction

Nematodes play an important role in ecosystem function by regulating decomposition and nutrient mineralization (Beare et al., 1992). For ecological studies, the structure of nematode communities may be expressed in terms of the trophic groups present (Parmelee et al., 1995; Yeates et al., 1993b) because relative abundance of these groups affect the abundance of the mineralizing microbes. Generally, fungal- and bacterial-feeding nematodes are the most abundant trophic groups in forest and agricultural fields, respectively (Popovici, 1984). The relationship between bacteria and fungi and their grazers may be complex. Bacterivores may control the number of bacteria through grazing but will

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also control fungi by affecting the outcome of fungal–bacterial competition (Wardle and Yeates, 1993). Theoretically, trophic structure, abundance and activity of nematodes should be determined by the soil environment, e.g., organic matter (Griffths et al., 1995; Hendrix et al., 1990; Wasilewska, 1979) or bulk density (Jones and Thomasson, 1976). However, there may be little canonical correlation between soil environmental factors and nematode trophic structure (Neher and Campbell, 1994) at any given time, although there may be a temporal lag between nematode populations and nitrogen availability (Wardle et al., 1995; Yeates et al., 1993a).

There are only a few studies that have examined the impact of soil pore size and volume on nematode colonization, activity and feeding behavior (e.g., Griffiths et al., 1995). Beare et al. (1995) tested the importance of the inter- and intra-aggregates in nematode distribution. Inter- and intra-aggregates are defined as pore space between and within aggregates, respectively. Inter-aggregates correspond to a transient niche, where nematodes migrate to their food sources. We assume that microbes are present as food in all but the smallest pores. Hassink et al. (1993) showed that bacteria and nematodes are correlated with pore sizes of 0.3–1.2 and 30 minus 90 μm, respectively. Inter-aggregate pores within an adequate pore size range offer more suitable space than intra-aggregate pores for nematode movement (Quénéhervé and Chotte, 1996). Nematodes are restricted to moving within the existing soil matrix (Anderson, 1988), primarily in water-filled pores >30 μm in diameter (Killham, 1994; van der Linden et al., 1989; Wallace, 1958). Pores of 200–1000 μm diameter may constrain colonization and habitation by nematodes because pores with diameters much greater than nematode diameters may impede nematode movement (Quénéhervé and Chotte, 1996).

In this study, we investigated the influence of different soil water matric potentials on (1) nematode community composition and (2) nematode grazing on micro-organisms involved in nitrogen mineralization. Pore space in soils is partitioned into water- and air-filled compartments; information about one compartment may yield information on the other. For this reason, we investigated Collembola and enchytraeids in addition to nematodes. Nematodes are ubiquitous in most ecosystems (Freckman and Caswell, 1985; Proctor, 1990; Söhlenius, 1980) and are restricted to movement within water-filled pore spaces. Soil drying and the accompanying reduction in water-filled pore sizes may lead to exclusion of nematodes (the 'exclusion hypothesis') and to lower accessibility of their microbial food resources (Darbyshire, 1976; Elliott et al., 1980; Hassink et al., 1993). Exclusion may occur when water-filled pore spaces become smaller than the nematode grazer body diameter as soils dry. Food web interactions, thus, become a function of moisture and matric potential (Elliott et al., 1980). We hypothesized that changes in water-filled pore space affect the abundance of soil biota (e.g., Hassink et al., 1993). In particular, we expected nematode abundance to decrease with decreasing moisture content, and Collembola and enchytraeid abundance to increase.

Materials and methods

Study site

The study was conducted at an old field on Peckham Farm, part of the University of Rhode Island's Agricultural Experiment Station (Kingston, RI, USA). The field is dominated by perennial grasses on a Hinckley sandy loam. A 20-m by 40-m area of the old field was divided into fifty 16-m^2 plots. In May, August and November 1997 and March 1998, cores were taken from 40 randomly selected plots (Table 1). Each sampling location was chosen randomly within a plot. Three undisturbed soil cores (5 cm diameter, 10 cm depth), arranged in an equilateral triangle, were extracted at each sampling point. Two of each core triplet were used to determine nematode community structure at different soil matric potentials. The third core was set aside for other analyses not included in this report. Plant stems were clipped at the soil surface prior to laboratory procedures. Ten pairs of cores each were first saturated and then equilibrated to matric potentials of -3 and -10 kPa on a sand table and to -20 and -50 kPa on a sand/kaolin table (Eijkelkamp, Giesbeek, The Netherlands) at field soil temperatures (Table 1). For each sampling date, the -3 and -20 kPa treatments were processed first. After approximately 7 days, when these cores had reached stable weights at the applied tension, they were put in canning jars, and the -10 and -50 kPa cores were placed on tension tables to be saturated and subsequently equilibrated to -10 and -50 kPa matric potential. Moisture contents were defined as stable when core weight for each matric potential varied less than 1 g per core within a 24-h period. One of each core pair was harvested from its canning jar after 21–28 and 42–58 days incubation for determination of microbial biomass and nematode

Table 1. Environmental conditions (mean values) at the study site on the four sampling dates

Parameter	May 12, 1997	Aug. 12, 1997	Nov. 11, 1997	March 2, 1998
Soil temperature (°C)	13.6	21.9	6.5	6
Air temperature (°C)	17.9	28.8	8.2	12
Volumetric moisture (%)	17.2	10.5	18.8	22

community structure. Incubations at equilibrium matric potentials were implemented because most community theory is based upon coefficients derived from stable environmental conditions (May, 1981; Moore et al., 1996). Soil samples for microbial biomass and nematode classification and enumeration were shipped overnight express to University of Toledo (Toledo, OH, USA). Microbial biomass samples were shipped on ice and nematode samples in an insulated cooler without ice. Upon arrival, microbial and nematode samples were stored at 4 and 15°C, respectively, until processed.

Laboratory procedures

Nematodes were extracted using Cobb's decanting and sieving method (Ayoub, 1980; Thorne, 1961) modified by duplicate passes through 850-, 250-, 150-, 75-, and 44 μm mesh sieves. The final pass through the sieves was followed by centrifugal-flotation (Caveness and Jensen, 1955) modified by using a 1:1 (v:v) sugar solution and centrifuging for 1 min (Neher and Campbell, 1994). Nematodes were identified and enumerated by taxonomic family and genus where possible for 120–250 g fresh soil and were not corrected for extraction efficiency. Numbers were standardized by gravimetric soil moisture. Nematodes were identified to taxonomic family according to Bongers (1987), Hunt (1993), Nickle (1991), Goodey (1963), Maggenti (1983, 1991), Maggenti et al. (1987), and Andrássy (1968, 1979, 1980, 1984). Taxonomic families were assigned to a trophic group (root-feeding, bacterial-feeding, fungal-feeding, omnivores and predators) according to Yeates et al. (1993b). To obtain additional data that might strengthen our grazer-microbe analysis, we also measured the abundance of enchytraeids and Collembola, i.e. grazers which reside in air-filled pore spaces.

Measurements of soil microbial biomass were obtained by direct microscopy coupled with staining techniques. Bacteria in soil suspensions were stained with fluorescein isothiocyanate and filtered onto 0.2-μm polycarbonate membranes (Poretics Corp., Livermore, CA 94550) (Babiuk and Paul, 1970). Total bacterial biomass was determined by counting numbers and measuring the diameters of bacteria. Total fungal biomass was determined by measuring the length and diameter of hyphae in agar-film soil suspensions using a combination of epi-fluorescent and phase-contrast microscopy. Active fungal biomass was determined by measuring the length and diameter of fluorescein diacetate-stained hyphae (Ingham and Klein, 1984; Lodge and Ingham, 1991).

Statistical analysis

Three indices were computed for the nematode community in each soil sample. Trophic group diversity was estimated as $N_1=\exp[-\Sigma P_i(\ln P_i)]$, where P_i is the proportion of trophic group i in the total nematode community (Shannon and Weaver, 1949). Successional maturity was estimated as MI (Bongers, 1990) and MI25 (Bongers et al., 1995). Nonparametric statistics were used to analyze data because distributions were skewed. Spearman correlations were performed between direct counts of microbial biomass and nematode trophic groups using SAS Ver. 6.12 (SAS Institute, 1990). Kruskal–Wallis tests were performed on trophic diversity, abundance of each trophic group, and numbers of each nematode taxon, collembolans, enchytraeids and microbial biomass. Single degree contrasts were performed to determine significant differences among matric potential treatments, month sampled, and duration of incubation. A full model was defined with three main effects: month sampled, incubation period and matric potential; and two-way interactions between matric potential and (a) month and (b) incubation period.

Results

Nematode community composition

Bacterial-feeding nematodes were several orders of magnitude more abundant than fungal-feeding nematodes. The most abundant taxa within these two

Table 2. Nematode taxa present in bulk soil collected near Kingston, Rhode Island. Mean abundance (per 100 g (±standard deviation)) and numeric rank by trophic group are presented for both 21–28- and 42–58-day incubation periods combined. Trophic group categories were assembled according to Yeates et al. (1993b)

	Rank	Abundance		Rank	Abundance
Bacterial-feeders			Root-feeders		
Alaimus[1]	10	1.3(6.8)	*Criconemella*	6	63.5(189.8)
Aphanolaimus[3]	14	0.6(9.4)	Hoplolaimidae		
Bunonema[3]	7	11.9(47.3)	*Helicotylenchus*	13	2.8(17.2)
Cephalobidae[2,4,6]	1	928(912)	*Hoplolaimus*	20	0.3(3.5)
Acrobeles[6]			*Lelenchus*	10	11.3(25.4)
it Acrobeloides[6]			Longidoridae		
Cervidellus			*Longidorus*	21	0.2(2.5)
Chiloplacus[6]			*Xiphinema*	7	50.3(109.9)
Eucephalobus			*Paratylenchus*[1]	8	35.4 (111.3)
Heterocephalobus			*Psilenchus*[3]	19	0.3(2.6)
Dauerlarvae[2]	3	122.9(377.0)	Pratylenchidae		
Microlaimus	9	1.8(10.7)	*Hirschmanniella*	16	1.0(6.4)
Monhysteridae[1]	11	0.8(4.3)	***Pratylenchus***[2]	1	292(337)
Neodiplogasturidae	12	0.02(0.4)	*Pungentus*	11	10.9(23.3)
Panagrolaimidae[2,6]	6	43.1(90.2)	*Rotylenchus*[1]	17	0.7(5.4)
Plectidae[6]	2	196(266.4)	***Tylenchorhynchus***[3]	4	101(219)
Anaplectus			Tylenchidae		
Plectus			*Coslenchus*	5	70.5(351.7)
Wilsonema			***Filenchus***[2]	3	139.8(250.1)
Prismatolaimus[1,4]	5	86.4(238.4)	*Tylenchus*	12	8.1(33.4)
Rhabditidae[3,4]	4	102.0(303.0)	Total Root-feeders		841.4(929.3)
Teratocephalobidae	8	9.5(79.7)			
Total Bacterial-Feeders		1401.7(1291.0)	Predators		
			Anatonchidae		
Fungal-Feeders			*Anatonchus*	8	0.1(1.1)
Aphelenchoides[2,4,6]	1	99.9(141.2)	*Miconchus*	11	0.01(0.2)
Aphelenchus[2,6]	2	36.6(74.3)	Aporcelaimidae		
Diptherophora	3	3.8(14.2)	***Aporcelaimellus***[3,4]	1	492(3222)
Huntaphelenchoides[2]	6	0.06(1.0)	***Paraxonchium***[1,4]	3	35.7(89.6)
Paraphelenchus[2,6]	4	3.7(14.2)	*Sectonema*[2]	5	5.8(41.1)
Tylencholaimus[3,4]	5	1.5(6.4)	Mononchidae		
Total Fungal-Feeders		144.2(192.6)	*Clarkus*	10	0.1(1.7)
			Coomansus[2,4]	2	51.8(164.5)
Root-feeders			*Mylonchus*	6	0.3(4.3)
Aglenchus[1]	14	2.8(25.7)	*Nygolaimus*	4	10.5(24.7)
Anguinidae[5,6]			*Seinura*	7	0.2(4.2)
Ditylenchus[1,5]	2	249.1(87.9)	*Tripyla*[2]	9	0.1(1.4)
Axiochium	18	0.6(3.4)	Total Predators		590.8(3213.1)
Belondiridae					
Dorylaimellus[1]	15	1.4(8.6)	Omnivores		
Oxydirus[3]	9	16.6(44.3)	Dorylaimidae		
Dorylaimoides[1,4]	2	4.0(36.7)	***Enchodelus***	1	29.5(51.6)
Eudorylaimus[2]	3	0.3(3.9)			
Total omnivores		31.4(60.2)			

[1]Significant matric main effect ($P \leq 0.05$).
[2]Significant month interaction (plus main effect).
[3]Significant month interaction (no main effect).
[4]Illustrated graphically.
[5]Facultative fungal-feeder (Yeates et al., 1993b).
[6]Considered anhydrobiotic (Aroian et al., 1993; Demeure et al., 1979; Freckman, et al., 1977; Nicholas, 1998; Tobar et al., 1996; Wharton, 1996; Wharton and Barclay, 1993).

trophic groups were Cephalobidae, Plectidae, Rhabditidae, *Aphelenchoides* and *Aphelenchus* (Table 2). Omnivorous nematodes were equally as abundant as fungal-feeding nematodes. Predacious nematodes were similar in abundance as fungal-feeding and omnivorous nematodes at all matric potentials except −20 and −50 kPa in May when they were similar in abundance as bacterial-feeding nematodes. *Aporcelaimellus, Coomansus* and *Paraxonchium* predominated the predacious nematodes and *Enchodelus* and *Dorylaimoides* were the most common omnivorous nematodes.

The effect of matric potential on numbers of bacterial-feeding (P=0.0012), fungal-feeding (P=0.0001), omnivorous (P=0.0064) and predacious (P=0.0001) nematodes was seasonal (Figure 1) identified as a significant two-way interaction of matric potential with month sampled. No consistent patterns of matric potential on numbers of bacterial-feeding nematodes occurred among seasons. Numbers of fungal-feeding nematodes were greater at −50 kPa than other matric potentials in August, November and March, but not May. Omnivorous nematodes were absent in May but present in August, November and March. Relative abundance was greater at −10 and −20 kPa than −3 and −50 kPa consistently among the later three months. Number of predacious nematodes were most abundant in May with greatest numbers at −20 and −50 kPa matric potential.

Matric potential explained relative abundances of nematodes in several genera and families (Table 2). Matric potential tended to have little affect on uncommon or rare taxa. Three trends were evident. First, there was a consistent effect of all matric potentials for all seasons for *Alaimus* (P=0.0082), Monhysteridae (P=0.0236), *Prismatolaimus* (P=0.0001), *Paraxonchium* (P=0.0006), and *Dorylaimoides* (P=0.0285). *Prismatolaimus, Paraxonchium* and *Dorylaimoides* are illustrated as representatives of the most abundant taxa in each free-living trophic group (Figure 2). *Prismatolaimus* (P=0.0001) was more abundant at −3 kPa than −10, −20 or −50 kPa as predicted by the exclosure hypothesis. *Paraxonchium* was greater at −10 and −20 kPa than −50 and −3 kPa (P=0.0005). *Dorylaimoides* was present at −10 and −20 kPa but absent at −3 and −50 kPa not behaving in accordance with the exclosure hypothesis. Second, some effects of matric potential behaved consistently for all seasons and others were inconsistent among seasons (significant interaction between matric potential and month sampled) for *Aphelenchoides* (P=0.0001 matric, 0.0019 matric·month), *Aphelenchus* (P=0.0414, 0.7705), Cephalobidae (P=0.0001, 0.0001), *Coomansus* (P=0.0001, 0.0001), *Eudorylaimus* (P=0.0066, 0.0088), *Huntaphelenchoides* (P=0.0368, 0.0496), Panagrolaimidae (P=0.0122, 0.0001), *Paraphelenchus* (P=0.0002, 0.0004), *Sectonema* (P=0.0132, 0.0003) and *Tripyla* (P=0.0401, 0.0460) (Table 2). Only Cephalobidae, *Aphelenchoides* and *Coomansus* are illustrated as representatives of the most abundant taxa in each free-living trophic group (Figure 3). Numbers of Cephalobidae were greater in moist (−3 and −10 kPa) soils in May, but more abundant in drier (−10, −20 and −50 kPa) soils in August, November and March. *Aphelenchoides* were more abundant in dry (−50 kPa) than moist soils in all months except May. *Coomansus* was most abundant in wet (−3 kPa) soils in May, August and November but were similar among soil moisture conditions in March. For these nematode taxa, the exclosure hypothesis was not a reliable predictor of abundance. Third, effects of matric potential were always inconsistent among seasons (significant interaction between matric potential and month sampled) for numbers of *Aphanolaimus* (P=0.0352), *Aporcelaimellus* (P=0.0002), *Bunonema* (P=0.0202), Rhabditidae (P=0.0052), and *Tylencholaimus* (P=0.0264). Only Rhabditidae, *Tylencholaimus* and *Aporcelaimellus* are illustrated as representatives of the most abundant taxa in each free-living trophic group (Figure 4). Rhabditidae were most abundant at −20 kPa in May and −10 kPa in March, and least abundant at −10 kPa in August and −3 kPa in November. Although relatively uniform in abundance in November and March, numbers of *Tylencholaimus* were greatest in wet (−3 kPa) and dry (−50 kPa) soils in May and August, and conspicuously absent in at least one soil moisture–season combination for each month. Numbers of *Aporcelaimellus* were greatest in dry (−20 and −50 kPa) soils in May and uniformly scarce in moist soils and in other months sampled. In general, abundance of most nematode taxa did not agree with the exclosure hypothesis.

There were significant effects of matric potential on H' (P=0.0038) with greater trophic diversity at −50 kPa than −3, −10 and −20 kPa (P=0.0004). Increases in trophic diversity at −50 kPa correlated positively with abundance of predators at this matric potential. In contrast, matric potential had no significant effect on MI (P=0.0757) or MI25 (P=0.0944) suggesting that maturity indices are not sensitive to soil moisture.

Collembola occurred in quantities of 0–26.6 (median=0.18) per soil sample. Five families were present,

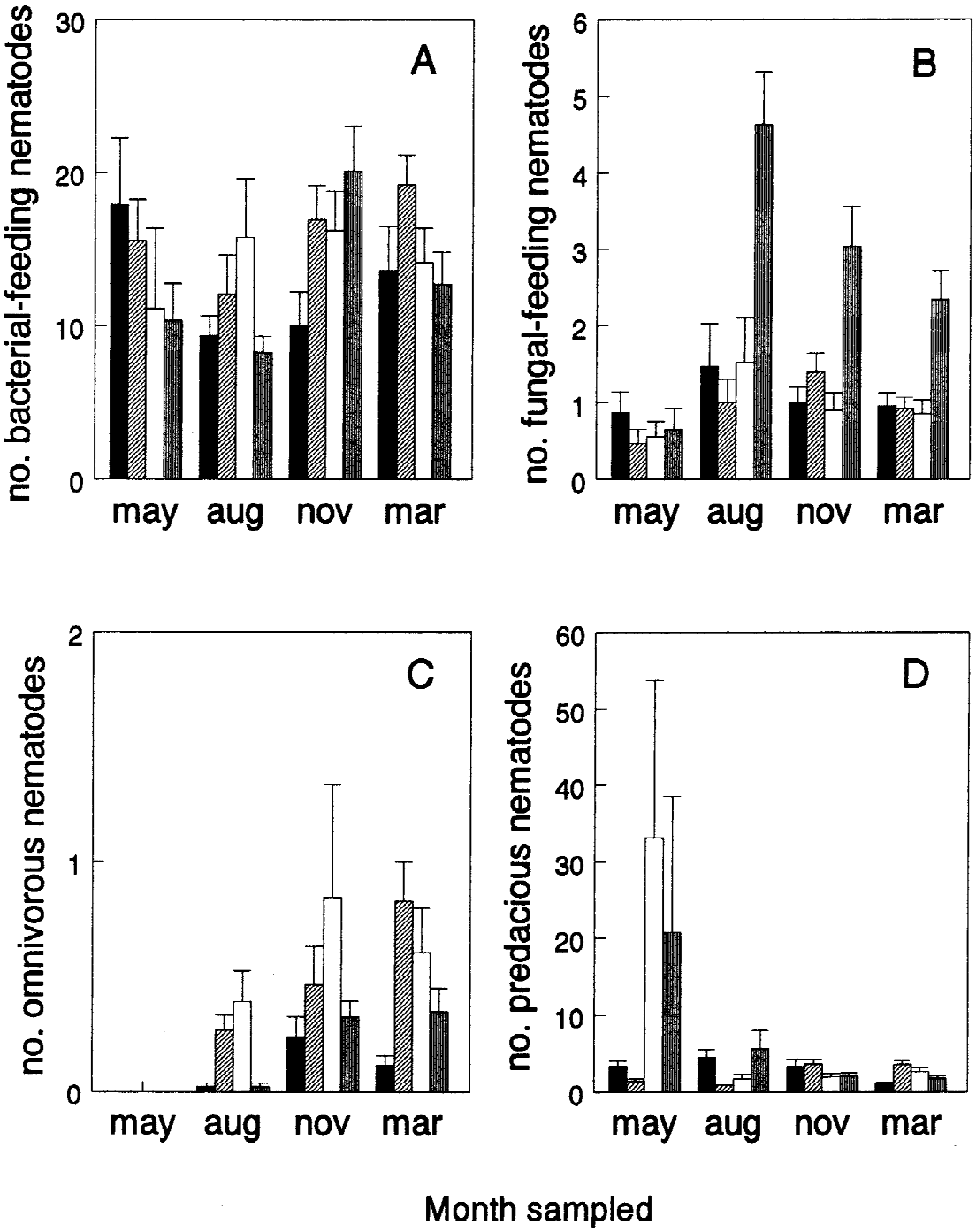

Figure 1. Illustrated are average abundance and standard error of (A) bacterial-feeding, (B) fungal-feeding, (C) omnivorous, and (D) predacious nematodes. All trophic groups showed a significant ($P<0.05$) two-way interaction of matric potential and season. Bar fills represent −3 (solid black), −10 (diagonal), −20 (open) and −50 (striped) kPa matric potential.

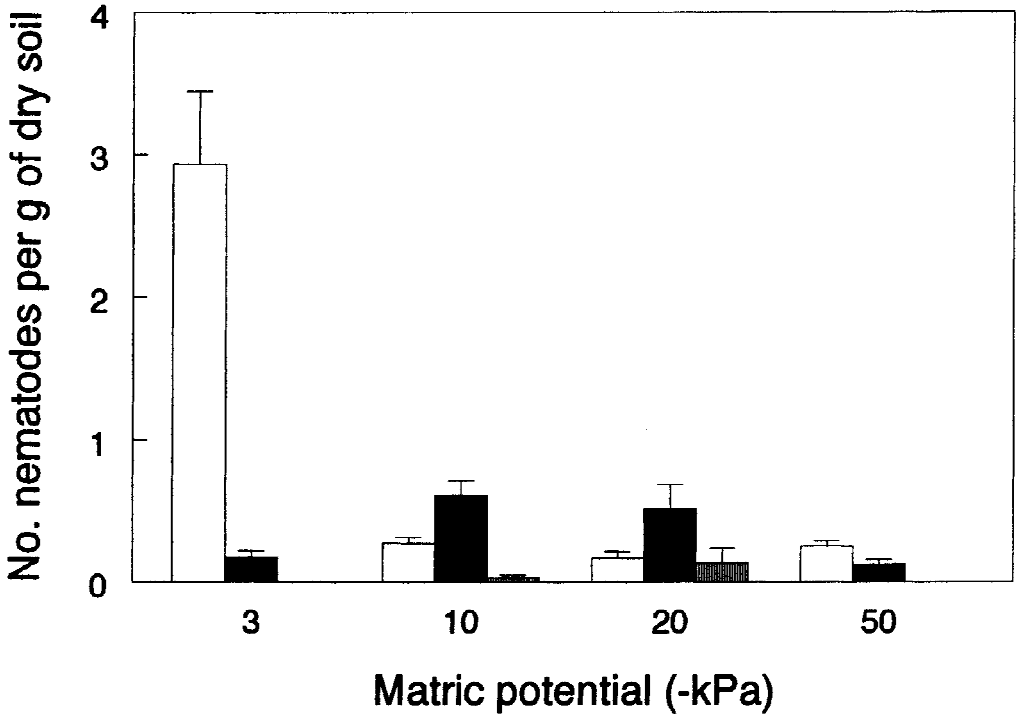

Figure 2. Numbers of *Prismatolaimus* (open, left-axis), *Paraxonchium* (black), and *Dorylaimoides* (vertical stripe) per gram of dry soil are plotted as a function of matric potential (−kPa) across months sampled. Means and standard error estimates are illustrated.

Onychiuridae, Entomobridinae, Isotomidae, Hypogasturinae and Neelidae. Onychiuridae accounted for 92.8±20.4% (mean±standard deviation) of the total number of collembolans. Collembola were affected by matric potential (P=0.0001), although inconsistently among seasons (P=0.0001). Numbers are greater at −10 and −20 than −3 kPa (P=0.0001). No differences in abundance were observed at −50 kPa and any combination of other matric potentials. Zero to 8.0 (median=0) enchytraeids were observed in each nematode sample. Numbers of enchytraeids were affected significantly by matric potential (P=0.0050) although inconsistently among seasons (P=0.0022). Enchytraeids were less abundant at −50 kPa than −3, −10 and −20 (P=0.0005).

Availability of microbial food source

As predicted, fungal and bacterial biomass responded oppositely to matric potential. Total bacterial biomass was greater at −3 kPa than −10, −20 and −50 kPa (P=0.0095, Figure 5). Total fungal biomass was greater at −50, −20 and −10 kPa than at −3 kPa (P=0.0095, Figure 5). Although not significant statistically, active fungi appeared to respond to matric potential (P=0.0996). Active fungi comprised a median of 5% of total fungi. The effect of matric potential on total fungal biomass was confounded by seasonal effects (a significant interaction with month sampled, P=0.0028).

Correlations between nematodes and microbial prey by matric potential

Numbers of omnivorous nematodes correlated positively with numbers of bacterial nematodes at −50 kPa (r=0.29, P=0.0244) but not numbers of fungal-feeding nematodes. Numbers of predacious nematodes correlated positively with numbers of bacterial-feeding nematodes at −3 (r=0.29, P=0.0162), −10 (r=0.32, P=0.0036), −20 (r=0.25, P=0.0346), and −50 (r=0.23, P=0.0427) kPa and numbers of fungal-feeding nematodes at −10 (r=0.47, P=0.0001) and −20 kPa (r=0.51, P=0.0001). Numbers of collembolans correlated positively with numbers of bacterial-feeding nematodes at −20 kPa (r=0.50, P=0.0001) and numbers of fungal-feeding nematodes at −10 (r=0.33, P=0.0027), −20 (r=0.48, P=0.0001) and −50

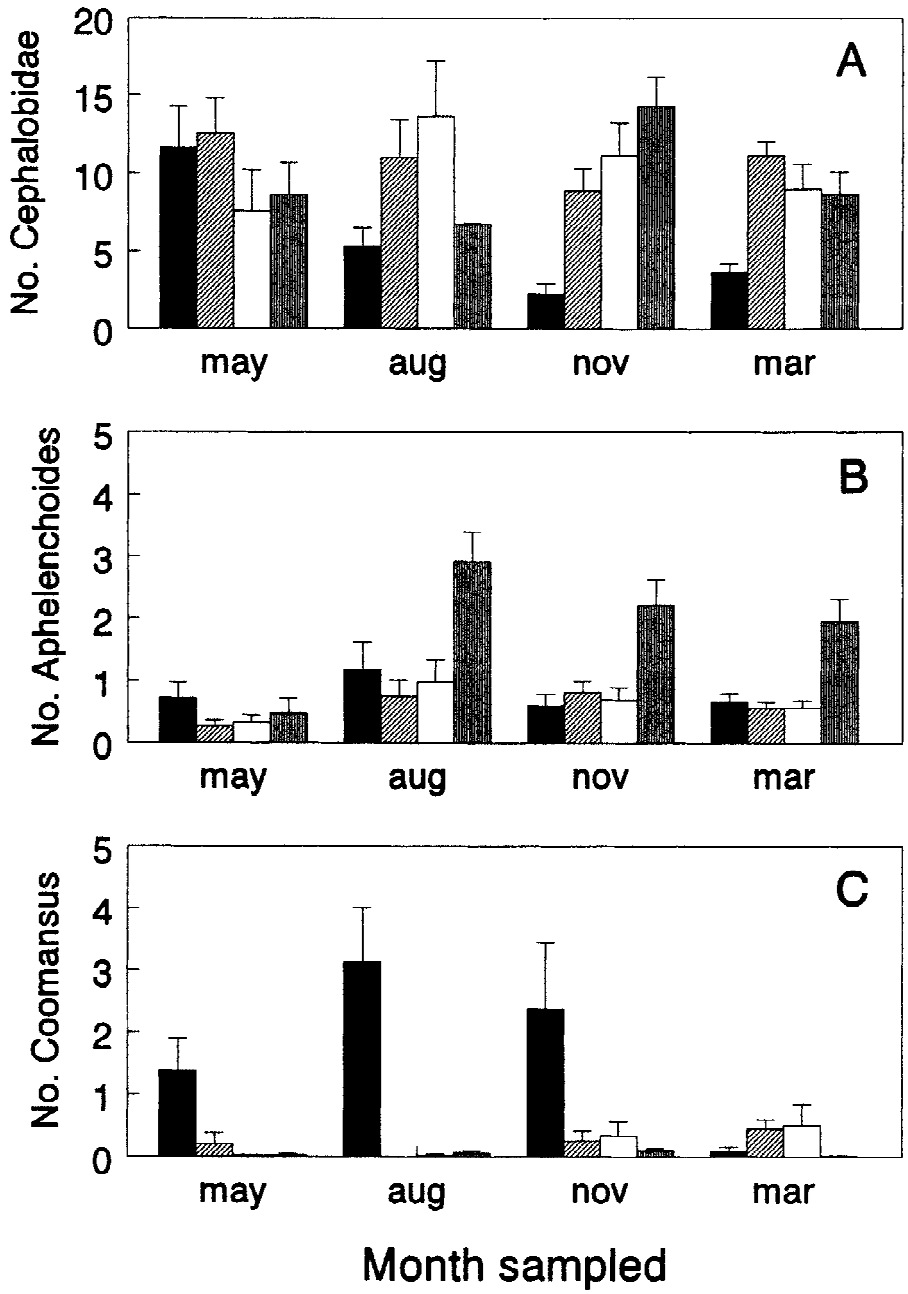

Figure 3. Illustrated are selected nematode taxa whose abundance was affected by a two-way interaction of matric potential and season plus a main effect of matric potential. Illustrated are means and standard error for numbers of (A) Cephalobidae, (B) *Aphelenchoides*, and (C) *Coomansus*. Bar fills represent −3 (solid black), −10 (diagonal), −20 (open), and −50 (striped) kPa matric potential.

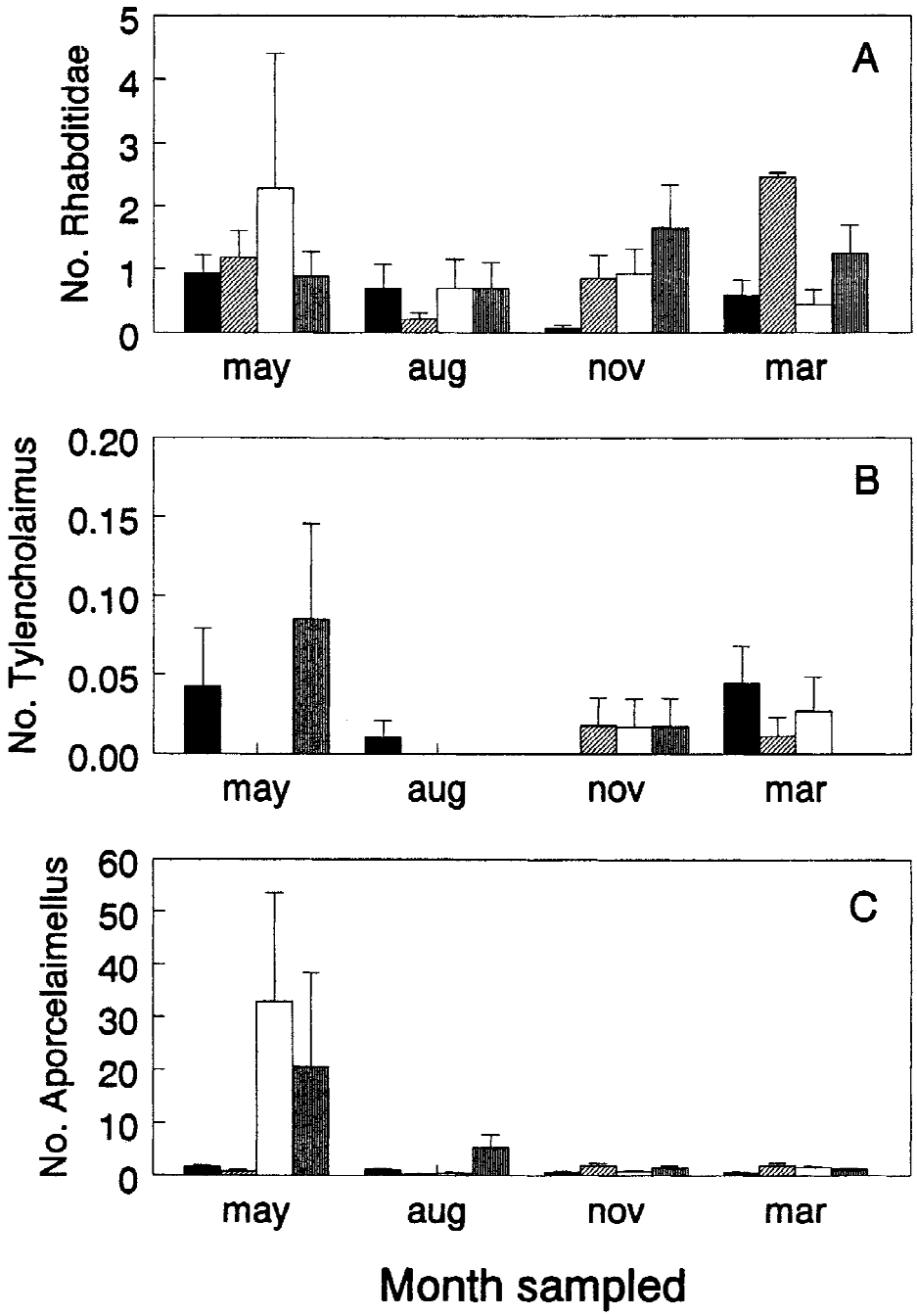

Figure 4. Illustrated are selected nematode taxa whose abundance was effected by a two-way interaction of matric potential and season but no main effect of matric potential was evident. Illustrated are means and standard error for numbers of (A) Rhabditidae, (B) *Tylencholaimus*, and (C) *Aporcelaimellus*. Bar fills represent −3 (solid black), −10 (diagonal), −20 (open), and −50 (striped) kPa matric potential. Standard error bars are illustrated.

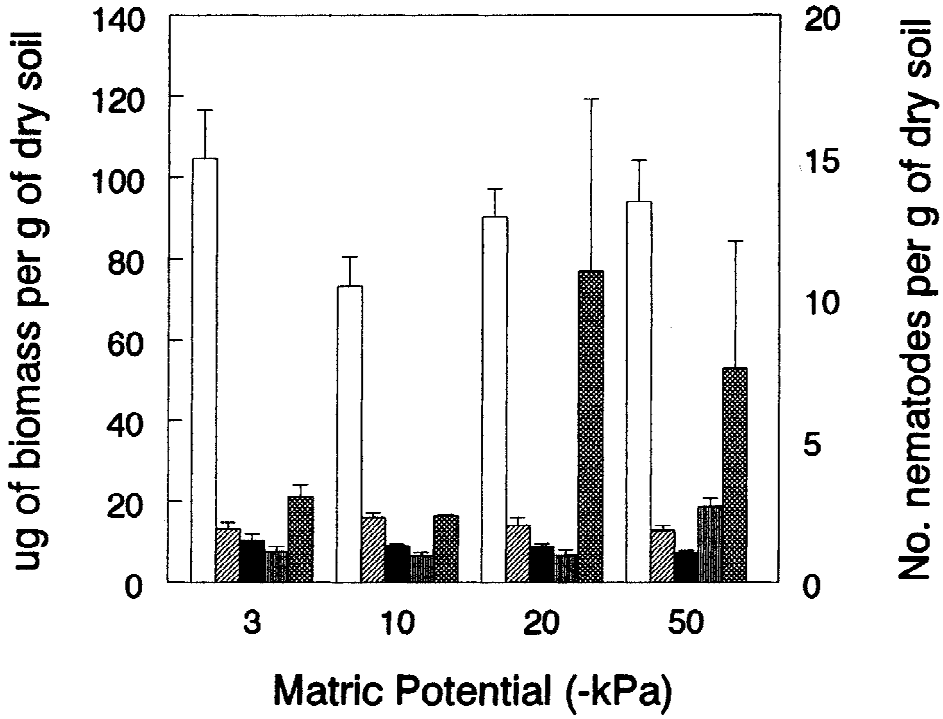

Figure 5. Microbial biomass and numbers of microbial grazing nematodes are illustrated as a function of matric potential pooling all months sampled. Total bacterial (open) and total fungal (diagonal) biomass are expressed as μg per g of dry soil and plotted relative to the left-axis. Numbers of bacterial- (black), fungal- (vertical stripe), and predacious (cross-hatched) nematodes are expressed as numbers per g of dry soil and plotted relative to the right-axis. Means and standard error estimates are illustrated.

(r=0.40, P=0.0003) kPa. Numbers of enchytraeids correlated positively with numbers of bacterial-feeding nematodes at −20 (r=0.29, P=0.0158) and −50 (r=0.41, P=0.0001) kPa and numbers of fungal-feeding nematodes at −10 (r=0.37, P=0.0007) and −20 (r=0.28, P=0.0191) kPa. No significant correlations were observed for treatment combinations not mentioned ($P>0.05$).

Total fungal biomass correlated positively with active fungal biomass (r=0.53, P=0.0037) and total bacterial biomass (r=0.64, P=0.0004) at −3 kPa but no significant correlations were observed for −10, −20 or −50 kPa ($P>0.05$). Total bacterial biomass correlated with active fungal biomass at −50 (r=0.61, P=0.0036) kPa, negatively at −10 kPa (r=−0.45, P=0.0426), and not significantly at −3 or −20 kPa. Neither bacterial-feeding, fungal-feeding or predacious nematodes correlated significantly with total fungal or total bacterial biomass ($P>0.05$, Figure 5). However, numbers of collembolans correlated positively with total fungal biomass at −10 kPa (r=0.42, P=0.0318) and positively with total bacterial biomass at −20 kPa (r=0.50, P=0.0144) but no other matric potentials. Numbers of enchytraeids correlated positively with total fungal biomass at −10 (r=0.65, P=0.0003) and −50 (r=0.39, $P<0.0476$) kPa and total bacterial biomass at −50 kPa (r=0.54, P=0.0042) but no other matric potentials ($P>0.05$).

Incubation effects

Relative to field samples, numbers of bacterial-feeding and omnivorous nematodes increased with any incubation consistently for each month sampled. In contrast, numbers of fungal-feeding and predacious nematodes increased with incubation in May, November and March but decreased with incubation in August. Numbers of some nematode taxa were affected simply by incubating soil at any equilibrium matric potential. For example, numbers of Cephalobidae, *Coomanus*, *Paraxonchium* and *Prismatolaimus* increased consistently with incubation. Numbers of Rhabditidae, *Wilsonema* and *Aporcelaimellus* increased or decreased but inconsistently with incubation. Effects

of incubation ranged from 2- to 30-fold change in numbers.

Differences between the two incubation periods were apparent for some taxa but not for others. Total bacteria were more abundant after 42–58 days than 21–28 days of incubation (P=0.0039) but incubation period did not impact either total (P=0.1818) or active (P=0.1625) fungi. Numbers of *Tylencholaimus* (P=0.0178) and *Sectonema* (P=0.0131) were reduced by incubation; numbers of *Aporcelaimellus* (P=0.0327), *Microlaimus* (P=0.0051), *Paraxonchium* (P=0.0012), Panagrolaimidae (P=0.0010), and fungal-feeding nematodes (P=0.0496) increased. The effect of incubation was confounded by matric potential for numbers of *Aphelenchoides*, *Tripyla*, Monhysteridae and predacious nematodes but not with other trophic groups or nematode taxa ($P>0.05$). Numbers of *Aphelenchoides* (P=0.0367) and predacious (P=0.0001) nematodes increased with incubation and Monhysteridae (P=0.0449) decreased with 42–58 days of incubation. *Tripyla* was present in bulk soil before, but not after, incubation (P=0.0401).

Seasonal effects

Bacterial biomass was least in May and increased progressively in the months of August, November, and March (P=0.0001, Figure 6). The proportion of total fungi that were active tended to be greater in August and November than March and May (P=0.1413). Numbers of total nematodes were greatest in May and more abundant in November than March or August (P=0.0038).

As a sole effect, seasonal patterns impacted nematode taxa in a variety of ways ($P<0.05$). Teratocephalobidae were the only bacterial-feeding nematode taxon affected solely by season (P=0.0001). Numbers of Teratocephalobidae were greater in May than August (P=0.0001) and absent in November and March. Dorylaimidae (omnivores) were more abundant in November than August (P=0.0321) and absent in March and May. *Nygolaimus* tended to be more abundant in early spring (March) and fall (November) than during summer (May and August) months (P=0.0144).

Seasonal fluctuations were observed for numbers of all five trophic groups ($P<0.01$) and all nematode taxa ($P<0.05$) that showed effects of matric potential varying with season (Figures 3 and 4), i.e., *Aphanolaimus*, *Aphelenchus*, *Aphelenchoides*, *Aporcelaimellus*, *Bunonema*, Cephalobidae, *Coomansus*, dauerlarvae, *Eudorylaimus*, *Huntaphelenchoides*, Panagrolaimidae, *Paraphelenchus*, Rhabditidae, *Sectonema*, *Triplya* and *Tylencholaimus*. Any nematode trophic groups or taxa not mentioned above were not affected significantly by season ($P>0.05$).

Discussion

Two mechanisms could explain equivalent nematode community composition in soils of contrasting matric potentials. First, an enclosure hypothesis suggests that drying of soil generates pockets of moisture in aggregates that become isolated from one another enclosing nematodes and their food in relatively high concentrations creating patches of activity separated by larger areas of inactivity (Griffths et al., 1995). Second, anhydrobiosis may account for large numbers of nematodes under dry conditions but inactivity of the animals would correspond (Demeure et al., 1979).

Nematodes survived even when soils were dry enough to exclude all nematodes (Görres et al., this volume). If water-filled pores of a size capable of containing these genera were the limiting factor for grazing, we would expect their activity, but not necessarily numbers, to be greater at -3 kPa than -10 to -50 kPa. Numbers of relatively large nematodes did not decrease consistently in number as soils dried and we are uncertain about patterns associated with activity. For example, numbers of *Coomansus* declined in dry soils but *Aporcelaimellus* remained numerous. Because both genera were abundant in August soils, which were quite dry (Table 1), we know that both genera are capable of surviving dry soils. Based on relative abundance of relatively large-size nematodes in soils held at -50 kPa, we must reject the notion that the nematode size is the sole factor determining whether or not it will inhabit only large water-filled pores. At -50 kPa, water-filled pore structure may contain isolated water-filled pores that act as enclosures for nematodes from which they cannot leave (Görres et al., this volume). These conclusions generally agree with those of Griffiths et al. (1995) who observed survival and activity of nematodes at matric potentials down to -1000 KPa. However, in contrast to Griffiths et al. (1995), we did not observe a subsequent decrease in proportion of Rhabditidae and increase in proportion of Cephalobidae as matric potentials dropped to -10 kPa or drier. Three important differences in methods employed by Griffiths et al. (1995) and our study are noted. First, we used undis-

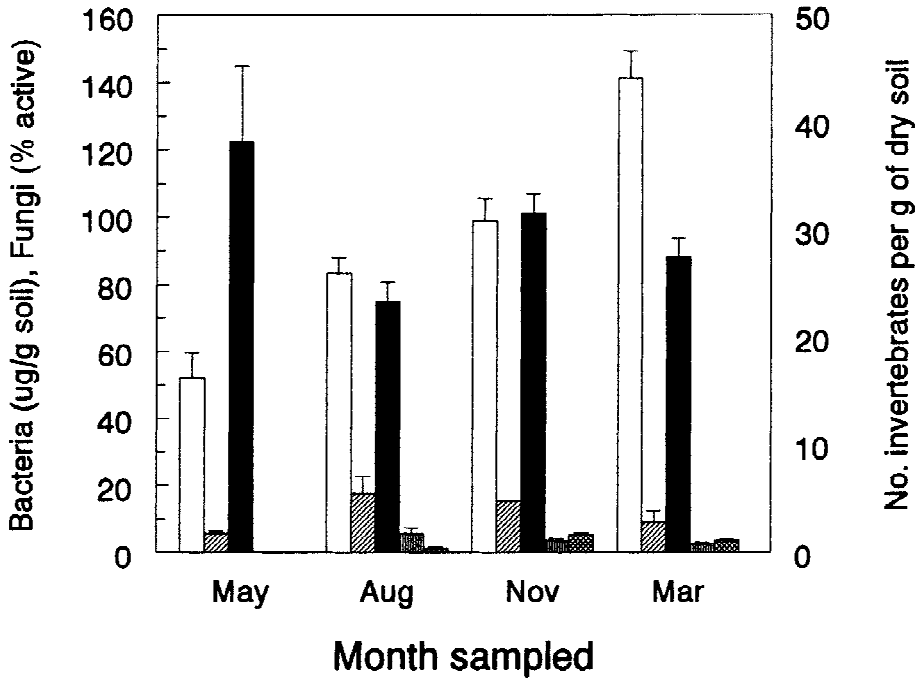

Figure 6. Relative abundance of microbial biomass and microbial grazers by month of sampling. Numbers of total bacterial biomass expressed as μg per g of dry soil (open) and proportion of total fungi that are metabolically active (diagonal) are plotted as a function of the left axis. Total numbers of nematodes (black), Collembola (vertical stripe) and Enchytraeidae (cross-hatched) are plotted relative to the right-axis. Means and standard error estimates are illustrated.

turbed, intact cores in contrast to sieved soil. Second, Griffiths et al. (1995) amended soil with substrate before imposing matric potential treatments permitting subsequent development of a few rapidly responding bacterial-feeding nematodes. We did not add any substrate and the nematode community represented that of field populations and tended to remain similar despite imposed matric potential treatments. Third, we characterized nematode communities to family and genus rather than trophic group (Griffiths et al., 1995). An alternative mechanistic approach would be to separate effects of connectivity from tortuosity, each of which describe a different perspective on pore saturation models. To quantify connectivity, it is necessary to measure connectivity independently at each matric potential.

Effects of the interaction between matric potential and season were more consistent among bacterial- and fungal-feeding nematodes than predacious nematodes (Figures 1 and 3). However, genera within trophic groups responded to matric potential and season differently (Figures 1 and 2). Therefore, these data do not support the extreme redundancy hypothesis that functional roles of nematodes are dependent on trophic groups but not species composition (Ettema, 1998; Walker, 1992). Rather, particular genera within trophic groups may have similar grazing function but differ in the water potential and season in which they are active.

We had hoped that abundance of enchytraeids and Collembola would provide additional information on the relationship between water-filled pore structure and grazing, i.e. by inspecting the abundance of soil animals inhabiting the complementary air-filled porosity. The abundance of enchytraeids was smallest at -50 kPa, probably because of the sensitivity of these worms to moisture (Kilham, 1994). However, a positive correlation between abundance of enchytraeids and bacterivorous nematodes at -50 kPa may represent a micro-scale pore habitat effect. Enhancement of water-filled pore habitat for bacterial-feeding nematodes may co-occur with the development of improved conditions in air-filled habitat for enchytraeids. Greater fragmentation of water-filled habitat upon drying may create more water-filled enclosures that favor microbial-feeding nematodes and improving their

foraging efficiency (Görres et al., this volume). Fragmentation of water-filled pores would also result in a more connected air-filled pore space improving conditions for both enchytraeids and Collembola. Whether this effect is one of resource availability, i.e. more fungal hyphal length in air-filled space or pore structure, cannot be determined from this study.

Demeure et al. (1979) found that *Acrobeloides* spp., *Aphelenchus avenae*, and *Scutellonema brachyurum* started coiling at gravimetric water contents of 3.7% (−300 kPa), 9% (−30 kPa), and 15% (−10 kPa) gravimetric water content, respectively. In our study, Cephalobidae (including *Acrobeloides* spp.) were the most abundant bacterial-feeding nematodes and present in large numbers at −50 kPa in August, November and March. At this matric potential, gravimetric moisture was 16%, which represent gravimetric moisture well above those that Demeure et al. (1979) observed the onset of anhydrobiosis in *Aphelenchus avenae* and *Acrobeloides* spp. Greater moisture at a common matric potential with Demeure et al. (1979) might be explained partly by our experiment being conducted on temperate and intact soil cores that contain natural aggregates whereas Demeure et al. (1979) examined arid and sieved soils that may have less defined aggregate structure. Maximum levels of anhydrobiosis were observed by Demeure et al. (1979) at −600 kPa, ranging from 2% nematodes at 3.7% gravimetric water content (−300 kPa) in anhydrobiosis to 90% nematodes at 3.4% gravimetric moisture (−600 kPa). While we cannot exclude the possibility that some nematodes may have entered the state of anhydrobiosis in our study, the findings of Demeure et al. (1979) suggest that only a small portion of nematodes would have been affected in our study. Extraction methods used in this study did not permit us to determine a proportion of nematodes that were anhydrobiotic. Extraction procedures to measure anhydrobiosis are involved and cumbersome and would require additional experiments (Freckman et al., 1977).

Incubation affected numbers of bacterial-feeding (Cephalobidae, *Prismatolaimus*, Rhabditidae and *Wilsonema*) and fungal-feeding (*Tylencholaimus*) nematodes in opposite ways. These findings correspond with impacts of matric potential on bacterial and fungal food sources. In our study, bacterial biomass was greater in wet (−3 kPa) than drier (−10, −20, and −50 kPa) soils; the opposite pattern was observed for total fungal biomass. Fungal activity was similar among matric potentials ranging from −3 to −50 kPa. Bacterial habitat is largely restricted to capillary water in soil, which is present at matric potentials of −20 to −100 kPa (Wong and Griffin, 1976a,b). Within this range, nutrients are able to diffuse toward and waste products away from bacteria (Wong and Griffin, 1976a,b). The driest soil (−50 kPa) in our study is within the moisture range where both bacteria and fungi are both active. However, drier soils (<-1000 kPa) would be more favorable to fungal than bacterial activity. Hyphal extension occurs at much more negative matric potentials allowing fungi to bridge air-filled pores and actively explore for nutrients (Griffin, 1969).

It is well-established that nematode and microarthropod populations are affected by climatic shifts brought by seasonal change and plant phenology (Kastner and Germershausen, 1989). For example, numbers of Cephalobidae decreased in progressively drier soils in May but increased in abundance with drier soils the other three months. Relative numbers of Cephalobidae at matric potentials of −10, −20, and −50 were similar for all months. An aberration occurs at −3 kPa in May which corresponds with an exceptional number of bacterial-feeding nematodes. Cephalobidae are the most abundant taxa among bacterial-feeding nematodes and, perhaps, are responding to shifts in competitive advantage that correspond with seasonal differences.

Nematodes compete with other organisms for their fungal and bacterial food sources. Based on significant correlations between fungi, bacteria, fungal grazers, bacterial grazers, we conclude that enchytraeids and Collembola play important roles in the soil community. Furthermore, temporal associations between total fungal biomass and collembolans were observed. Although protozoa are major consumers of bacteria, our study was not designed to enumerate their abundances. Protozoa may out-compete nematodes for consumption of bacteria because they have much shorter generation times (1–2 compared to 4–7 days) (Griffiths, 1994). However, it is assumed that nematodes and protozoa do not compete directly. Nonetheless, protozoa, especially amoebae, are responsible for 20–40% of net nitrogen mineralization under field conditions (Griffiths, 1994). Protozoa mineralize approximately 30 and 43 kg of nitrogen per year in conventional and integrated farming trials (Beare, 1997). Our estimates likely underestimate total faunal contributions to net mineralization because we did not consider contributions by protozoa (Griffiths, 1994). Further experiments are necessary to quantify the impact of enchytraeids, collembolans and protozoan and rotifer

(which were also noted in large numbers) impacts on nitrogen mineralization as affected by matric potential.

In summary, our data do not support the exclosure hypothesis or the extreme redundancy hypothesis. Our work agrees with other studies (Anderson et al., 1997; Görres et al., this volume; Hassink et al., 1993; Killham et al., 1993) that suggest that the interaction between pore structure and trophic interactions affects nutrient cycling. However, the relationship between grazer abundance, grazing activity and pore structure is more complex than expected by the exclosure hypothesis. More experimental and theoretical studies of the effect of pore structure on grazing and community structure should be conducted. In particular, such studies might include the complementarity of air-filled and water-filled pore space.

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