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SOIL NEMATODES OF NORTHERN ROCKY MOUNTAIN ECOSYSTEMS: GENERA AND BIOMASSES

T. Weaver¹ and J. Smolik²

ABSTRACT.—Soil nematode populations were larger and more diverse in two grasslands than in three forests of the northern Rocky Mountains. As we moved from *Festuca idahoensis* grassland through progressively higher zones of vegetation dominated by *Artemisia tridentata*, *Populus tremuloides*, and *Pseudotsuga menziesii*, and then to *Abies lasiocarpa* forests, numbers of nematode genera declined from 31 to 26 to 20 to 21 to 13; numbers of individuals in the top 50 cm of the soil were 6.0, 5.3, 1.7, 1.5, and 1.6 million/m², and biomasses of nematodes in the top 50 cm of the soil were 0.83, 0.88, 0.58, 0.35, and 0.19 g/m². Biomasses of nematodes were often well correlated with root biomass as well as soil depth; of the nematodes in the 0–50-cm horizon, 38 to 70% were in the 0–20-cm layer. The effects of light grazing on nematode populations were small or nonexistent.

While the plant component of major Rocky Mountain communities has been characterized (Mueggler and Stewart 1979, Pfister et al. 1977), their soil nematode composition has not been described (cf. Table 1). To repair this deficiency, we have compared the generic composition, densities (number/m²) by feeding group, and biomasses (g/m²) by feeding group of nematodes in major vegetation types spanning the altitudinal zone from foothills to timberline. On a complex gradient of increasing altitude, increasing precipitation, and decreasing temperature (Weaver 1980), these include: *Festuca idahoensis* grasslands, *Artemisia tridentata* shrublands, *Populus tremuloides* forests, *Pseudotsuga menziesii* forests, and *Abies lasiocarpa* forests. Strengths of our study include the diversity of ecosystems compared, the use of uniform methods to compare them, and the sampling of a thicker soil layer (0–50 cm) than is usually studied (cf. Table 1).

METHODS

To describe soil nematode populations associated with Rocky Mountain vegetation, we sampled soils under near-climax communities representing major vegetation zones along the altitudinal gradient. From foothills upward, these were *Festuca idahoensis*–*Agropyron caninum*, *Artemisia tridentata*–*Festuca idahoensis*, *Populus tremu-*

loides–*Poa pratensis*, *Pseudotsuga menziesii*–*Symphoricarpos alba*, and *Abies lasiocarpa*–*Vaccinium scoparium* habitat types. All stands were in the Bridger Mountains, within 22 km of Bozeman, Montana, and at altitudes of 2,330, 1,570, 1,810, 1,650, and 1,820 m, respectively. Pfister et al. (1977) and Mueggler and Stewart (1979) describe the plant associations indicated. Soil water regimes of all stands (Weaver 1977) and nutrient regimes of the *Artemisia*, *Pseudotsuga*, and *Abies* stands (Weaver and Forcella 1979) have been characterized previously. The soils were classified as Typic Cryoborolls, Pachic Argiborolls, Udic Haploborolls, Typic Haploborolls, and Mollic Cryoborolls, respectively.

Soil cores used in characterizing the nematode populations were collected in all stands on 30 July 1973. A second sample was collected at the *Festuca*–*Agropyron* site on 2 October 1972. At each site six cores were taken using a soil-sampling tube with a 2.1-cm inside diameter. Cores were taken to a depth of 50 cm at 3-m intervals along a line passing through the stand studied. Each core was divided into 10-cm increments: 0–10 cm, 10–20 cm, etc. The cores were refrigerated at 4 C until they were analyzed.

Nematodes were extracted from the soil by wet screening followed by Baermann funnel extraction (Christie and Perry 1951). The efficiency of the wet screening was determined

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TABLE 1. Nematode numbers and biomasses in various vegetation types.

Vegetation type		Densities (millions/m ²)	Biomasses (g/m ²)	Depth ¹ (cm)	Source
Desert	Mojave	0.4-1.1	0.1-0.2	30	Freckman et al. 1975
	Colorado	0.5-0.8	0.1	30	Freckman et al. 1975
Grasslands	Andropogon	0.1-0.3	0.2-1.5	20	Coleman 1971
		0.1-0.5	0.5-3.0	80	Coleman 1971
	Phalaris	0.1-0.3	—	25	King and Hutchinson 1976
	Swiss	—	5.0	15	in Banage 1963
	Danish	4-20	6-18	5	in Banage 1963
	Irrigated field	0.8-1.7	0.15	20	Freckman et al. 1975
	Artemisia-Agropyron	4.7-5.3	0.4-0.5	40	Smolik and Rodgers 1976
	Agropyron-Büchloe	3.8-7.9	0.5-1.8	60	Smolik 1974
Deciduous forests					
	Beech	0.4	0.08	6	Phillipson 1977
	Beech	1.1	0.28	6	Yeats 1972
	Beech	12	4.0	25	in Banage 1963
	Oak	30	15	25	in Banage 1963
	Oak-hornbeam	—	4-13	?	Saly 1975
	Liriodendron	1-6	0.6-1.4	16	McBrayer et al. 1977
Coniferous forests					
	Picea	0.01	—	?	Eroshenko 1976
	Pseudotsuga	1.3	—	16	McBrayer et al. 1977
Moor	Danish	1-3	1.5-4.5	5	in Banage 1963
	British	2-3	0.5-0.8	6	Banage 1963
Tundra	Bare soil	0.07	0.3	85	Kuznin 1976
	Bare soil	0.01	—	10-100	Chernov et al. 1977
	Moss lichen	2-4	—	10-100	Chernov et al. 1977
	Moss	0.5	—	6	Spaull 1973
	Moss	0.6-3	6-31	85	Kuznin 1976
	Herb-grass	0.8-8	1.1-7.5	85	Kuznin 1976
	Deschampsia	7.4	—	6	Spaull 1973

¹Sampling was from the top of the soil to the depth given.

by reextracting the soil sample. Efficiency of the Baermann funnel was established by examining approximately 10% of the residues to determine the number of nematodes that failed to pass through the screen. Nematode numbers were then corrected for the overall extraction efficiency, which varied with vegetation type from 60 to 70%. Density estimates were made by counting the number of nematodes (60X magnification) in three 1-ml aliquots of a 50-ml suspension on Scott hook-worm larvae counting slides. Biomass estimates were made following the method of Andrassy (1956) and were converted to dry weight by multiplying by 0.25 (Smolik 1974). Generic identifications and measurements for biomass determinations were obtained from permanent mounts (Thorne 1961) of approximately one thousand randomly selected individuals. Nematodes were assigned to feeding

groups by reference to standard catalogues listed by Smolik (1974).

Although our study is based on samples taken on one date near midsummer (30 July 1973), we believe the data fairly approximate the general numbers, biomasses, and generic compositions that might be found in another summer month or in the same month of another year. The following statements support our belief. (1) Most studies in which successive samples have been taken from sites with undisturbed vegetation show relatively small differences (less than a factor of two) between nematode populations in successive summer months: differences observed by Coleman (1971), King and Hutchinson (1976), Phillipson et al. (1977), Banage (1963), and Ferris and McKenry (1976) were not statistically significant; some differences observed by Yeats (1972) were statistically significant; differ-

TABLE 2. Nematode genera present in five vegetation types.

Feeding group and genus	Community type					
	FEID ¹	FEID ²	ARTR ¹	POTR ¹	PSME ¹	ABLA ¹
Herbivore						
<i>Ditylenchus</i>	+	+	+	+	+	+
<i>Helicotylenchus</i>	+	+	+	+	+	+
<i>Merlinius</i>	+	+	+	+	+	+
<i>Tylenchus</i>	+	+	+	+	+	+
<i>Tylenchorhynchus</i>	+	+	+	+	+	
<i>Aglenchus</i>	+	+	+	+		
<i>Nothotylenchus</i>	+	+	+	+		
<i>Dorylainellus</i>	+	+	+			
<i>Paratylenchus</i>	+	+	+			
<i>Tylencholaimellus</i>	+	+	+			
<i>Criconemoides</i>	+	+				
<i>Euchodelus</i>	+	+				
<i>Hemicycliophora</i>	+	+				
<i>Pratylenchoides</i>	+					
<i>Axonchium</i>		+				
<i>Diphtherophora</i>			+	+		
<i>Xiphinema</i>			+	+		
<i>Trichodorus</i>				+	+	
<i>Tylencholaimus</i>	+				+	
<i>Boleodorus</i>		+	+		+	
<i>Leptonchus</i>					+	
Number of genera	15	15	13	11	9	4
Predaceous						
<i>Aporcelaimellus</i>	+	+	+	+	+	+
<i>Eudorylainus</i>		+	+	+	+	+
<i>Dorylaimoides</i>	+		+	+	+	
<i>Nygolaimus</i>	+	+	+			
<i>Thonus</i>	+	+				
<i>Mesodorylainus</i>		+				
<i>Tripyla</i>					+	
<i>Mylonchulus</i>				+		+
<i>Miconchus</i>						+
<i>Mononchus</i>	+	+				+
Number of genera	5	6	4	4	4	5
Microvore						
<i>Acroboloides</i>	+	+	+	+	+	+
<i>Plectus</i>	+	+	+	+	+	+
<i>Aphelenchoides</i>	+	+	+		+	+
<i>Panagrolaimus</i>		+	+	+		+
<i>Aphelenchus</i>	+	+	+	+		
<i>Eucephalobus</i>	+	+	+	+		
<i>Acrobeles</i>	+	+	+			
<i>Bastiani</i>		+				
<i>Prismatolaimus</i>		+				
<i>Wilsonema</i>	+					
<i>Anaplectus</i>	+	+			+	
<i>Chiloplacus</i>	+	+			+	
<i>Rhabditis</i>		+			+	
<i>Cervidellus</i>	+		+		+	
<i>Cephalobus</i>	+	+	+		+	
Number of genera	11	13	9	5	8	4
Total genera	31	34	26	20	21	13

¹Ungrazed vegetation types were *Festuca idahoensis* (FEID), *Artemisia tridentata* (ARTR), *Populus tremuloides* (POTR), *Pseudotsuga menziesii* (PSME), and *Abies lasiocarpa* (ABLA).²Grazed vegetation of an adjacent *Festuca idahoensis* stand (FEID).

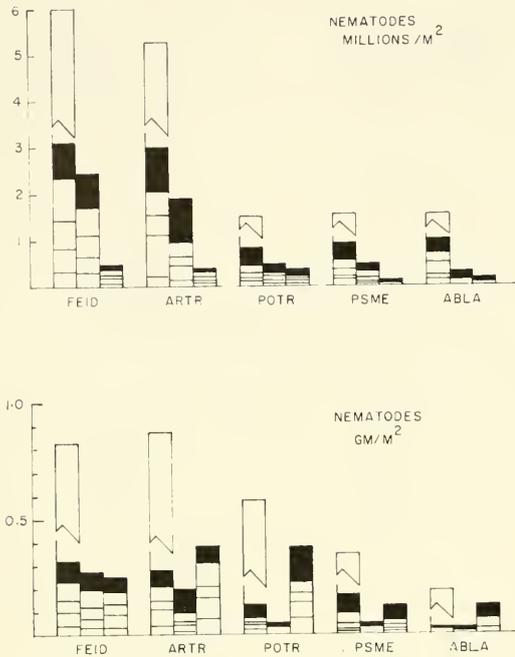


Fig. 1. Nematode numbers and biomasses in five vegetation types: A, Nematode numbers in millions; B, Nematode biomasses in grams per square meter. The first bar in each type presents herbivore data, the second microvore data, and the third predator data. Each bar is subdivided into a shaded portion and four clear portions below it indicating successively lower 10-cm horizons. Above the first bar is an unshaded bar indicating total nematode numbers or biomasses. The vegetation types are *Festuca idahoensis* (FEID), *Artemisia tridentata* (ARTR), *Populus tremuloides* (POTR), *Pseudotsuga menziesii* (PSME), and *Abies lasiocarpa* (ABLA).

ences observed by Smolik and Rodgers (1976) and McBrayer (1977) might have been statistically significant if they had been tested. (2) Numbers and biomasses measured in our *Festuca idahoensis* grassland changed little with season; on 2 October 1972, for example, they were 1.2 times as large as those measured on 30 July 1973. (3) Weather data from a station representative of the region (USDC 1973, Bozeman MSU, Montana) were normal: April–July precipitation was 100% of normal, June precipitation was 140% of normal, and July precipitation was 33% of normal; the average May temperature was normal, the average June temperature was 1.2 C above normal, and the average July temperature was 0.8 C above normal.

Root biomass data correlated with nematode population parameters were mea-

sured by coring, washing out small roots (< 1 mm), and determining their ash-free weights. Detailed methods and results were reported by Weaver (1977).

RESULTS AND DISCUSSION

DIVERSITY.—The generic diversity of plant-feeding and microbe-feeding nematodes declined as we moved from steppelands (*Festuca* and *Artemisia*) to a *Populus* forest to coniferous forests (*Pseudotsuga* and *Abies*), but the diversity of predaceous nematodes remained constant (Table 2). The difference appears to be due principally to the failure of steppe genera under forest conditions, since the number of genera endemic to steppelands (15) was three times greater than the number restricted to forest lands (5). The major nematode genera appearing in each vegetation type are listed in Table 2.

DENSITY.—Total numbers of nematodes present in the upper 50 cm of the soil declined from grasslands to forests (Fig. 1); they were 6.0, 5.3, 1.7, 1.5, and 1.6 million/m² in *Festuca*, *Artemisia*, *Populus*, *Pseudotsuga*, and *Abies* stands, respectively. The nematodes were similarly partitioned into plant-feeders, microbe-feeders, and predators in steppe vegetation (55, 38, and 7%, respectively) and coniferous forests (65, 25, and 10%, respectively). Given differences in the methods used and the depths considered, our data generally agree with those from other regions (Table 1). Note especially that Egunjobi (1971) and Razzhivin (1976) also found lower nematode densities in forests than in grasslands and that Novikova (1970) also observed similar nematode densities in deciduous and coniferous forests.

BIOMASS.—Total nematode biomasses present in the upper 50 cm of the soil declined from grasslands to forests (Fig. 1, Table 3); they were 0.83, 0.88, 0.58, 0.35, and 0.19 g/m² in *Festuca*, *Artemisia*, *Populus*, *Pseudotsuga*, and *Abies* vegetation, respectively. These biomasses are similar to those reported in other regions (Table 1). The nematodes were similarly distributed among plant-feeders, microbe-feeders, and predators in steppe communities (35, 28, and 37%, respectively) and coniferous forests (35, 15, and 50%, respectively). These masses may be better appreciated by comparing them with the

TABLE 3. Mean¹ nematode and root biomasses (g/m²) of five vegetation types.²

		Soil depth (cm)					CV ³	r ^{2,4}	
		0-10	10-20	20-30	30-40	40-50			0-50
FEID	herbivore	0.087	0.079	0.056	0.065	0.035	0.322	0.10	0.59
	microvore	0.080	0.066	0.049	0.040	0.029	0.266	0.13	0.83**
	predator	0.056	0.056	0.042	0.061	0.033	0.247	0.05	0.14
	total	0.223	0.201	0.147	0.166	0.097	0.835	0.06	0.62**
	root	902.0	391.0	143.0	51.0	95.0	158.2	0.01	
ARTR	herbivore	0.056	0.061	0.044	0.075	0.047	0.283	0.12	0.01
	microvore	0.102	0.033	0.019	0.035	0.014	0.203	0.16	0.87**
	predator	0.070	0.102	0.059	0.093	0.075	0.399	0.14	0.00
	total	0.228	0.196	0.122	0.203	0.136	0.885	0.03	0.55*
	root	202.0	118.0	58.0	54.0	44.0	476.0	0.03	
POTR	herbivore	0.060	0.021	0.012	0.021	0.021	0.135	0.35	0.90**
	microvore	0.022	0.004	0.010	0.010	0.006	0.052	0.22	0.68**
	predator	0.017	0.040	0.038	0.065	0.079	0.239	0.22	0.56*
	total	0.099	0.064	0.060	0.096	0.106	0.426	0.19	0.24
	root	355	409	37	12	23	836	0.23	
PSME	herbivore	0.083	0.037	0.033	0.007	0.009	0.169	0.19	0.96**
	microvore	0.021	0.014	0.008	0.007	0.003	0.053	0.21	0.80**
	predator	0.064	0.026	0.028	0.007	0.005	0.130	0.17	0.96**
	total	0.168	0.077	0.069	0.021	0.017	0.352	0.13	0.95**
	root	231	81	88	42	48	490	0.14	
ABLA	herbivore	0.010	0.005	0.008	0.003	0.004	0.030	0.48	0.67**
	microvore	0.021	0.006	0.001	0.004	—	0.032	0.36	0.90**
	predator	0.064	0.041	0.020	—	—	0.125	0.42	0.95**
	total	0.095	0.052	0.029	—	—	0.176	0.35	0.99**
	root	245	123	75	45	57	545	0.06	

¹Average coefficients of variation for herbivore-microvore-predator and root data are FEID (19-1%), ARTR (28-40%), POTR (55-33%), PSME (41-45%), and ABLA (76-40%).

²Vegetation types are FEID - *Festuca idahoensis*, ARTR - *Artemisia tridentata*, POTR - *Populus tremuloides*, PSME - *Pseudotsuga menziesii*, and ABLA - *Abies lasiocarpa*.

³Coefficients of variation (SD/X) for the 0-50 cm layer.

⁴The square of the correlation coefficient (r²) of nematode biomass against root biomass by layer. Statistical significance is indicated by asterisks. ** - significant at the 1% level, and * - significant at the 5% level.

biomass of cattle grazing in a *Festuca* meadow, that is, approximately 4-5 g/m² on an annual basis.

COMMUNITY STRUCTURE.—The functional composition—microvore, phytovore, predator—of the nematode population showed no consistent changes with changes in community type. Phytovores comprised about 60% of the herbivore (microvore and phytovore) biomass; this proportion was 56, 58, 67, 78, and 50% in *Festuca*, *Artemisia*, *Populus*, *Pseudotsuga*, and *Abies* communities, respectively. Predator weights usually exceeded 50% of the herbivore weights; they were 42, 82, 216, 60, and 197% in *Festuca*, *Artemisia*, *Populus*, *Pseudotsuga*, and *Abies* communities, respectively. The large predator/herbivore ratios suggest that herbivores turn over rapidly, that the predators consume other foodstuffs including plant material (Smolik 1974), and/or that the predators have low respiration rates (Klekowski et al. 1972). The

pyramid (predator/herbivore ratio) of biomass is less steep than the number pyramid because predators (0.96 g/million) are nine times larger than herbivores (0.11 g/million). For comparison, the weight of a predatory wolf is about 40 kg, and his herbivorous prey range in weight from 0.03 kg (voles) to 5 kg (rabbits) to 100 kg (deer) to 700 kg (bison) (Burt and Grossenheider 1964).

ENVIRONMENTAL FACTORS CORRELATED WITH NEMATODE DISTRIBUTION.—We do not know what environmental factors are responsible for the decline in nematode diversity, numbers, and biomass from grasslands to forests. Evidence suggesting that low temperatures may be the controlling factor is summarized below. (1) Soil temperatures, like nematode numbers, are lower under our forests than in adjacent (or lower) grasslands (Munn et al. 1979). (2) Our data (Fig. 1, Table 3) are inconsistent with other obvious hypotheses. Soil water, said to favor nematodes (McBrayer

et al. 1977), becomes more available as one moves from nematode-rich steppelands to nematode-poor forests (Weaver 1977). Soil organic matter and pH are lower in nematode-poor coniferous forests, but not in nematode-poor aspen forests, than in nematode-rich steppelands. Though they are high in nematode-rich *Festuca* grasslands, root biomasses of the nematode-rich *Artemisia* community did not exceed those of the nematode-poor forests. Nutrient elements (e.g., N, P, K) are probably available in larger quantities in nematode-rich steppelands, and in nematode-poor aspen forests, than in nematode-poor coniferous forests (Weaver 1979). (3) Egunjobi's (1971) observation that nematodes were fewer in forests of New Zealand than in adjacent cleared land planted to grasses supports the temperature hypothesis: soils of the cleared area probably differ little in pH, organic matter content, nutrient availabilities, water availabilities, etc., but they are probably warmer. (4) An alternate, but doubtful, hypothesis is that trees have evolved nematode-inhibiting structures or chemicals, perhaps in response to a greater initial susceptibility associated with their relatively long lives.

Total nematode biomasses decreased regularly with depth in *Festuca*, *Pseudotsuga*, and *Abies* communities, but not under *Artemisia* and *Populus* (Table 3). Of nematode biomasses in the 0–50-cm horizon, the 0–20-cm horizon contained 51, 48, 38, 70, and 67% in *Festuca*, *Artemisia*, *Populus*, *Pseudotsuga*, and *Abies*, respectively. Similar decreases were observed by Coleman (1971), who emphasized the need for examination of subsurface horizons, as well as by Smolik (1974) and Ferris and McKenry (1976).

One might expect nematode biomasses to be well correlated with root biomasses, which also decline with depth, either because roots serve as a food source or because warm, moist, oxygen-rich conditions favoring roots should favor nematodes as well. The correlation between microvores and root biomass data from the same sites (Weaver 1977) is highly significant in every vegetation type (Table 3). The correlation of both herbivore and predator biomasses with root biomass was significant in forest communities, but not in steppe communities (Table 3).

Small differences in nematode numbers between grazed and ungrazed parts of our

meadow, if they are biologically significant, could be due to light grazing or to the relatively shallow soils of the grazed plots. Total numbers were significantly less at the 1% level in October 1972 (grazed 6.3 million/m², ungrazed 7.2 million/m²) and in July 1973 (grazed 4.8 million/m², ungrazed 6.0 million/m²). Total autumn 1972 biomasses were 1.04 g/m² in the grazed area plots and 1.05 g/m² in ungrazed plots; total summer 1973 biomasses were 0.72 g/m² grazed and 0.83 g/m² ungrazed. Numbers of plant-feeders were lower in the grazed plot in both years and significantly so in 1972. Numbers of microbe-feeders were significantly greater in the grazed area in 1973, but were lower in 1972. Numbers of predators were lower in the ungrazed area in 1972, higher in the ungrazed area in 1973, and did not differ significantly between treatments in either year. Plant-feeding nematode biomasses were apparently reduced by grazing in a South Dakota *Agropyron smithii*–*Büchloe dactyloides* grassland (Smolik 1974), but not in a Washington *Artemisia tridentata*–*Agropyron spicatum* grassland (Smolik and Rodgers 1976).

CONCLUSIONS

Soil nematode populations were more dense, heavier, and more diverse under steppe than forest vegetation. The decline occurred under both deciduous and coniferous vegetation. The drop in soil temperature may be a major influent. Grazing is apparently not.

Within a soil, nematodes are most numerous in surface horizons. This could be due to conditions which favor roots, to the presence of roots, or to the presence of organisms associated with the roots.

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