

Soil fauna communities in two distinct but adjacent forest types on northern Vancouver Island, British Columbia

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The composition of major soil fauna groups throughout the soil profile in adjacent old growth western red cedar (*Thuja plicata* Donn) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and mature hemlock – amabilis fir (*Abies amabilis* (Dougl.) Forbes) forests on northern Vancouver Island was compared as part of an integrated study on the possible causes of poor growth of plantation Sitka spruce (*Picea sitchensis* (Bong.) Carr.) on cedar–hemlock cutblocks. In addition, we examined seasonal changes in vertical distribution of soil fauna within the forest floor of both forest types. At five times between August 1989 and March 1991, four methods were used to extract soil fauna: hand sorting, high-gradient extraction, modified Baermann funnel, and the Formalin method. Forty-one faunal groups were identified in both forest types. The hemlock – amabilis fir forest maintained a higher abundance and biomass of soil fauna than the cedar–hemlock forest. Nematoda were numerically dominant in both forest types followed by Acari, Collembola, and Copepoda. Diplopoda, Enchytraeidae, Diptera larvae, and Acari dominated soil fauna biomass in both forests. Similarity indices indicated that the forest types have similar group diversity. The majority of Nematoda, Acari, and Collembola were found in the LF and H horizons in both forest types. On average, more than 50% of the Acari and Collembola populations were found in the LF horizon while approximately 30% of the Nematoda were found there.

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La composition des principaux groupes de la faune du sol de tout le profil de sol d'une vieille forêt de cèdre rouge occidental (*Thuja plicata* Donn) – pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et d'une forêt mature de pruche – sapin gracieux (*Abies amabilis* (Dougl.) Forbes) adjacentes et situées dans le nord de l'île de Vancouver a été comparée dans le cadre d'une étude intégrée sur les causes possibles de la faible croissance de l'épinette de Sitka (*Picea sitchensis* (Bong.) Carr.) plantée dans des blocs coupés de forêts de cèdre–pruche. De plus, les changements saisonniers dans la distribution verticale de la faune du sol dans la couverture morte des deux types forestiers ont été examinés. Quatre méthodes ont été utilisées pour extraire la faune du sol pour les cinq échantillonnages effectués entre août 1989 et mars 1991 : le tri manuel, l'extraction à fort gradient, l'entonnoir modifié de Baermann et la méthode à la formaldéhyde. Dans les deux types forestiers, 41 groupes fauniques ont été identifiés. La forêt de pruche – sapin gracieux a maintenu une abondance et une biomasse de faune du sol plus élevées que celles observées dans la forêt de cèdre–pruche. Les nématodes étaient numériquement dominants dans les deux types forestiers, suivis par les acariens, les collemboles et les copépodes. La biomasse des diplopodes, des enchytréides, des larves de diptères et des acariens dominaient la faune du sol dans les deux types forestiers. Les indices de similarité indiquent que les types forestiers ont une diversité similaire au niveau des groupes fauniques. La majorité des nématodes, des acariens et des collemboles se trouvaient dans les horizons LF et H dans les deux types forestiers. En moyenne, plus de 50% des populations d'acariens et de collemboles se trouvaient dans l'horizon LF tandis qu'approximativement 30% des nématodes se trouvaient dans cet horizon.

[Traduit par la rédaction]

Introduction

Soil fauna play an important role in forest litter decomposition, nutrient cycling, maintenance of soil structure, and may also prove to be excellent indicators of soil quality (Price 1973; Petersen and Luxton 1982; Setälä and Huhta 1990; Smith et al. 1990; Paoletti et al. 1991). The soil fauna may comminute as much as 68% of the litter within some ecosystems (Seastedt 1984; Anderson 1988). Soil fauna convert microbial biomass and detritus into smaller fragments and feces, increasing surface area and modifying substrates for further microbial colonization and use (Parkinson 1988).

Litter decreases, microbial activity increases, and more nutrients are mineralized and picked up by roots or mycorrhizal fungi as a result of soil fauna activity (Seastedt and Crossley 1981). Even though soil fauna may be responsible for less than 5% of the total decomposer respiration (Petersen and Luxton 1982), their biomass is generally positively correlated with decomposition rate (Schaefer and Schauermaun 1990).

During the late 1970s, it was observed that Sitka spruce (*Picea sitchensis* (Bong.) Carr.) plantations were stagnating on old-growth western red cedar (*Thuja plicata* Donn) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (CH) cutblocks within 5 years after planting while those on mature hemlock – amabilis fir (*Abies amabilis* (Dougl.) Forbes) (HA) cutblocks were growing well. The CH sites were gen-

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erally deficient in available nitrogen and phosphorous and plantations on these sites responded well to fertilization (Germain 1985). This suggested a nutrient cycling problem, perhaps related to litter decomposition, in the CH. Preliminary research by Western Forest Products (WFP), University of British Columbia (UBC), and Pacific Forestry Centre (PFC) lead to the establishment of the Salal–Cedar–Hemlock Integrated Research Project (SCHIRP) and the development of appropriate research projects, including one on soil fauna.

Despite the importance of soil fauna in soil development and maintenance of soil fertility, they have been largely ignored in Canadian forestry. Canadian studies that examine more than one group of forest soil fauna are few. Exceptions include Behan et al. (1978) in a coniferous forest in Quebec; Bird and Chatarpaul (1986, 1988) and Tomlin and Miller (1987) in mixed forests in Ontario; Aitchison (1979a, 1979b, 1979c) in a hardwood stand in Manitoba; and Vlugg and Borden (1973) and Marshall (1974) in coastal forest soils in British Columbia. The purpose of this study is to compare the composition of major soil fauna groups in old-growth CH and mature HA forest types, and to examine seasonal changes in vertical distribution of soil fauna in the forest floor of both forest types where most of the tree feeder roots are found.

Materials and methods

Study site

The study was conducted on Western Forest Products' Tree Farm License No. 25 (block 4) northwest of Port McNeill, B.C. (50°36'N, 127°20'W), on northern Vancouver Island. The area is located in the Very Moist Coastal Western Hemlock biogeoclimatic subzone (CWH_{vmt}) (Klinka et al. 1991), which covers much of northern Vancouver Island (Messier and Kimmins 1991). The area has a maximum elevation of 300 m. The climate consists of cool, moist summers and mild, wet winters with minor snowfalls (Fig. 1). Rainfall seems sufficient through the growing season to prevent any soil moisture deficit (Messier 1991).

Within this subzone, Lewis (1982) identified the western red cedar – western hemlock – amabilis fir – salal (*Gaultheria shallon* Pursh.) – lanky moss (*Rhytidiadelphus loreus* (Hedw.) Warnst.) or “salal–moss” (S1) ecosystem association. Approximately 60% of block 4 is dominated by the S1 ecosystem association (Lewis 1982). This association contains two distinct forest types: cedar–hemlock (S1_{CH}) and hemlock – amabilis fir (S1_{HA}). These two forest types develop side by side on soils with similar parent material and underlying deposits. The transition between them is often abrupt with the HA occurring on upper slopes and the CH downslope, usually in depressions.

The CH is characterized by large, old-growth western red cedar and western hemlock. The canopy is relatively open and produces an understory of dense shrub dominated by salal with minimal herb (*Blechnum spicant* (L.) and moss (*Hylocomium splendens* (Hedw.) B.S.C. and *R. loreus*) layers (Germain 1985; Messier 1991). The CH is equivalent to the CWHb₁₍₃₎ described by Green et al. (1984).

The HA is characterized by dense, even-aged stands of western hemlock and amabilis fir. The closed canopy results in sparse shrub (*Vaccinium alaskaense* Smith and *Vaccinium parvifolium* Howell) and herb (*B. spicant*, *Polystichum munitum* (Kaulf.) Presl, and *Tiarella trifoliata* L.) layers while the forest floor is dominated by a continuous moss covering, mainly *H. splendens* and *Stokesiella oregana* (Sull.) Robins. (Germain 1985; Messier 1991). The HA is more susceptible to periodic windthrow disturbances, the most recent occurring around 1908, which produce friable soils (Lewis 1982). The HA is equivalent to the CWHb₁₍₄₎ of Green et al. (1984).

The soils of the S1 ecosystem have been variously classified (see Lewis 1982; Germain 1985; Messier 1991). The parent material is dominated by sandy loam glacial tills with a deep, permeable, reddish-brown mineral Bf horizon in both the CH and HA. This horizon is friable in the HA but firm in the CH (Lewis 1982).

Because the accumulation of organic material in both forest types ranged from less than 15 cm to greater than 70 cm (see Lewis 1982; Germain 1985; Fox et al. 1987; Messier 1991), the soil may be classified as a complex of Podzol, folic phase, and Lignic Folisol to cover the variation that occurs throughout both forest types (R. Trowbridge, B.C. Ministry of Forests, Smithers, personal communication).

The organic (L, F, and H) horizons show the greatest variation between the two forest types. (See deMontigny et al. (1993) for physical descriptions of organic horizons of CH and HA sites.) In the HA, wood is sometimes incorporated into the organic horizons, possibly as a result of treefall. In the CH, however, abundant wood material results in the formation of Fw, Hrw, and Hhw horizons (w is a horizon containing >35% of the volume as coarse woody debris in various stages of decomposition) (Green et al. 1993). Messier (1991) classified the humus forms of the CH and HA as Lignohumimor and Humimor, respectively, based on the humus form classification system of Klinka et al. (1981).

Sampling

Sampling for soil animals was carried out five times: August 9 and 10, 1989; May 24 and 25, 1990; July 22 and 23, 1990; October 14 and 15, 1990; and March 4 and 5, 1991. Four 2.5 × 2.5 m plots were established in each forest type. Sampling plots were at least 50 m from the forest type boundary and not in the ecotone between the CH and HA. These plots were divided into 25 microplots (0.5 × 0.5 m). Each microplot was sampled only once during the study. At each sampling time, three microplots were selected at random from each of the eight plots.

Two of the selected microplots from each plot were sampled using a 1 m long metal soil corer, which had a 5.1 cm internal diameter cutting edge. The main body of the corer was recessed to reduce compaction of the sample. Because each soil profile did not contain all possible horizons, soil samples for extraction were taken from certain combined horizons for consistency between the two forest types. The horizons for both CH and HA were divided into LF, H, and mineral soil layers. From each of the LF, H, and mineral layers at least one 3-cm sample was removed to include all or at least the middle of the horizon.

A 0.3 × 0.3 m sample was removed from the third microplot for hand sorting of macrofauna in the laboratory. The depth of these samples ranged from 5 to 10 cm as most of the macrofauna would be expected to occur here.

At each sampling time, a separate 0.5 × 0.5 m plot was established at least 5 m away from each plot to sample for Oligochaeta using the Formalin method (Raw 1959). During the last four sampling periods the litter layer was removed from each plot to increase the absorption of Formalin into the soil and to enhance observation of emerging worms. Oligochaeta specimens were hand collected and then preserved in 4% Formalin for further identification.

Soil samples were packed into coolers and transported to PFC in Victoria for the Baermann funnel extraction and to UBC in Vancouver for high-gradient extraction and hand sorting. Extractions were begun within 72 h of sampling. The single exception was the March 1991 wet funnel samples, which were stored in a cold room (4°C) for 10 days before extraction.

Laboratory analyses

One set of soil cores was extracted with a high-gradient extractor (Lussenhop 1971). Microarthropods were collected into a 1:1 (v:v) saturated aqueous picric acid (1.2% w/v) – distilled water solution and then transferred to 70% ethanol by washing out

the collecting dishes with distilled water through a 50- μ m sieve until no picric acid remained. The contents of the sieve were then rinsed into glass shell vials (1 dram) using 70% ethanol and stored for counting and identification. Soil cores were weighed prior to extraction. Extracted soil cores were oven-dried for at least 24 h at 105°C and weighed. The gravimetric moisture content for each sample was calculated as percentage of the soil dry weight (Hillel 1980).

The other set of soil cores was extracted for nematodes and enchytraeid worms using modified Baermann funnels (O'Connor 1962) at room temperature and humidity with no additional light or heat. Soil samples were placed in a double-walled sample holder with the bottom screen lined with facial tissue. Each sample was placed in a glass funnel and partly submerged in distilled water. After 24 h, the bottom 30 mL of water was drawn off. Five millilitres of 4% Formalin was added to preserve the specimens for future counting and identification. After 5 days another 30-mL sample was drawn off. Both samples were then transferred to 70% ethanol using a fine porosity sintered glass funnel.

The 0.3 \times 0.3 m soil samples were hand sorted for macrofauna (e.g., Coleoptera, Isopoda, Chilopoda, Diplopoda, etc.) in a white, enamel tray. Specimens were preserved in 70% ethanol.

All samples were counted and identified using a dissecting microscope (8–150 \times) with fibre optic lighting through a dark-field plate (manufactured by CHU Technical Corp.). Arrangement of taxa for all arthropods to class and order follows Scudder et al. (1979) except the Acari, which follows Evans et al. (1961). Collembola and Oligochaeta were identified to family. Arachnida, Crustacea, and Insecta were identified to order. Mollusca, Myriapoda, Stelechopoda, and the remaining Hexapoda (Protura and Diplura) were identified to class. Nematoda and Rotifera were identified to phylum.

Data analyses

Faunal counts were extrapolated to include the total depth of the specified horizon (LF, H, and mineral) as measured in the field. Numbers of organisms per sample were used to calculate relative abundance, abundance per square metre and biomass per square metre. Biomass was calculated from median individual dry mass (milligrams) values obtained from Petersen and Luxton (1982).

Three similarity indices were used to compare group diversity between the two forest types. Morisita's index of similarity (C_s) (Morisita 1959) was calculated from the actual counts of individuals in higher taxa (i.e., family and above). The counts were then log transformed using $\ln(x + 1)$, where x is the actual counts of individuals. These new values were used to calculate the simplified Morisita's index of similarity (C_H) (Krebs 1989; Wolda 1981). The C_H -values were calculated also for the biomass values for higher taxa. Renkonen index (PS) was calculated using the relative abundances of soil fauna in higher taxa (Krebs 1989; Wolda 1981) for the two forest types.

Distribution of Acari, Collembola, and Nematoda within the LF, H, and mineral soil horizons was examined also. The number of individuals per square metre and the percentage of the total population in the LF horizon were plotted against sampling time.

Nitrogen content

We estimated nitrogen content of the soil fauna biomass from values presented by Persson (1982) and Teuben and Verhoef (1992). The values for whole-body nitrogen concentration for Collembola, Diplopoda, and Isopoda are 12.6, 6.9, and 8.3%, respectively, of biomass (Teuben and Verhoef 1992). For all remaining groups, nitrogen content is about 10% of biomass on a dry weight basis (Persson 1982).

Results

Abundance and biomass

Forty-one major groups of soil animals were extracted and identified during the study (Table 1). Overall, the HA

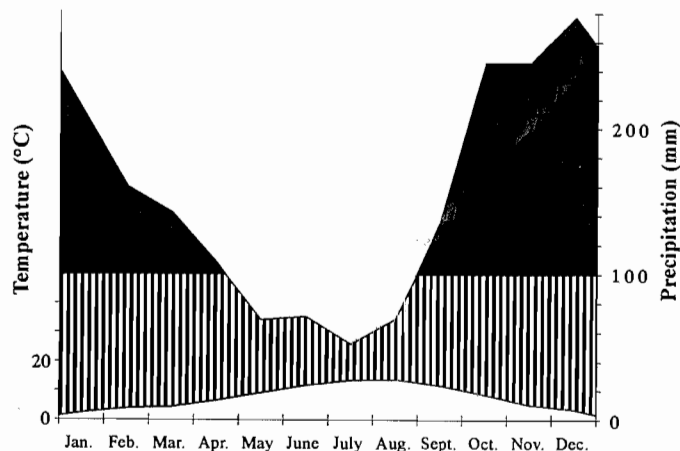


FIG. 1. Ecological climate diagram based on 30-year means from the Port Hardy, B.C., airport (elevation 22 m) in the style of Walter (1979). Abscissa is months, beginning with January. The mean annual temperature was 7.9°C and the mean annual precipitation was 1728.8 mm. Vertical line pattern indicates relatively humid periods. Solid areas indicates perhumid periods. Data are from Environment Canada (1982).

maintains a higher abundance of soil fauna per square metre than the CH. Owing to the large variation accompanying most of the abundance values, the data from this study can only be used to suggest trends in the soil fauna communities in these forest types.

Nematodes (Nematoda) maintained the highest relative abundance overall in both forest types followed by the mites (Acari), springtails (Collembola), and copepods (Copepoda) (Table 2). The HA showed a greater relative abundance of mites than the CH; springtails were equal in both forest types and copepods maintained greater abundances in the CH than the HA. These four groups accounted for approximately 98% of the total number of soil fauna in both the CH and the HA.

Millipedes (Diplopoda) maintained the highest biomass values in the CH forest type followed by potworms (Enchytraeidae), mites, and springtails. The distribution of biomass in the HA presents a different pattern with the mites having the highest relative biomass followed by potworms, millipedes, and dipteran larvae. In each forest type, these top four groups represent about 80% of the biomass in the CH and HA. Adding the values for the other two groups in this table increases the total to about 90%. The missing 10% of the relative biomass is made up by the remaining groups.

Although nematodes are the most abundant group numerically, they are responsible for only a small portion of the total biomass in both forest types (about 4%). In contrast, the millipedes, which account for a large amount of the biomass (31% in the CH and 20% in the HA), are responsible for less than 0.01% of the total number of fauna in the soil.

Three orders of crustaceans (Crustacea) were identified during the study. Copepoda were found in both forest types. This is the first record of soil copepods in Canada (C. Shih, Zoology Division, Canadian Museum of Nature, Ottawa, Ont., personal communication). While their presence in soils is not considered to be unusual (Kühnelt 1976), copepods are not generally searched for in soils. Abundances in the CH ranged from a high of 94 000 / m² in May to a low of

TABLE 1. Range of mean abundances (individuals $\times 10^3 / m^2$) of soil fauna, sampled in August 1989, May 1990, July 1990, October 1990, and March 1991, in cedar-hemlock (CH) and hemlock - amabilis fir (HA) forest types near Port McNeill, B.C.

	CH	HA
Phylum Rotifera	2.5-20.4	2.9-30.7
Phylum Nematoda	1660-4160	2440-5790
Phylum Mollusca		
Class Gastropoda	0-0.01	0-0.003
Phylum Annelida		
Class Oligochaeta		
Family Enchytraeidae	9.5-42	19.4-45.8
Family Megascolecidae	0-0.008	0-0.001
Superphylum Arthropoda		
Phylum Stelechopoda		
Class Tardigrada	3.4-44.3	8-15.7
Phylum Entoma		
Subphylum Chelicerata		
Class Arachnida		
Subclass Acari		
Order Mesostigmata	3.7-10.5	3.4-20.5
Order Prostigmata	1-22.4	2-135.8
Order Astigmata	0-17	0-19.6
Order Cryptostigmata	30-140	48-472
Undetermined	0.2-16.2	0-14
Total Acari	38.6-189	60.3-629
Subclass Araneida		
Order Aranea	0.02-0.07	0.02-0.06
Subclass Chelonethida		
Order Pseudoscorpionida	0.1-1.5	0.4-2.9
Subphylum Crustacea		
Order Branchiopoda	Present	Absent
Order Copepoda	55.4-93.6	16.6-95.7
Order Isopoda	0-0.1	0-0.01
Subphylum Uniramia		
Superclass Myriapoda		
Class Pauropoda	0-1.5	0-8
Class Diplopoda	0.03-0.09	0.02-0.1
Class Chilopoda	0.03-0.09	0.04-0.09
Class Symphyla	0-1.3	0-3.8
Superclass Hexapoda		
Class Protura	0-0.6	0-1
Class Collembola		
Order Arthropleona		
Family Anurididae	0.3-1.1	0.1-3.3
Family Entomobryidae	0-5.3	0-22.3
Family Hypogastruridae	0.09-9.7	0.5-15.6
Family Isotomidae	8-20.9	11.1-43.8
Family Neanuridae	0.3-0.8	0-5
Family Onychiuridae	9.6-99.9	32.4-226.7
Family Tomoceridae	1.4-2.8	0.3-6
Order Symphypleona		
Family Neelidae	0-3.3	0-4.4
Family Sminthuridae	0-1.8	0-4.2
Undetermined	3.8-9.9	3.8-15.9
Total Collembola	34.8-140.3	61.1-339.8
Class Diplura	0-0.1	0-0.5
Class Insecta		
Order Homoptera	0-0.006	0-0.006
Order Diptera (A)*	0-0.003	0
Order Diptera (L)*	0-0.7	0.1-1.7

TABLE 1. (concluded)

	CH	HA
Order Coleoptera (A)	0-0.03	0.003-0.04
Order Coleoptera (L)	0-0.006	0.003-0.02
Order Hemiptera	0.003-0.006	0-0.003
Order Hymenoptera	0-0.006	0-0.006
Order Lepidoptera (L)	0-0.006	0-0.003
Order Thysanura	0-0.1	0
Overall total	1970-4634	2805-6864

*A, adult; L, larvae.

55 000 / m² in July. Abundances in the HA had a wider range from 96 000 / m² in May to 16 000 / m² in October. Copepods were more abundant in the CH during August, October, and March and in the HA during May and July. Pillbugs (Isopoda) were found mostly in the CH; ranging from 100/m² in May to zero in July. Pillbugs were only collected once in the HA during October (10/m²). Two specimens of Branchiopoda were found during July in the CH, but none in the HA forest.

Megascolecidae (an earthworm family with many native North American species, as opposed to the more commonly known Lumbricidae) were observed in both the CH (1/m² for May and 8/m² for July) and the HA (1/m² only in July). Only one species was found. It was identified as *Arctiostrotus perrieri* Benham by W.M. Fender (Soil Biology Associates, McMinnville, Oreg.).

Potworms were the dominant segmented worms. Abundances ranged in CH from 42 000 / m² in May to 9500/m² in August. In the HA, the high abundance occurred in May (46 000 / m²) and the low in October (19 000 / m²). The abundance of potworms was greater in the HA during August, May, and July while being higher in the CH during March and October. The Formalin method, which was used to extract earthworms, also forced large potworms, ranging in length from approximately 3 to 8 cm, to the soil surface.

Vertical distribution

Mites, springtails, and nematodes were selected for detailed presentation because of their high abundance or biomass (Table 2, Fig. 2). Millipedes were not included because they were collected mainly from the hand-sorted samples and usually occupy the upper litter layers (Hoffman 1989). Figure 2 shows that most of the population of nematodes, mites, and springtails were found in the LF and H horizons throughout the study. A high percentage of nematodes also appear in the mineral soil compared with the mites and springtails. The greatest number of individuals for all three groups were found during August. Generally, numbers increased from March until August and then decreased in October. All three groups show the same trend in vertical distribution; a low percentage of individuals in the LF during May and August and a greater percentage of individuals in the LF during March, July, and October.

Nematode populations within the LF represent about 30% of the total nematode population within the soil profile (Figs. 2a and 2b). Fluctuations in nematode numbers in the LF horizon remained relatively small except for a large peak observed in the CH during July. This peak also represents the time when the population estimate for the Nematoda is the lowest (1 660 000 / m²). The August sample for the nematodes in the CH indicates a low percentage of individuals in the LF,

TABLE 2. Summary of mean relative abundance and biomass for the dominant groups of soil fauna from all sampling times in the cedar-hemlock (CH) and hemlock - amabilis fir (HA) forest types

	Relative abundance*		Relative biomass	
	CH	HA	CH	HA
Nematoda	89.4	87.8	4.7	4.0
Acari	3.2	5.9	14.2	23.3
Collembola	3.1	3.4	8.7	8.4
Copepoda	2.5	1.3	ND**	ND
Enchytraeidae	0.76	0.75	25.5	22.0
Diptera larvae	0.01	0.02	6.7	15.3
Diplopoda	<0.01	<0.01	30.8	19.8
Total***	98.2	98.4	79.2	80.4

*Relative abundance and relative biomass are expressed as percentage of the total abundance and biomass on the CH and HA, respectively.

**ND, not determined.

***Total values represent sum of highest four values in each column.

while this same time period also represents the largest population estimate for the nematodes.

A similar pattern was observed for the mites (Figs. 2c and 2d) and springtails (Figs. 2e and 2f). Generally, more than 50% of the total population was found in the LF at all sampling times. While the largest numbers of mites and springtails per square metre occurred in August, this sampling time also showed a low percentage of individuals in the LF. The highest percentage of individuals in the LF occurred in July.

Similarity indices

As Morisita's index (C_x) ranges from 1 (similar) to 0 (dissimilar), the values of generally >0.90 (Table 3) indicate that soil fauna communities of CH and HA ecosystems are similar in composition when this index is calculated with taxa identified at high taxonomic levels (i.e., family and above). In May, there is a lower similarity value (0.86) than at the other four sampling times (all greater than 0.99); however, this does not suggest a large difference in the faunal composition between the two forest types.

The simplified Morisita's index of similarity (C_H) values calculated for the transformed values (Table 3) again suggest a similar community of soil fauna in the two ecosystems (all values >0.93). The C_H values calculated for the biomass (Table 3) show a range of results from a high of 0.92 in August to a low of 0.59 in October. This suggests sea-

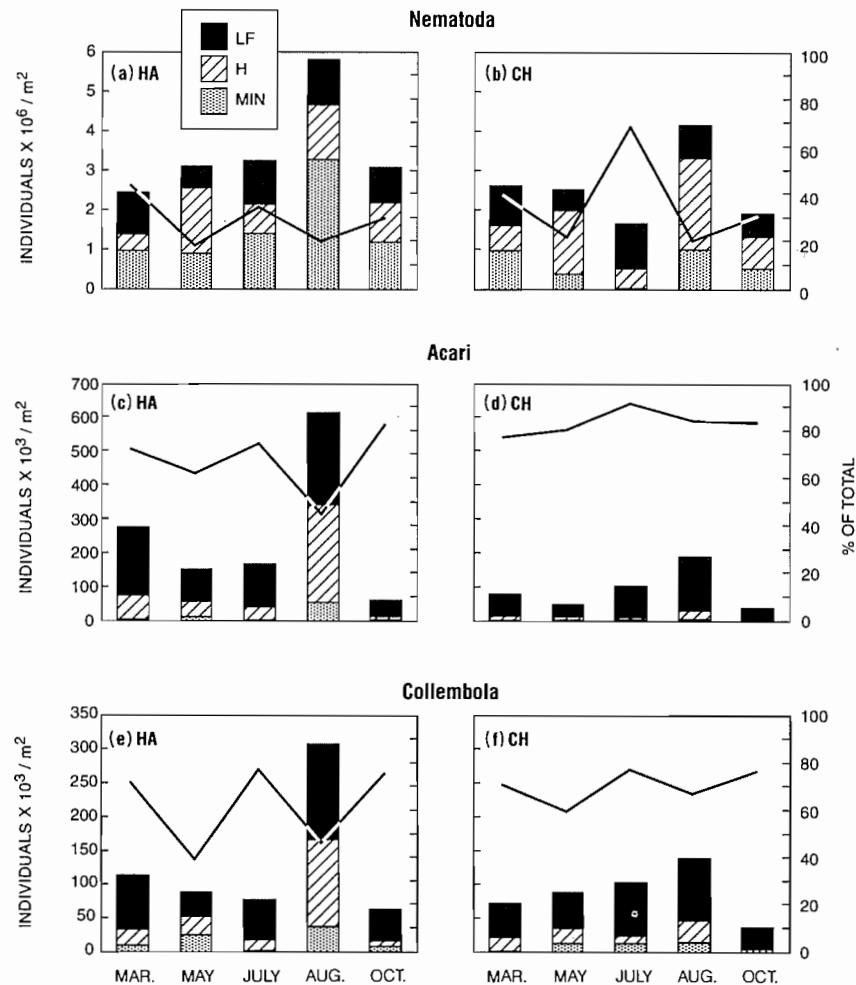


FIG. 2. Total number of individuals (vertical bars; left ordinate), and percentage of individuals found in the LF horizon (plotted line; right ordinate) of Nematoda, Acari, and Collembola plotted against sampling time for cedar-hemlock (CH) and hemlock – amabilis fir (HA) forest types.

sonal fluctuation in biomass between the two forest types. The Renkonen index (Table 3), which compares the relative abundance of organisms between the two forest types, shows there is little difference between the two forest types with values ranging from 91% in March to 96% in May.

Moisture content

In general, the CH maintained a higher soil moisture content than the HA throughout the study (Table 4). This was also evident for all soil horizons of both the CH and HA.

Nitrogen content

Total nitrogen content of soil fauna was estimated to be 2.3 kg N/ha in CH and 4.0 kg N/ha in the HA (Table 5). In the CH, both mites and millipedes contribute about the same amount of nitrogen (0.4 kg N/ha), while the numerically abundant potworms contribute 0.7 kg N/ha. However, in the HA the mites maintain a greater biomass and, therefore, contribute most of the total nitrogen held in fauna (1 kg N/ha). This is followed closely by the potworms and dipteran larvae (0.9 and 0.7 kg N/ha, respectively).

Discussion

At the level of taxonomic resolution (family and above) attained in this study, most of the 41 groups are present in both forest types at some point during the sampling. Based

on this information, it would suggest that the soil fauna communities of the CH and HA are roughly the same. However, a distinct separation of the communities might be observed if identification of the fauna in these forest types is done at the species level. Anderson (1977) considered most classes and orders of soil organisms to be widely distributed, whereas families are more restricted and genera and species are highly endemic to isolated habitats or land masses. Although it is sometimes difficult to separate soil fauna communities in adjacent soils that are different (Wood 1966), such soils may, nevertheless, be characterized by their fauna when the species have been carefully identified (Rusek 1989).

Unfortunately, the creation of a complete species list of soil fauna for a particular habitat is quite difficult for many reasons. Soil fauna are incorporated closely into the soil structure and some species are not easily extracted (Edwards 1991). The biogeography of Canadian soil fauna is poorly known and local checklists and regional monographs are not available. Canadian soil zoologists commonly encounter many species previously not known to science. For example, Behan-Pelletier and Bissett (1992) estimated that of the 48 500 species of soil arthropods expected to occur in North America, only 53% have been described. Furthermore, Danks (1988) reported that there are 1915 species of mites identi-

TABLE 3. Similarity indices calculated for higher taxa of soil fauna of both forest types for each sampling time

Index ^a	Aug. 1989	May 1990	July 1990	Oct. 1990	Mar. 1991
C_{λ}	0.99	0.86	0.99	0.99	0.99
C_H (transformed counts) ^b	0.95	0.94	0.96	0.95	0.96
C_H (faunal biomass; $\text{mg} \cdot \text{m}^{-2}$)	0.92	0.91	0.84	0.59	0.75
PS (%)	93	96	94	93	91

^a C_{λ} , Morisita's Similarity Index (Morisita 1959); C_H , simplified Morisita's Similarity index (Krebs 1989); PS, Renkonen index (Krebs 1989; Wolda 1981).

^bThe transformation used was $\ln(x + 1)$.

TABLE 4. Gravimetric soil moisture contents (%) for the sampled horizons in the cedar-hemlock (CH) and hemlock - amabilis fir (HA) forest types

	Mar. 1991		May 1990		July 1990		Aug. 1989		Oct. 1990	
	CH	HA	CH	HA	CH	HA	CH	HA	CH	HA
LFm	424	313	256	175	138	176	189	142	330	227
F	NA ^a	NA	NA	NA	320	275	295	163	418	319
H	351	285	NA	NA	343	192	233	224	351	236
Mineral	147	126	NA	NA	78	75	132	92	90	71
Average	307	241	256	175	219	180	212	155	297	213

^aNA, data not available.

fied in Canada and estimated that there were also some 7600 species still undescribed or unrecorded. Well over 250 species of arthropods alone per square metre of forest floor may be expected in a mature coniferous forest soil (Moldenke 1990).

Both Morisita's similarity index and the Renkonen index generally indicated that the soil fauna communities are similar in the CH and HA forest types with respect to higher taxa. However, there were differences when the biomasses were compared for the CH and HA. The variation in the biomass calculation for the simplified Morisita's index of similarity (Table 3) is the result of a single group, the millipedes, which had a fourfold greater biomass in the CH than in the HA during October. Biomass values calculated for March also indicate a lower similarity between the two forest types. The lower similarity values could result from cryptostigmatid mite biomass being over three times higher in the HA than the CH, or the dipteran larva biomass being over eight times higher in the HA.

Numerical abundance and biomass of the groups provide a better picture of the structure of the soil fauna communities in the CH and HA than does simple presence or absence of higher taxa or similarity indices based on higher taxa. The HA tended to maintain a higher abundance and biomass throughout the study period. While nematodes were the most numerous soil animals in both forest types (1 700 000 - 5 800 000 / m^2), they are only responsible for about 4% of the faunal biomass. In the CH, millipedes account for nearly 31% of the biomass followed by the potworms, which are responsible for 26%. The HA shows a more even distribution of biomass among the dominant groups, which may create a more "balanced" ecosystem that could produce consistent decomposition and nutrient cycling throughout the year. A single group responsible for a large portion of the biomass may create a "bottleneck" in decomposition and nutrient cycling, thus limiting the productivity of the system.

Although microarthropod feeding favourably influences mineralization (Seastedt 1984), the rate of decomposition

TABLE 5. Mean biomass and nitrogen content of soil fauna (kg/ha) of cedar-hemlock (CH) and hemlock - amabilis fir (HA) forest soils

Fauna	CH		HA	
	Biomass	Nitrogen	Biomass	Nitrogen
Acari	3.8	0.38	10.2	1.02
Aranea	0.4	0.04	0.3	0.03
Diplopoda	8.4	0.42	8.7	0.44
Collembola	2.4	0.24	3.7	0.37
Diptera larvae	1.8	0.18	6.7	0.67
Nematoda	1.3	0.13	1.8	0.18
Mollusca	0.3	0.03	0.1	0.01
Enchytraeidae	6.96	0.7	9.7	0.97
Megascolecidae	0.3	0.03	0.03	0.003
Others	1.64	0.16	2.67	0.27
Total*	27.3	2.31	43.9	3.96

*Includes those fauna for which biomass data were provided by Petersen and Luxton (1982). Other groups however are of low biomass and thought included in the total, were not listed separately.

also depends on the type of material being broken down and the environment in which it is found. In the CH, there is a large amount of standing and fallen western red cedar wood which is known to be decay-resistant due to the presence of phenolic acids, such as thujaplicins, in the heartwood (Harmon et al. 1986). Furthermore, Prescott et al. (1993) found that cedar foliar litter decomposes slowly and tannins were present in the forest floor of the CH. These compounds may play a role in depressing the soil fauna community. Furthermore, the CH generally maintains a higher soil moisture content than the HA, possibly high enough to fill soil pores, impede gas diffusion, and slow microbial and faunal activity, thereby reducing the rate of decomposition. The high moisture content in the CH, however, would create an excellent habitat for the Crustacea, such as Copepoda and Branchiopoda, that were found primarily there. Copepoda were the fourth most relative abun-

dant group in both the CH and HA (2.5 and 1.3%, respectively) and should not be ignored in faunal studies. While copepods are generally collected from wet soils (Watson et al. 1966; Kühnelt 1976), they have also been found in drier soils in the CWH zone on southern Vancouver Island (V.G. Marshall, unpublished data). These aquatic animals could act as indicator species for environments in which decomposition could be impeded by a high water content.

Generally, abundance and biomass values calculated for the CH tend to be lower than those reported by Petersen and Luxton (1982) for temperate coniferous forests, whereas values in the HA tend to be closer to published averages. Among the metazoa, nematodes generally maintain the highest numerical abundance followed by the mites and the springtails (Kevan 1965; Tomlin and Miller 1987; Marshall 1993) and we found a similar pattern.

Soil fauna show a characteristic negative binomial distribution (Huhta et al. 1967; Abrahamson and Strand 1970). Equations to estimate sample size for populations that fit a negative binomial distribution (Krebs 1989) indicate that we achieved $\pm 50\%$ accuracy in estimating the total soil fauna population in CH and HA by taking four samples. This level of accuracy ($\pm 50\%$) is considered adequate for preliminary surveys (Robson and Reiger 1964). To achieve $\pm 90\%$ accuracy, a minimum of 80 samples from both forest types would have been necessary, requiring many person-years of work to simply count the fauna, let alone to identify them.

Soil fauna populations in many temperate regions are generally highest during the spring and fall (Wallwork 1976; Edwards 1991). However, populations in West Coast forests might not follow this pattern (Marshall 1974). In our study, total faunal abundances peaked in August for both forest types. In the CH, a smaller peak in abundance occurred in March also, whereas the HA showed a steady increase in numbers from March until August. The total population of soil fauna decreased in both forest types in October. From the climate diagram (Fig. 1) we know that May shows spring-like conditions (increasing temperature and decreasing precipitation) while August maintains summer-like conditions with high temperatures and relatively low precipitation. However, information on the specific years studied was not collected. Sampling regularly over a number of years might be necessary to better characterize the soil fauna communities of these two forest types.

Spring and late-summer peaks in soil fauna populations might be related to increased activity in root and fungal growth, which provide food sources for most soil animals. With increased food availability, populations could increase until food becomes a limiting resource. On average, more than 60% of the microarthropod population is present in the LF horizon. This horizon contains a great amount of fine roots and fungal hyphae and perhaps behaves similarly to ectomycorrhizal fungal mats of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in supporting large faunal populations (Cromack et al. 1988). Fluctuations in the soil fauna population in the LF horizon may be the result of the fauna migrating to find a better food source or changes in mortality and natality depending upon the time of year or specific life histories. The presence of nematodes in the mineral soil could be due to their small size, which would permit them to use the small soil pores to access this horizon and utilize this environment while the mites and spring-

tails, owing to their relatively larger size, would be unable to do so.

The HA is considered to be a more productive forest type than the CH, possibly because the CH is N and P deficient for good tree growth (Germain 1985). Better tree growth in the HA could be the result of more rapid or complete decomposition caused by a larger soil fauna community present in the HA. Although Prescott et al. (1993) found virtually no difference in litter-bag mass loss between the CH and HA, this tells little about nutrient availability and nutrient turnover. The lower N availability in the CH suggests that more N is immobilized in the humus of the CH, thereby reducing the amount available for tree growth. Setälä et al. (1990) showed that soil fauna significantly increased the release of N and P in microcosms that simulated coniferous forest floors. Furthermore, Setälä and Huhta (1991) showed that soil fauna positively influenced nutrient uptake and net production in birch (*Betula pendula* Roth.) seedlings in similar microcosm studies. The turnover rate of the animal biomass is another important factor when considering nutrient content of the ecosystem (Lousier and Bamforth 1989; Teuben and Verhoef 1992).

The animals themselves also serve as a reservoir of nutrients (Teuben and Verhoef 1992) and Petersen and Luxton (1982) consider them to be important for the internal retention and cycling of most major nutrients, but especially N and P. Persson (1982) found about 1.7 kg N/ha in the soil fauna in a podzol with a mor humus form of a 120-year-old Scots pine (*Pinus sylvestris* L.) forest in central Sweden. This is lower than the amount of nitrogen in the standing crop of soil fauna of the CH (2.3 kg N/ha), and less than half of that found in the HA (4.0 kg N/ha). Assuming a 10% N content for biomass, the nitrogen content of the HA is much higher than the 3.0 kg N/ha estimated from the data of Tomlin and Miller (1987) for a mature *Pinus-Quercus-Acer* stand in Ontario.

This preliminary survey provides further support for the concept that forest site productivity is positively related to soil fauna biomass. More research is required in two major areas: (i) trophic level studies that examine the contribution of different feeding groups to soil structure and (ii) species level studies to determine how species diversity influences and is influenced by the development of CH and HA humus forms. The Collembola are now being identified to species to test the latter hypothesis.

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