THE INFLUENCE OF SOIL FAUNA ON NITROGEN MINERALIZATION AND
DECOMPOSITION IN SOIL FORMED UNDER WESTERN REDCEDAR, WESTERN
HEMLOCK, SITKA SPRUCE AND DOUGLAS-FIR FORESTS ON THE WEST
COAST OF VANCOUVER ISLAND

by

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We accept this thesis as conforming
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The influence of soil fauna on indices of N mineralization and decomposition in soil developed under four tree species (western redcedar, western hemlock, Sitka spruce and Douglas-fir) from the west coast of Vancouver island, B. C. was evaluated over a 5-month period. The soil was either defaunated, or given an assemblage of mites, collembola, nematodes and enchytraeids extracted from soil collected from the study site, or given the latter plus one millipede (*Harpaphe haydeniana haydeniana*). The experiment was carried-out in pots (microcosms) in a greenhouse. Water-leached, KCl-extractable and total N concentration (leached N plus KCl-extractable N plus plant N content) increased with increasing faunal community complexity. The effect was more apparent in the presence of the millipede. The millipede enhanced the rate of decomposition to a statistically significant degree. Rates of N mineralization did not differ significantly between combinations of soil fauna and soil type (tree species). Both decomposition and microbial biomass were significantly enhanced in the presence of *H. h. haydeniana* (and other fauna) in Sitka-spruce soils. Western redcedar soil mineralized the most N. The use of cabbage plants as indicators of N availability did not prove to be a good choice; plant biomass was extremely variable and not related to other measures of N availability. The abundance of soil fauna was low and this may have reduced the potential for statistically significant differences between fauna treatments.
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Nutrient cycling in forests is accomplished through the decomposition and mineralization of organic matter. This involves the combined activities of a decomposer community composed of soil microorganisms and soil fauna, the latter being made up largely of mites and collembola (Swift et al. 1979). Research has focused on the effects of bacteria and fungi during decomposition and less on soil fauna. However, studies have illustrated significant effects due to faunal activity and there is general acceptance that soil fauna play an important role in the processes of decomposition and nutrient cycling (Seastedt, 1984; Lussenhop, 1992).

The following will review a significant portion of the literature dealing with the effects of soil fauna in nutrient cycling, with carbon (C) and nitrogen (N) dynamics being the focus.

Mechanisms

There is general acceptance that soil fauna influence rates of decomposition and N mineralization through a number of mechanisms (Lussenhop, 1992; Anderson, 1988; Verhoef and Brussard, 1990). Indirectly, soil fauna will regulate decomposition and N mineralization by grazing the microbial population and dispersing fungal and bacterial inoculum. Direct effects include mixing and fragmentation of organic matter, and mobilization of nutrients through excretion. Inherent in these “mechanisms” are the
ecological attributes of soil fauna, which are many and varied (Hasegawa and Takeda, 1995; Rihani et al., 1995; Leonard and Anderson, 1991). For example, the organisms’ capacity to digest fungal chitin will affect the impact it has on the fungal community (Siepel and Maaskamp, 1994).

**Grazing**

Consumption of whole or partial bacterial cells and fungal hyphae by soil fauna, or “grazing”, can potentially regulate soil microbial biomass and community structure (Lussenhop, 1992; Seastedt, 1984). A decrease in microbial biomass and concomitant rise in faunal population is common where overgrazing has occurred (Ineson et al. 1982; Bardgett et al. 1993). Low to intermediate degrees of grazing result in elevated rates of CO$_2$ production (Ineson et al. 1982; Hanlon and Anderson, 1979; Setala et al. 1988), most of which is attributed to the microbial population. Carbon mineralized through faunal activity is negligible compared to microbial respiration (Persson, 1989), although the potential for fauna to influence decomposition is substantial. Soil fauna have a lower C to N ratio than their microbial food source (Lavelle, 1997). As a result soil fauna contribute N in the form of urine and feces (Anderson et al. 1981), and upon molting (Teuben & Verhoef, 1992). Several authors have suggested that faunal grazing may be of particular importance where the release of microbially immobilized N is inhibited by substrate with a high C to N ratio (Persson, 1989; Teuben & Verhoef, 1992; Seastedt, 1984). The net result is largely determined by a balance between nutrient release due to grazing, and the size and activity of the microbial population (Siepel & Maaskamp, 1994).

Food choice among soil fauna is varied (Dindal, 1990; Kaneko et al. 1995). Walter (1987) noted that “opportunistic polyphagy” may be more common than is
thought; mycophagous fauna likely consume the fungal hypha as well as the variety of organisms intimately associated with the fungus. Nonetheless some research has illustrated the existence of food preference among soil fauna. Aitchinson (1983) noted that certain collembolans and mites preferred darkly pigmented fungi. Klironomos et al. (1992) noted a similar response in collembola to darkly pigmented fungi. A later study by Klironomos and Kendrick (1995) provided additional support for food preference by showing that the presence of collembola in the field was related to fungal distribution, and “apparent importance” of darkly-pigmented fungi was suggested. This research raises the question of a possible relationship between fungal growth and succession during decomposition and the selective pressures of faunal grazing. A study by Newell (1984) revealed that fungal dominance and rates of decomposition were dependent upon the presence of a collembolan species. She found that in the field the fungus *Mycena galopus* was more abundant in the upper forest floor layers than *Marasmius androsaceus*. This was reversed in the laboratory in the absence of grazing. *M. galopus* decomposed litter more slowly than did *M. androsaceus*, suggesting that a shift in dominance (if collembolans were not present) would speed the rate of decomposition. Mclean et al. (1996), in contrast to the above studies, found no indication that fungal succession is related to grazing pressures.

The digestive systems of faunal species will influence their feeding activities, and hence the resulting impact on decomposition. For example, a symbiotic relationship between the collembola *Folsomia candida* and a certain chitin-degrading microorganism allows *F. candida* to make greater use of nutrients available in fungal hyphae (Borkott and Insam, 1990). It is likely that a more complete mineralization of nutrients is encouraged by
this relationship. Siepel and Maaskamp (1994) noted differences in the CO₂ evolved from microcosms containing mites of varying enzymatic capacity. A distinction was made between “browsers” and “grazers”: “browsers” are capable of digesting cell contents only and as a result leave damaged fungal hyphae, whereas “grazers” can effectively digest both the cell contents and the cell wall. The “browsers” had an eventual negative effect on CO₂ production whereas the “grazers” increased CO₂ production. Addition of NH₄NO₃ also increased CO₂ production although not when added with mites. The authors concluded that the additional availability of cell wall-derived N due to “grazing” stimulated the microbial population, and that this was dependent upon the assimilation efficiency of each mite species (see Peterson & Luxton, 1982). Very little information exists regarding the physiological response of fungi to grazing. Grazing may release portions of the fungal mycelium from metabolic stasis (Dix and Webster, 1995), or perhaps stimulate the production or release of enzymes involved in nutrient acquisition (Hedlund et al. 1991).

Fungal response to grazing is noted to vary depending on the nutrient content of its biomass (Hanlon, 1981). In sterile soil inoculated with the fungus Mortierella isabellina, enchytraeid worms had a positive effect on respiration and hyphal length, as compared to the natural soil. High amounts of nutrient-rich organic material in the inoculated soil (due to the death of organisms upon sterilization) may have provided for the growth of M. isabellina, and supplied enchytraeids with young hyphae of high nutrient content.
Fragmentation, mixing and dispersal

Depending on body size and type, on mouth parts and on the extent of mobility, soil fauna will affect decomposition to varying degrees through fragmentation and mixing of organic matter, and by dispersal of microbial propagules (Anderson, 1988). Feeding reduces the particle size of organic matter thereby increasing the surface area for microbial growth (Hanlon, 1981). A reduction in particle size also increases infiltration of organic matter in percolating water. Feeding and eventual excretion enable the movement of material, thus promoting microbial growth in uncolonized areas (Swift et al. 1979).

Arthropod feces have been shown to contain higher nutrient contents than the original food source (Teuben & Verhoef, 1992). Teuben and Verhoef (1992) found that collembolan feces could increase the availability of $\text{NO}_3^-$ in the forest floor by a factor of 2.4, and that this was due to nitrifier microflora in the collembolan gut. Fungal spores are found upon gut analysis suggesting possible dispersal by soil fauna, although spore survival is variable (Dix and Webster, 1995).

Faunal community dynamics and decomposition

The structure of the soil decomposer community may change as the substrate progresses from fresh to decomposed litter (Hagvař & Kjondal, 1981; Garrett, 1981). The dynamics of this succession depend on many things, one of which is the food source, or varied forms of organic matter (Swift et al. 1979). The physical, chemical and biological nature of litter will help determine the community of fauna that feed on organic matter, as well as the microbial community upon which many fauna depend (Seastedt &
Fauna have been shown to stimulate microbial respiration in early-stage litter with a high C content (Couteaux et al. 1991), and decrease this activity in later-stage litter (low C to N ratio) (Van Wensem et al. 1993).

Battigelli et al. (1994) studied the soil fauna of two forest types. The research was initiated to discover why stagnation of Sitka spruce trees on old-growth western-red cedar/western-hemlock cutblocks (CH) occurred while the opposite was true on adjacent mature western-hemlock/amabilis fir cutblocks (HA). Previous research had revealed lower N and P availability on CH sites (Germain, 1985, cited by Batigelli et al., 1994). The study revealed differences in soil fauna between the two sites, although these were quite variable suggesting trends only. HA sites possessed a more general richness in faunal groups. The authors suggested that this may allow for a more balanced process of decomposition, whereas the presence of large numbers of certain faunal groups in the CH sites encouraged immobilization of nutrients and as such limited site productivity.

As the faunal community develops in decomposing litter, interactions between groups, and between species within groups will determine the make-up of the faunal and microbial community (Santos & Whitford, 1981; Petersen & Luxton, 1982). Other factors such as temperature (Laasko et al. 1995) and moisture (Argyropoulou et al. 1993), or perturbations to the system (Ponge et al. 1993), will play a determining role in the resultant community structure. Hasegawa and Takeda (1995) employed litterbags to study the population dynamics of four collembolan species during the decomposition of pine needles in field enclosures. Fungal colonization followed three phases: initial growth, followed by a steady-state and finally a collapse of the fungal population during the last 3 months of the 24-month experiment. Two litter-dwelling collembola were predominant.
during the initial growth phase of the fungi. Gut analysis showed that fungal hyphae comprised a large proportion of the food consumed by the collembola. As decomposition proceeded populations of two new collembolan species grew and continued to do so until the end of the experiment. Very little fungal material was found upon gut analysis. These later two species were considered detritivores while the first colonizers were fungivores. Changes in collembolan populations thus corresponded to the stage of decomposition and resource type available to the soil animals. During the steady-state phase animal feces and humus accumulated. Coprophagy and use of more recalcitrant material were suggested to have occurred during the mobilization phase. Faber and Verhoef (1991) also looked at the functional differences in feeding among two litter-dwelling and one humus-dwelling collembola. They used field enclosures to study the three collembolan species, either separately or grouped together. Results for decomposition were distinctly different depending on the influence of each collembolan species.

Santos and Whitford (1981) found that soil fauna had a marked effect on the rate of decomposition measured in buried litter bags in the Chihuahuan desert. Buried litter was viewed as an “island” where conditions were favorable enough to harbor a diverse community of arthropods and microorganisms. They found several interesting relationships between faunal groups, which helped to elucidate the mechanisms involved in faunal control over decomposition. A consistent colonization sequence was correlated with mass-loss of organic matter. Mite groups present during the later stages of decomposition were closely related in terms of their feeding habits and being prey to one another. Non-predatory generalist feeders such as collembola and Oribatid mites (Dindal, 1990) were last to colonize the litter bags. An early stage colonizer, the Tydeid mite, was
found to prey on bacteriophagic nematodes. This significantly increased decomposition as the mites kept nematode densities low enough to prevent overgrazing of bacteria (Santos et al. 1981). The authors suggested that desert fauna have a large effect on decomposition by grazing and dispersing the microbial population, and in the early stages of decomposition, by controlling bacteriophagic nematode abundance. They further concluded that a diverse faunal population “uncouples” the relationship between abiotic factors and decomposition, as the rate of decomposition in litter bags from which the fauna were excluded correlated well with abiotic influences. Elkins and Whitford (1982) similarly found changes in the faunal population as decomposition proceeded. They also noted the importance of predators as regulators of nematode abundance and their potential to overgraze the microbial population.

**Faunal effects on decomposition and N mineralization**

**Simple systems**

The use of microcosms to study faunal effects on soil processes allows the researcher to simulate the complexity of a natural soil environment while still allowing for the control of many factors that affect decomposition in the field. The system can be greatly simplified in order to study specific faunal activities.

Ineson et al. (1982) used fragmented oak leaves and one species of collembola in a simple microcosm. Fungal growth and nutrient dynamics were studied in the presence and absence of collembola. Grazed fungal populations increased rapidly, beyond that of the ungrazed systems, then dropped significantly whereas ungrazed populations remained at a consistent level. The initial rise was viewed as a response to low-intensity grazing. The
drop in fungal mass coincided with a sharp increase in collembola numbers. Ammonium and \( \text{NO}_3^- \) released from the grazed systems increased markedly along with the collembolan population, and by the end of the eight-week experiment was twice that of the ungrazed microcosms. The authors concluded that collembola likely play a significant role in acid forest soils where nutrients in organic matter are mobilized slowly. Teuben (1991) also found that soil fauna (collembola and isopods) increased microbial respiration and nutrient release while levels of corresponding parameters in systems lacking soil fauna were low.

Protozoa have a significant impact on the mineralization of bacterially immobilized nutrients (Elliott et al. 1979; England et al. 1993). They are present in all experimental systems unless selectively excluded (with mesh sizes of 5-50 \( \mu \text{m} \)). Kuikman et al. (1991) studied the effects of protozoan activity on bacterial populations and N mineralization under varying moisture regimes. Sterilized loamy sand was used as substrate. Their experiment clearly illustrated that in the presence of protozoa, N was mineralized to a far greater extent than in their absence, except where soil moisture content fell below 7% (v/v). Both reduced accessibility of protozoa to bacteria in pores lacking water and the disruption of protozoan cellular metabolism were suggested as reasons for the reduced rates of N released under low moisture conditions.

The effects of enchytraeid worms were studied in microcosms containing grassland litter, soil or both together (Forster et al. 1995). The combination of soil, litter and enchytraeid worms induced the highest production of \( \text{CO}_2 \), although microbial biomass at the end of the experiment was the smallest in this system. The effect of combining the three components was synergistic as adding up the \( \text{CO}_2 \) produced from the three one component systems gave a smaller number. Addition of \( \text{KNO}_3 \) induced a respiration rate
similar to that of adding enchytraeids, suggesting that the worms enhanced the growth of active microbial biomass.

**Complex systems**

Of primary importance in studying the faunal role in nutrient cycling is the interactions between faunal groups and between the microbial and faunal populations. For this reason, microcosm-based experiments should include a complex community of organisms if the study is going reflect the field. Individual effects of each faunal group are difficult to assess in these systems. Complex systems provide results that differ from those of simple systems (Laakso et al. 1995; Hyvonen & Persson, 1996). This can be attributed to the dynamics that exist within the soil food web, with predator-prey dynamics and a varied microbial response to faunal activities. Setala and Huhta (1990) emphasized the importance of complex faunal populations in microcosm experiments. He also suggested that soil structural properties should be simulated as faunal behavior is greatly affected by spatial constraints, as well as a host of other soil properties.

Setala et al. (1991) studied the mineralization of C, N and P in one- and two-component faunal systems in a coniferous forest soil. The microcosms contained nematodes, enchytraeids or collembolans alone or in combination. The effect of predatory nematodes on microbivorous nematode activity was also tested. All two-component systems produced more CO₂ than the control, which contained microbes and protozoans, suggesting that predation of the decomposer community increased overall respiration. Nutrient leaching in this study was not significantly enhanced in the presence of fauna although two-component systems leached more nutrients than their single-component
activity. Other studies have noted significant correlations between microbial biomass and
the abundance of soil fauna (Setala et al., 1991; Hanlon and Anderson, 1979), often
suggesting that this is due to faunal grazing and its varied impacts on the microbial
population. Abiotic variables in the study by Sulkava et al. (1996) may have clouded any
faunal effects. Nitrogen mineralization correlated well with enchytraeid biomass in both the
simple and complex systems. Setala et al. (1991) noted enhanced release of N from
coniferous forest soil material in the presence of enchytraeids, beyond that released due to
collembolan activity. Enchytraeid worms are important members of the faunal community,
both in terms of their abundance and role in the break down of organic matter (Dash,
1990). Like termites and larger worms, enchytraeids can alter the physical structure of
soil, although to a lesser degree.

Using 3-mm mesh litter bags, Hasegawa and Takeda (1996) assessed the dynamics
of decomposing pine litter in a four year field study. Fungal growth correlated well with
immobilization of N and P roughly from the third to the eighteenth month of
decomposition. This was also the period of faunal population growth, suggesting that
grazing contributed to fungal stimulation and concomitant immobilization of nutrients.
Faunal densities generally increased as decomposition progressed, with mites and
collembola being dominant.

Blair et al. (1985) studied decomposition of three types of litter, separately and in
all possible combinations, in litterbags. Dynamics of N in mixed vs. single species litter
showed significant differences. The initial release of N was greater in mixed litterbags,
and less N was immobilized at later stages of decomposition. The fungivorous nematode
population was significantly larger in mixed litter samples and fungal abundance was
significantly smaller. A relationship between nematode numbers, fungal abundance and N release was suggested and related to the effects of mixing species of litter. The authors found little to support the hypothesis that soil faunal abundance is correlated with litter mass loss.

Setala et al. (1996) assessed the effect of different faunal assemblages on decomposition and N mineralization. By using $^{15}$N tagged Douglas-fir litter and litter baskets embedded within a pot of forest floor material they were able to track the movement of material into and out of the litter baskets. Inclusion of macrofauna did not increase mass loss or N mineralization and the authors suggested that the greatest influence on these processes was through the regulation of microorganisms, this being effected largely by collembola, mites, nematodes and enchytraeids.

Single- and two-component studies aid in understanding the existence of interactions between faunal groups but present a somewhat artificial snapshot of faunal activities in the soil. Field research is far more laborious and difficult to interpret but gives more realistic results. Mesocosms provide a system that allows for greater variability in experimental conditions. Vedder et al. (1996) conducted an eight-month mesocosm study in the field. They used defaunated soil monoliths and controlled for faunal migration-emigration by wrapping the monoliths in nets of various mesh sizes. Substrate-induced respiration and fumigation-extraction were used to assess characteristics of the microbial population. These methods correlated well in systems containing only a microbial population but in the presence of soil fauna only substrate-induced respiration was enhanced. Soil fauna therefore stimulated microbial activity but not biomass. An increase in the N turnover rate further supported this conclusion. Microbial N mineralization
during an anaerobic incubation was not significantly enhanced by soil fauna although extractable $\text{NH}_4^+$ was, suggesting that faunal excretion could account for the increased $\text{NH}_4^+$ in the system. This study also demonstrated the impact of earthworms on N mineralization; both extractable $\text{NH}_4^+$ and microbial N were enhanced in their presence.

RATIONALE FOR THE PRESENT STUDY

Little is known about the relationships between tree species, soil faunal activities, and rates of decomposition and N mineralization. In general, the diversity of soil mesofauna (mites, collembola and enchytraeids) increases from deciduous to coniferous forest soils (Paquin and Coderre, 1997; Seastedt, 1984). Blair et al. (1994) found significant differences among the soil faunal populations of three tree species and a mixed forest. The differences were related to forest floor characteristics such as pH, organic matter content, moisture content and bulk density. Faunal activity seems to prevent the use of decomposition and N mineralization rates in pure litter to predict these rates in mixed litter (Blair et al., 1990; Saetre, 1998). This would suggest that soil fauna are key organisms in unraveling the mysteries of these soil processes.

Faunal-mediated nitrogen dynamics and interactions with resource quality have not been studied in coastal B.C. forests. Single-species stands on the same site provide for such an assessment. Pure stands of western red cedar, western hemlock, Douglas-fir and Sitka spruce on the west coast of Vancouver island were used for this study. This study has employed microcosms in which temperature and moisture were controlled. Soils formed under the four tree species were defaunated and then fauna were added at three levels: 1) microorganisms only, 2) microorganisms, soil mites, collembola, enchytraeids
and nematodes, and 3) all of the above plus a millipede (*Harpaphe haydeniana*).

Indices of N mineralization and decomposition were measured over a 5-month period.

The objectives of this study were: 1) to compare rates of decomposition and N mineralization in the presence and absence of soil fauna, and to discover the importance of *Harpaphe haydeniana*, a millipede common to the west coast of Canada and the northern United States, with respect to these rates, 2) to determine if the faunal influences were consistent with different types of soil (i.e., under different tree species), and 3) to examine N mineralization and decomposition in forest floors under common tree species in coastal BC.
Soil was collected from an area on the west coast of Vancouver Island, British Columbia. The site (UK Main) is near Franklin River (latitude 48° 50'-54’N; longitude 124° 46'-54’W; elevation m). The area is located within the Windward Submontane Maritime Wetter Coastal Western Hemlock variant (Klinka et al. 1991). The climate is cool and wet and the soils Humo-Ferric or Ferro-Humic Podzols. The original old-growth forest of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn) and Sitka spruce (*Picea sitchensis* (Bong.) Carr) was logged between 1958 and 1960, and slashburned in 1961. In 1962, 81 seedlings were planted in each plot, in 9 rows of 9 trees. Two plots of each tree species (Sitka spruce, western red cedar, western hemlock and Douglas-fir) were planted at 3 spacings (2.7 m, 3.7 m and 4.7 m) resulting in a total of 24 plots. The 8 plots with a spacing of 3.7 m were used for this experiment.

METHODS

EXPERIMENTAL DESIGN

Four soil types and three faunal treatments were established. There were 6 microcosms of each soil type x faunal treatment combination, for a total of 72 microcosms.
On October 24 and November 11, 1997, soil samples were collected from the two plots of each tree species (soil type). The sampling was staggered to facilitate the survival of soil fauna, as only half of the full number of samples could be processed at once. Sampling was spread between two plots for each soil type, and collection was random within each plot. Thirty intact soil cores (10 cm high and 10 cm in diameter) per soil type were collected and placed into plastic pots (12.7 cm high and 12.7 cm in diameter). The samples consisted of forest floor material and 1-2 cm of mineral soil. Eighteen of the thirty soil cores were used as microcosms and the remaining 12 were used for extracting mesofauna (mites and collembola). An additional 12 soil samples per soil type, similar in size to the cores, were collected to extract microfauna (nematodes and enchytraeids). Finally, 6 bulked soil samples per soil type were collected for microbial inoculations and chemical analysis. All samples were kept cool and were stored for no more than 8 days before being processed.
Several methods have been used to defaunate soil samples and usually one settles for a reduction in faunal numbers. Freezing to -80 °C is time-consuming and requires significant freezer space. Freezing with liquid nitrogen (-196 °C) has been used with some success although references to samples as large as 10 x 10 cm do not exist. This method was decided upon as freezer space was limited. Liquid nitrogen was poured into each sample until the liquid no longer evaporated upon contact, and the assumption was made that the sample had reached -196 °C (the core temperature of several samples was measured to verify that the sample had reached -196 °C). Following freezing each microcosm was remoistened as freezing tended to leave the soil very dry.

To reinoculate the soils with microorganisms, 60 g of humus from the forest floor of each tree species was blended for 30 seconds in 500 mL of tap water. The soil and water suspension was then filtered through a 10 μm filter to eliminate nematodes and enchytraeids. Fifty mL of the suspension was then added to the appropriate microcosm and left for 5-6 days to allow for colonization.

A modified Burleson funnel method was used to extract microfauna. Soil samples were placed in 1 L plastic containers with 54 μm mesh closing one end. These were then immersed in water-filled containers until the water just covered the soil. This apparatus was placed under heating lamps and cool water was circulated around the base of the containers. The extraction lasted 24 h whereupon the extracted nematodes and enchytraeids were added along with some water, to the appropriate microcosms.
Mesofauna extractions were carried out with the use of a modified Tullgren funnel. The soil cores were separated into three parts, inverted and placed into polyester tubing with mesh (2-mm openings) closing the bottom. The tubes were placed under a heat lamp which slowly dried the soil, causing the fauna to move away from the heat source and thereby fall into the collection vial that was bathed in cool water. The mesofauna were collected daily and all mites and collembola were added to the intact soil core corresponding to the soil from which they were extracted.

Millipedes (*Harpaphe haydeniana haydeniana*) were collected in October, 1997 from the Malcolm Knapp Research Forest of the University of British Columbia. The forest is located in the District Municipality of Maple Ridge and lies within the Coastal Western Hemlock biogeoclimatic zone. The millipedes were added to one-third of the microcosms (6 microcosms per soil type), resulting in the addition of 24 millipedes.

Birch leaf litter was used to estimate the rate of decomposition. Intact but senesced leaves were rinsed thoroughly under tap water and air-dried. Between 0.1 and 0.25 g (d.w.) were then placed under the top 2-4 cm of forest floor material in each microcosm.

Three-week-old cabbage (*Brassica oleracea* var. *capitata*) plants grown from seed. On January 4, 1998 they were weighed and one was planted in each microcosm. Cabbage was chosen because it is non-mycorrhizal and fast-growing. Including a mycorrhizal plant could have confounded results for plant N content as some soil fauna would have grazed the hyphae.

On January 5, 1998 all 72 microcosms were placed in the “controlled” environment of the UBC greenhouse for five months. The soil was kept moist throughout the experiment.
experiment. The temperature was relatively stable at 18 °C and the room received 18 hours of light/day. Between May 5 and June 1, 1998, all microcosms were destructively sampled in batches of 12 (one replicate of each treatment combination).

LABORATORY ANALYSES

Prior to and following the 5-month incubation, soil samples were extracted with a 2M KCl solution (2:1 KCl:soil by volume), filtered to remove all particulate material and analysed for nitrate and ammonium concentrations on a Lachat autoanalyser.

At monthly intervals during the incubation, 100 mL of tap water was poured evenly over the surface of each microcosm and the exiting solution was collected, filtered and analysed for $\text{NO}_3^-\text{-N}$ and $\text{NH}_4^+$-N concentrations the same day using the Lachat autoanalyser.

The weight of the cabbage plant in each microcosm was measured after the roots were washed free of soil and the whole plant was oven-dried for 48 h at 80 °C. The plants were digested according to the semi-microKjeldahl method (Bremner and Mulvaney, 1982) and N concentrations were measured with the Lachat autoanalyzer.

To estimate the rate of decomposition all fragments of the added birch leaves were collected, rinsed, air-dried, weighed and compared to the initial weight.

Following harvesting of the plant and birch leaf fragments, rocks and twigs were removed from each microcosm and the soil was sieved through a 2 cm mesh. Initial and final moisture contents were calculated after oven-drying the soil at 100 °C for 24 h.

Samples collected for N and pH analyses were frozen, while those collected for microbial
analyses were refrigerated for no more than 24 h. Mites and collembola were extracted as described above from 40-60 g (wet mass) of soil and preserved in 80% ethanol until they could be counted. A 20-30 g (wet mass) sample of soil was used to assess nematode and enchytraeid numbers (as described above)

The active microbial biomass of each sample was determined by the substrate-induced respiration (SIR) technique (Anderson and Domsch, 1978). Five-gram (dry mass equivalent) portions of each sample were placed in canning jars (Kerr wide mouth, 1 pint (0.6 dm$^3$)) and sealed with air-tight lids mounted with rubber septa. The soil was left at 22 °C for one hour, after which time a 1 mL portion of the headspace was removed with a syringe and the concentration of CO$_2$ measured with a model infrared gas analyzer (Clegg et al. 1978). Ten mL of a 40 g L$^{-1}$ glucose solution was then added to each soil sample, resulting in the addition of 80 mg glucose per g of sample. Prior to this the soil was tested to determine the glucose concentration necessary to provide maximum respiration, as outlined by Anderson and Domsch (1978). CO$_2$ was then measured every hour for the next 2 hours. Carbon dioxide was converted to mg of carbon respired per g of sample in one hour using the equation: $R = AC \cdot V \cdot K / (T \cdot W)$.

Where: $\Delta C =$ change in CO$_2$ concentration in head space air (uL/L)
$V =$ volume of jar (0.4 L)
$K =$ conversion factor $5.35 \times 10^{-4}$ mg C/uL CO$_2$
$T =$ time in hours
$W =$ dry mass of soil sample (g)
To convert to active microbial biomass the equation: $x = 40.4y + 0.37$ was used, where $x$ is the active microbial biomass in mg/g and $y$ is the CO$_2$ respired in mg.g$^{-1}$.h$^{-1}$ (Anderson and Domsch, 1978).

STATISTICAL ANALYSIS

All indices were evaluated as to the effects of fauna, soil type and the presence of an interaction between these factors with 3 by 4 factorial analysis of variance followed by Duncan’s multiple range test. The factors were: 3 fauna treatments and 4 soil types. Homogeneity of variances were tested by Levene’s test. SPSS for Windows was used for all calculations. Due to the considerable variability in most measurements, the accepted level of significance was $p<0.1$.

RESULTS

COMPARISON OF FAUNA TREATMENTS

The various indices of N mineralization and decomposition are compared among faunal treatments in Table 1. Soil moisture and pH did not differ among fauna treatments. Concentrations of KCl-extractable NH$_4^+$-N and NO$_3^-$-N at the end of 5 months did not differ significantly between fauna treatments. There was a trend however, with concentrations of NH$_4^+$-N and NO$_3^-$-N, and their total being greatest in treatment 3 (mesofauna and $H. h. haydeniana$) and least in treatment 1 (defaunated) (Fig. 1).
Letters indicate a significant difference among fungi treatments at P<0.1. Values are averages and (standard deviations) of the four soil types (n=24).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Plant N content (%)</th>
<th>Total N (mg)</th>
<th>NH₄⁺-N (mg)</th>
<th>Extractable N (mg)</th>
<th>Microbial biomass (mg)</th>
<th>Total lignin (%)</th>
<th>Microbial N (%)</th>
<th>Total N (%)</th>
<th>Extractable N (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fungi</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Defaunated</td>
<td>3.8 (0.3)</td>
<td>2.3 (1.1)</td>
<td>0.7 (0.3)</td>
<td>3.9 (0.3)</td>
<td>2.9 (1.9)</td>
<td>11.0 (1.0)</td>
<td>9.6 (0.9)</td>
<td>11.1 (0.4)</td>
<td>1.3 (1.2)</td>
</tr>
<tr>
<td>Fungi</td>
<td>3.3 (0.1)</td>
<td>2.7 (1.7)</td>
<td>0.9 (0.3)</td>
<td>3.4 (0.3)</td>
<td>2.6 (1.9)</td>
<td>11.3 (1.1)</td>
<td>9.7 (0.9)</td>
<td>11.1 (0.4)</td>
<td>1.5 (1.2)</td>
</tr>
<tr>
<td>Fungi</td>
<td>3.3 (0.1)</td>
<td>2.7 (1.7)</td>
<td>0.9 (0.3)</td>
<td>3.4 (0.3)</td>
<td>2.6 (1.9)</td>
<td>11.3 (1.1)</td>
<td>9.7 (0.9)</td>
<td>11.1 (0.4)</td>
<td>1.5 (1.2)</td>
</tr>
<tr>
<td>Microcosm</td>
<td>3.3 (0.1)</td>
<td>2.7 (1.7)</td>
<td>0.9 (0.3)</td>
<td>3.4 (0.3)</td>
<td>2.6 (1.9)</td>
<td>11.3 (1.1)</td>
<td>9.7 (0.9)</td>
<td>11.1 (0.4)</td>
<td>1.5 (1.2)</td>
</tr>
<tr>
<td>Microcosm</td>
<td>3.3 (0.1)</td>
<td>2.7 (1.7)</td>
<td>0.9 (0.3)</td>
<td>3.4 (0.3)</td>
<td>2.6 (1.9)</td>
<td>11.3 (1.1)</td>
<td>9.7 (0.9)</td>
<td>11.1 (0.4)</td>
<td>1.5 (1.2)</td>
</tr>
<tr>
<td>Microcosm</td>
<td>3.3 (0.1)</td>
<td>2.7 (1.7)</td>
<td>0.9 (0.3)</td>
<td>3.4 (0.3)</td>
<td>2.6 (1.9)</td>
<td>11.3 (1.1)</td>
<td>9.7 (0.9)</td>
<td>11.1 (0.4)</td>
<td>1.5 (1.2)</td>
</tr>
<tr>
<td>Microcosm</td>
<td>3.3 (0.1)</td>
<td>2.7 (1.7)</td>
<td>0.9 (0.3)</td>
<td>3.4 (0.3)</td>
<td>2.6 (1.9)</td>
<td>11.3 (1.1)</td>
<td>9.7 (0.9)</td>
<td>11.1 (0.4)</td>
<td>1.5 (1.2)</td>
</tr>
</tbody>
</table>

Table 1. Indicators of nitrogen mineralization and decomposition in the three fungi treatments.
Figure 1. KCl-extractable NH$_4$-N, NO$_3$-N and NH$_4$-N + NO$_3$-N in each faunal treatment at the end of the 5-month incubation (1 = defaunated, 2 = mesofauna, 3 = mesofauna + millipede). Bars represent standard deviations from the mean (n=24). There were no significant differences between faunal treatments at p<0.1.
Neither NH\textsubscript{4}\textsuperscript{+}-N, NO\textsubscript{3}\textsuperscript{-}-N or the total NH\textsubscript{4}\textsuperscript{+}-N and NO\textsubscript{3}\textsuperscript{-}-N leached over 5 months differed significantly between treatments, but the same trend was apparent: treatment 3 mineralized the most N and treatment 1 the least (Fig. 2). Plant weight was greatest in treatment 2, while both treatments 1 and 3 had equal plant weights (Fig. 3). Nitrogen concentrations of plants in treatment 1 were high while those of treatment 2 were the low (Fig. 3). As a result, plant N content was greatest in treatment 2 due to the comparatively large plants (Fig. 3). Treatment 3 plants, although having high concentrations of N, had low plant N contents due to the small size of the plants.

The total amount of N mineralized during the incubation (leached N + final KCl-extractable N + plant N content) was not significantly different between treatments, but followed the predominant trend with treatment 3 mineralizing the most N and treatment 1 the least (Fig. 4).

Percent mass loss of birch leaves was significantly greater in treatment 3 than treatment 1 (Fig. 5). There were no differences among treatments in microbial biomass.

Collembola were significantly more numerous in the millipede treatment than in the defaunated soil. Mites were significantly more numerous in both the millipede and mesofaunal treatments than in the defaunated soil (Table 2).

**Table 2.** Abundance of soil fauna in each fauna treatment.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Collembola (per g)</th>
<th>Mite (per g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Defaunated</td>
<td>0.03 (0.08) \textit{b}</td>
<td>0.16 (0.21) \textit{b}</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>0.21 (0.36) \textit{ab}</td>
<td>0.86 (1.17) \textit{a}</td>
</tr>
<tr>
<td>Mesofauna &amp; millipede</td>
<td>0.53 (0.95) \textit{a}</td>
<td>1.22 (1.33) \textit{a}</td>
</tr>
</tbody>
</table>

Values are averages and (standard deviations) of the four soil types (\textit{n}=24). Letters indicate a significant difference among fauna treatments at p<0.1.
Figure 2. Mean values of NH$_4$-N, NO$_3$-N and NH$_4$-N + NO$_3$-N leached from each fauna treatment during the 5-month incubation (1 = defaunated; 2 = mesofauna; 3 = mesofauna + millipede). Bars represent standard deviations from the mean ($n$=24). There were no significant differences between fauna treatments at $p<0.1$. 
Figure 3. Weight, N-concentration and N-content of plants grown for the 5-month incubation in each fauna treatment (1 = defaunated; 2 = mesofauna; 3 = mesofauna + milliped). Bars represent standard deviations from the mean ($n=24$). There were no significant differences between fauna treatments at $p<0.1$. 
Figure 4. Total N mineralized in each fauna treatment during the 5-month incubation. (1 = defaunated; 2 = mesofauna; 3 = mesofauna + millipede). Bars represent standard deviations from the mean ($n=24$). There were no significant differences between fauna treatments at $p<0.1$. 

Fauna treatment

Total N mineralized (mg)
Figure 5. Decomposition of birch leaves over a 5-month period in each faunal treatment (1: defaunated, 2: mesofauna, 3: mesofauna + millipede). Bars represent standard deviations from the mean ($n=24$). The letters indicate a significant difference between faunal treatments at $p<0.1$. 

Mass loss (%)
The effects of the three faunal treatments on mineralization are presented separately for each soil type (tree species) in Tables 3 to 6. There were few significant differences among faunal treatments, but where they existed the four indicated greater N mineralization in treatment 3 than treatment 1. In cedar soils, KCl-extractable NH\textsubscript{4}\textsuperscript{+}-N was significantly greater in treatment 3 than treatment 1 (Table 3). The NO\textsubscript{3}\textsuperscript{-}-N leached from hemlock (Table 4) and from Douglas-fir soils (Table 6) over 5 months was significantly greater in treatment 3 than in treatment 1. In spruce soils (Table 5), microbial biomass was significantly greater in treatment 3 than in treatment 1.

COMPARISON OF SOIL TYPES

For all faunal treatments together, hemlock soil contained significantly more moisture than Sitka spruce; cedar and Douglas-fir were intermediate (Table 7). KCl-extractable NH\textsubscript{4}\textsuperscript{+}-N concentrations did not differ significantly between soil type, although concentrations were generally greatest in hemlock and least in Sitka spruce soils (Fig. 6). KCl-extractable NO\textsubscript{3}\textsuperscript{-}-N concentrations were significantly greater in cedar and Douglas-fir soils than in Sitka spruce. Total KCl-extractable N (NH\textsubscript{4}\textsuperscript{+}-N + NO\textsubscript{3}\textsuperscript{-}-N) concentrations in cedar, hemlock and Douglas-fir soil were significantly higher than those in spruce soil. Cedar soils leached significantly more NH\textsubscript{4}\textsuperscript{+}-N and NO\textsubscript{3}\textsuperscript{-}-N than spruce, hemlock and Douglas-fir (Fig. 7). The total amount of N (NH\textsubscript{4}\textsuperscript{+}-N + NO\textsubscript{3}\textsuperscript{-}-N) leached was greatest in cedar soils and least in Sitka spruce soil (Fig. 7).
<table>
<thead>
<tr>
<th>Treatment</th>
<th>Millipede</th>
<th>Microcosm (mg)</th>
<th>Microcosm (%)</th>
<th>Plan N</th>
<th>KCl-extractable</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meiospora</td>
<td>3.4</td>
<td>6.57 (3.2)</td>
<td>0.62 (1.04)</td>
<td>1.69 (1.57)</td>
<td>1.83 (1.75)</td>
</tr>
<tr>
<td>Defenestrated</td>
<td>2.9</td>
<td>6.89 (2.86)</td>
<td>0.10 (0.07)</td>
<td>1.60 (1.45)</td>
<td>1.34 (0.62)</td>
</tr>
<tr>
<td></td>
<td>0.42</td>
<td>0.42 (0.11)</td>
<td>0.36 (0.08)</td>
<td>0.38</td>
<td>0.34 (0.14)</td>
</tr>
</tbody>
</table>

Letters indicate a significant difference among fauna treatments at p<0.1.

Table 3: Indices of N mineralization and decomposition in western reedbed forest floor microcosms in the three fauna treatments.
Letters indicate a significant difference among fauna treatments at \( p < 0.1 \).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Micromass (mg)</th>
<th>Mass loss (%)</th>
<th>Nitrification (mg N/mg)</th>
<th>NH4+ (mg NH4+)</th>
<th>NO3- (mg NO3-)/N</th>
<th>Extractable N</th>
<th>KCl- N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Planar</td>
<td>(g)</td>
<td>(%)</td>
<td>(mg)</td>
<td>(mg)</td>
<td>(mg)</td>
<td>(mg)</td>
<td>(mg)</td>
</tr>
<tr>
<td>Planar, Artificialized</td>
<td>8.24 (3.05)</td>
<td>2.9 (1.2)</td>
<td>1.09 (0.36)</td>
<td>0.69 (1.19)</td>
<td>0.94 (0.88)</td>
<td>5.28 (5.97)</td>
<td>7.0 (6.17)</td>
</tr>
<tr>
<td>Planar, Natural</td>
<td>7.7 (2.53)</td>
<td>2.3 (1.3)</td>
<td>0.27 (0.29)</td>
<td>2.11 (1.82)</td>
<td>0.33 (0.42)</td>
<td>6.9 (1.75)</td>
<td>15.89 (1.42)</td>
</tr>
<tr>
<td>Planar, Artificial N</td>
<td>6.23 (5.48)</td>
<td>2.0 (1.1)</td>
<td>0.27 (0.29)</td>
<td>2.11 (1.82)</td>
<td>0.33 (0.42)</td>
<td>6.9 (1.75)</td>
<td>15.89 (1.42)</td>
</tr>
<tr>
<td>Planar, Natural N</td>
<td>7.7 (2.53)</td>
<td>2.3 (1.3)</td>
<td>0.27 (0.29)</td>
<td>2.11 (1.82)</td>
<td>0.33 (0.42)</td>
<td>6.9 (1.75)</td>
<td>15.89 (1.42)</td>
</tr>
</tbody>
</table>

Table 4. Indices of mineralization and decomposition in Western hemlock forest floor microcosms in the three fauna treatments.
Table 5. Indices of N mineralization and decomposition in Sitka-spurce forest floor microcosms in the three luna treatments

<table>
<thead>
<tr>
<th>Treatment</th>
<th>microcosm (%)</th>
<th>microcosm (mg)</th>
<th>microcosm (mg)</th>
<th>microcosm (mg)</th>
<th>microcosm (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant N</td>
<td>N↑, N↓</td>
<td>N↑, N↓</td>
<td>N↑, N↓</td>
<td>N↑, N↓</td>
<td>N↑, N↓</td>
</tr>
<tr>
<td>Total N</td>
<td>N↑, N↓</td>
<td>N↑, N↓</td>
<td>N↑, N↓</td>
<td>N↑, N↓</td>
<td>N↑, N↓</td>
</tr>
<tr>
<td>Treatment</td>
<td>Mass loss (%)</td>
<td>Micromass (mg/ft²)</td>
<td>Microcosm immobilized N (mg/ft²)</td>
<td>Microcosm total N (mg/ft²)</td>
<td>Plant N (%)</td>
</tr>
<tr>
<td>-----------</td>
<td>--------------</td>
<td>-------------------</td>
<td>-----------------</td>
<td>----------------------</td>
<td>-------------</td>
</tr>
<tr>
<td>Mesostalina a</td>
<td>2.73 (1.64)</td>
<td>0.42 (0.18)</td>
<td>1.25 (1.08)</td>
<td>2.10 (1.43)</td>
<td>0.76 (0.63)</td>
</tr>
<tr>
<td>Mesostalina b</td>
<td>2.73 (1.64)</td>
<td>0.42 (0.18)</td>
<td>1.25 (1.08)</td>
<td>2.10 (1.43)</td>
<td>0.76 (0.63)</td>
</tr>
<tr>
<td>Defaunated</td>
<td>2.73 (1.64)</td>
<td>0.42 (0.18)</td>
<td>1.25 (1.08)</td>
<td>2.10 (1.43)</td>
<td>0.76 (0.63)</td>
</tr>
</tbody>
</table>

Letters indicate a significant difference among fauna treatments at p<0.1.

Table 6. Indices of nitrogen mineralization and decomposition in Douglas-fir forest floor microcosms in the three fauna treatments.
Values are averages and (standard deviations) of the three replicate treatments \( (n=18) \).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Sika spruce</th>
<th>Hemlock</th>
<th>Western cedar</th>
<th>Douglas fir</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Microcosm</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mass</strong></td>
<td>20.95 (6.89)</td>
<td>19.35 (15.83)</td>
<td>20.52 (17.33)</td>
<td>20.27 (15.74)</td>
</tr>
<tr>
<td><strong>Biomass</strong></td>
<td>1.27 (0.9)</td>
<td>1.23 (0.9)</td>
<td>1.21 (0.9)</td>
<td>1.23 (0.9)</td>
</tr>
<tr>
<td><strong>Nitrogen</strong></td>
<td>13.3 (2.1)</td>
<td>13.2 (2.1)</td>
<td>13.2 (2.1)</td>
<td>13.2 (2.1)</td>
</tr>
<tr>
<td><strong>Microbial Mass</strong></td>
<td>1.4 (0.5)</td>
<td>1.4 (0.5)</td>
<td>1.4 (0.5)</td>
<td>1.4 (0.5)</td>
</tr>
<tr>
<td><strong>Extractable N</strong></td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
</tr>
<tr>
<td><strong>Total N</strong></td>
<td>1.9 (0.5)</td>
<td>1.9 (0.5)</td>
<td>1.9 (0.5)</td>
<td>1.9 (0.5)</td>
</tr>
<tr>
<td><strong>Total KCl</strong></td>
<td>1.0 (0.5)</td>
<td>1.0 (0.5)</td>
<td>1.0 (0.5)</td>
<td>1.0 (0.5)</td>
</tr>
<tr>
<td><strong>NH4+</strong></td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
</tr>
<tr>
<td><strong>NO3-</strong></td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
</tr>
<tr>
<td><strong>K+</strong></td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
</tr>
<tr>
<td><strong>Ph</strong></td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
</tr>
<tr>
<td><strong>Moisture</strong></td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
<td>1.6 (0.5)</td>
</tr>
</tbody>
</table>

*Letters indicate a significant difference among soil types at \( p<0.1 \).*

**Table 7.** Indices of N mineralization and decomposition in the four soil types.
Figure 6. KCl-extractable NH$_4^+$-N, NO$_3^-$-N and NH$_4^+$-N + NO$_3^-$-N in each soil type (tree species) at the end of the 5-month incubation (Cw = western redcedar; Hw = western hemlock; Ss = Sitka spruce; Fd = Douglas-fir). Bars represent standard deviations from the mean ($n=18$). Letters indicate a significant difference between soil types at $p<0.1$. 
Figure 7. Mean values of $\text{NH}_4$-$\text{N}$, $\text{NO}_3$-$\text{N}$ and $\text{NH}_4$-$\text{N} + \text{NO}_3$-$\text{N}$ leached from each soil type (tree species) during the 5-month incubation (Cw = western redcedar; Hw = western hemlock; Ss = Sitka spruce; Fd = Douglas-fir). Bars represent standard deviations from the mean ($n=18$). Letters indicate a significant difference between soil types at $p<0.1$. 
The average weight of plants in Sitka spruce soils was significantly greater than in the other three soils (Fig. 8). Plant N concentrations were significantly greater in cedar soils than in spruce soils (Fig. 8). The N contents of plants in Sitka spruce and Douglas-fir soils were significantly greater than those in cedar and hemlock soils (Fig. 8).

The total N mineralized (KCl-extractable + leachate + plant content) in Douglas-fir soils was significantly greater than that mineralized in spruce and hemlock soils (Fig. 9).

There were no significant differences among soil types in mass loss from birch leaves during the 5-month incubation (Fig. 10). The microbial biomass of Douglas-fir soils was significantly larger than cedar and hemlock soils (Fig. 11).

Abundances of collembola and mites followed the same trend, with Douglas-fir harboring the greatest number of mesofauna, and cedar the least (Table 8).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Collembola (per g)</th>
<th>Mite (per g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>western red cedar</td>
<td>0.03 (0.09) b</td>
<td>0.48 (0.77)</td>
</tr>
<tr>
<td>western hemlock</td>
<td>0.18 (0.28) ab</td>
<td>0.63 (0.72)</td>
</tr>
<tr>
<td>Sitka spruce</td>
<td>0.10 (0.20) ab</td>
<td>0.91 (1.17)</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>0.71 (1.10) a</td>
<td>0.97 (1.58)</td>
</tr>
</tbody>
</table>

Values are averages and (standard deviations) of the three fauna treatments (n=18). Letters indicate a significant difference among soil type at p<0.1.
Figure 8. Weight, N-concentration and N-content of plants grown for the 5 month incubation in each soil type (tree species) (Cw = western redcedar; Hw = western hemlock; Ss = Sitka spruce; Fd = Douglas-fir). Bars represent standard deviations from the mean ($n=18$). Letters indicate a significant difference between soil types at $p<0.05$. 
Figure 9. Total N mineralized in each soil type (tree species) during the 5-month incubation (Cw = western redcedar; Hw = western hemlock; Ss = Sitka spruce Fd = Douglas-fir). Bars represent standard deviations from the mean ($n = 18$). Letters indicate a significant difference between soil types at $p<0.1$. 
Figure 10: Decomposition of birch leaves over the 5-month incubation in each soil type (tree species) (Cw = western redcedar; Hw = western hemlock; Ss = Sitka spruce; Fd = Douglas-fir). Bars represent standard deviations from the mean ($n=18$). There were no significant differences between soil type at $p<0.1$. 
Figure 11. Microbial biomass in each soil type (tree species) at the end of the 5-month incubation (Cw = western redcedar; Hw = western hemlock; Ss = Sitka spruce; Fd = Douglas-fir). Bars represent standard deviations from the mean (n=18). Letters indicate a significant difference between soil types at p<0.1.
DISCUSSION

The trends apparent in this study support the idea that soil fauna stimulate N mineralization. Both leachate and KCl-extractable NH$_4^+$-N and NO$_3^-$-N concentrations were enhanced in the presence of soil fauna. In general, the literature provides evidence in support of the idea that soil fauna increase rates of N mineralization. Ineson et al (1982) found a positive correlation between collembolan density and N release. Sulkava et al. (1991) noted an increase in N mineralization in the presence of enchytraeid worms. More complex systems, i.e., microcosms where several faunal populations are represented, provide somewhat more variable results, although again the overriding indication is that fauna increase the release of N. I would suggest two possible mechanisms for the increased rates of N mineralization in the present study. Firstly, direct addition of nutrients via faunal excretion was likely related to the enhanced concentrations of available N; N immobilized in microbial tissue and organic matter is released through faunal grazing and excretion (Persson, 1989). Faber and Verhoef (1992) showed that NO$_3^-$-N in collembolan and isopod feces was 2.4 times greater than in the original food source. By comparing the influence of soil fauna on leached NH$_4^+$-N and the N mineralized through anaerobic incubation, Vedder et al. (1996) were able to show that greater concentrations of N in the presence of soil fauna were due to faunal excretion. Secondly, increasing the faunal complexity may have stimulated microbial activity (Ineson et al. 1982) and encouraged its development to a more diverse population. In a similar study (Hector Carcamo, pers. comm.) greater “richness” and “activity” of microbial cells (based on the
The millipede plus soil fauna treatment enhanced N availability to a greater extent than did the soil fauna alone. Carcamo (unpublished) noted higher levels of available \( \text{NH}_4^+ -\text{N} \) and \( \text{NO}_3^- -\text{N} \) in millipede feces than in the uneaten litter. The elevated levels of available N may have encouraged microbial growth, a factor that could explain the significantly greater abundance of soil fauna in microcosms containing a millipede. Also, physical changes to the soil caused by millipede activity may have influenced abiotic factors important in N mineralization and further enhancing this process. It was observed that \( H. \ h. \ haydeniana \), like termites and worms (Lavelle, 1997), significantly altered the physical state of the soil. Few studies have addressed the potential influence of \( H. \ h. \ haydeniana \) on soil processes. In view of the present findings, further study of these millipedes would certainly enhance our understanding of west coast forests.

Both decomposition and N mineralization increased with faunal complexity, in accordance with several other studies of the direct and indirect effects of faunal activity on decomposition and N mineralization (Anderson, 1988; Santos and Whitford, 1981; Lavelle, 1997). Fragmentation of litter by soil fauna and its redistribution through excretion provides material with high surface area to the microbial populations, which can enhance microbial growth and hence the release of C and possibly N. Carbon from cabbage root exudates was supplied to the microbial population to prevent any decline in microbial growth due to C limitation (Grayston and Jones, 1996) and to help encourage efficient decomposition and N mineralization. However, a plentiful supply of C may also
lead to N immobilization hence low rates of net N mineralization. For example, in Sitka-spruce soils rates of net N mineralization were low but the cabbage plants grew to be very large and there was a large microbial biomass. The C exuded from the cabbage roots may have promoted a larger microbial population with a high N requirement, leading to immobilization of N in the microbial tissue in Sitka-spruce soils. Mikola and Setala (1998) found that the addition of C as glucose to microcosms containing microbes and microbivorous nematodes increased both the microbial and the nematode populations and reduced the release of N. Microbial respiration was also stimulated by faunal grazing.

The active microbial biomass was assessed to discover the mechanisms responsible for higher rates of N mineralization and decomposition in the presence of soil fauna. Substrate-induced-respiration did not differ significantly between faunal treatments. This both supports (Vreeken-Buijs et al., 1997; Alphei et al., 1996) and contradicts other studies (Setala et al., 1991; Bengtsson et al., 1988). Mikola and Setala (1998, 1998a) noted an increase in microbial biomass in the presence of one species of bactivorous and one species of fungivorous nematode. Upon further examination they found that nematode grazing did not affect the bacterial biomass, whereas the fungal biomass had increased. The observed increase in microbial biomass therefore was largely a result of fungal growth. Wardle and Yeates (1993) noted an identical effect of faunal grazing on the microbial population. This factor may account for the lack of significant differences in the present study. Although the bacterial to fungal ratio was not assessed, several factors indicated that the microbial population was likely bacterial: the prevailing warm, moist conditions and most importantly, the dominant form of N was NO$_3^-$-N. Ingham et al. (1989) showed that the forms of N present in the soil could be related to the predominant
microbial population, either bacterial or fungal. Nitrate was associated with bacterial populations and \( \text{NH}_4^+ \)-N with fungal. They further noted that the density of consumer groups (bactivorous or fungivorous soil fauna) could be related to the dominant decomposer (either bacterial or fungal). In this study soil fauna were not identified to any appreciable degree and therefore little can be stated about the dominant groups that existed and the resulting decomposer community.

The influence of soil type (tree species) on N mineralization was significant, as has been reported in many studies (eg. Blair, 1988; Melillo et al., 1982). An earlier assessment (Prescott et al., 1995 unpublished) of N mineralization on this site found extractable N to be highest in cedar and lowest in hemlock. The present study also measured high amounts of extractable N (\( \text{NH}_4^+ \)-N + \( \text{NO}_3^- \)-N) in cedar, although unlike the previous study, spruce was lowest in extractable N. These findings are in accordance with other studies showing N mineralization in cedar forests (Turner and Franz, 1985).

There is no conclusive evidence to suggest that soil fauna prefer soil under one tree species to another, although there are differences in faunal populations among forest types (Blair et al., 1994). In the present study collembola were significantly more abundant in Douglas-fir than cedar soil. This supports a recent study conducted in these plots and other nearby sites, where collembolan density was lowest in cedar forest floors (Ph.D. thesis, Baumbrough, 1998). There was no indication that the number of fauna in each soil type influenced the processes of N mineralization or decomposition. Perhaps greater numbers of fauna would have revealed a significant relationship between N mineralization and faunal abundance, as it has with other studies (Bengtsson et al., 1994; Seasteadt, 1984). A larger faunal population may also have influenced substrate-induced
respiration. Many of the laboratory studies may have had unnaturally high populations of fauna, so the effect of the fauna may have been exaggerated. In this study, fauna were added to microcosms in the numbers which were extracted from field samples, so the subtle effects of fauna observed may be more in keeping with natural ecosystems.

A plant was included in this study to provide a measure of N availability and to provide a source of carbon for the microbial community. Plant growth and N content was not closely related to the other indices of N availability. Where leachate and KCl-extractable NH$_4^+$-N and NO$_3^-$-N levels were highest (treatment 3) the plant weight was low. *H. h. haydeniana* activity in treatment 3 may have hindered plant growth by moving through and damaging roots. It may also be that because cabbages do not grow in forests they were not well adapted to conditions in the forest floors and so were limited by factors other than N availability. The original plan was to use fireweed (*Epilobium angustifolium*) but this was abandoned after the plants became diseased prior to planting in the microcosms. Setala and Huhta (1991) used birch seedlings effectively in microcosm experiments. This might be a better choice of plant, although the mycorrhizal relationship would need to be addressed.

This study was designed in part to reflect the heterogeneous nature of soil and as such provide a better idea of N mineralization and decomposition in the field. However, the great variability between soil cores may have hindered expression of significant differences between treatments. Bulking of soil samples within a tree species would probably have reduced the variability, but would have weakened the application of results to the field.
Efficacy of faunal exclusion was of primary concern in this study. Liquid nitrogen was effective and the faunal treatments were achieved initially. However, at the end of the incubation, faunal abundance was lower than populations measured in the field at these sites (Baumbrough pers. commun.). This is probably the result of the fluctuating temperature and moisture conditions in the greenhouse which may have negatively impacted the soil fauna. Daily maximum temperatures in the greenhouse were often in the low 30s and reached 41 °C on one occasion. The soils dried out quickly between waterings during periods of high temperatures. Soil fauna are known to be negatively affected by high temperatures and low moisture (Christiansen, 1964). They will lose water through their cuticle at ambient humidity levels below 100%. Harpaphe haydeniana haydeniana were maintained throughout the study, although the death of a few required later additions of millipedes. If initial (field) levels of fauna had been maintained through the incubation, the effects of soil fauna might have been greater.

Any assessment of faunal-mediated decomposition and N mineralization should include a careful and thorough evaluation of the microbial population. There is still a great deal to learn about the relationship between soil fauna and microorganisms. There is some indication that soil fauna shift the ratio between fungal and bacterial biomass, and that this is related to an ability to resist grazing (Mikola and Setala, 1998) (with antibiotics, niche selection, growth response). The implications of this for C and N mineralization are still unknown as is the nature of this shift in dominance as affected by each faunal group. A fairly new tool exists, called BIOLOG® (Garland and Mills, 1991) can be used to assess the functional characteristics of bacterial populations. Soil is distributed on a plate containing several small indentations. Energy sources equipped with
a color indicator are added to each indentation and the microbial activity and biomass are
then measured according to color development. It has been used with some success and
requires further application to realize its potential in soil ecology research. As well, the
use of fumigation-extraction, substrate induced respiration and an evaluation of hyphal
content by fluorescence can provide information on the microbial biomass, activity and
ratio of fungi to bacteria. Greater knowledge of the effects of fauna on the microbial
community would enable us to better understand their effects of soil processes.

Monitoring the soil fauna population and taking several measurements of microbial
activity and biomass throughout the study period would serve to track the relationship
between the two decomposer groups. Measures of N mineralization could also be
correlated to faunal and microbial populations. Most studies are fairly short in duration
and therefore provide an information bias. Decomposition is slow, especially in coniferous
litter, and its accurate assessment may require several years time. The relationship
between resource quality and soil fauna will vary over time (Santos and Whitford, 1981;
Hasegawa and Takeda, 1995) and between sites (Battigelli et al. 1994). Long-term studies
and comparisons of ecosystem function (e.g. decomposition and N mineralization) in
identical substrates from different sites within the same biogeoclimatic zone would provide
further insight. The use of intact soil cores and the addition of fauna as they existed in the
field (minus the macrofauna) may have introduced variability between experimental units
that could not be compensated for by the sample size used. However, I believe that
factors such as predation, niche selection, competition and resource utilization (Mikola
and Setala, 1998b) relevant to the site were represented in the intact soil cores. A
comparison of food web development and ecosystem function in intact vs. homogenized soil might help test this idea.

Greater manipulation of food webs would prove useful for gaining insight into the importance of faunal groups in decomposition and N mineralization. The removal of a predator, for example, can alter its prey, which in turn can alter the microbial population upon which the prey feed. Classical food web theory lacks applicability in soil webs (Mikola and Setala, 1998; Polis, 1994) as there seem to be several factors acting on each branch of the soil food web which make predictions difficult. Further research into the members of each food web would be valuable for making predictions and determining the importance of biodiversity to ecosystem processes. There is currently a great deal of discussion concerning this controversial issue (Bengtsson, 1998; Wolters, 1998; Lawton, 1994; Mikola and Setala, 1998b).

This study showed simply the net result of adding a very broad group of fauna to soil. The resulting faunal influence could have been due to the activities of one species of fauna present, therefore stating that my results support the idea that a diverse faunal community is essential to soil processes is presumptuous. The millipede significantly increased rates of decomposition and enhanced those of N mineralization. It is logical to conclude that an organism capable of effecting such obvious physical changes to soil would be important in ways similar to those attributed to the earthworm, which is considered to be a keystone species (Huhta et al. 1998). There is, however, no conclusive evidence for this suggestion. This study was not designed to test the importance of biodiversity on decomposition and N mineralization. An experiment with this in mind requires careful manipulation of the organisms present. Mikola and Setala (1998; 1998a;
1998b) have done just this. Most importantly they showed that microbial and faunal biomass and N mineralization were dependent on the idiosyncratic influences of each species of soil fauna tested. The soil fauna were not redundant, nor was their impact on the system predictable, both lending support to the importance of biodiversity, or rather to the acknowledgment that an understanding of individual species is the only way to assess the real value of biodiversity.

This study has brought to light the relevancy of soil fauna to decomposition and N mineralization in coastal British Columbia western-red cedar, western hemlock, Douglas-fir and Sitka spruce forests. Of particular note is the impact the millipede had on the indices of N mineralization that were measured. The physiology and ecology of these organisms is little known. We do however, have some ideas of their obvious presence in the EP571 sites from field observations. It is therefore important to consider the impact that forest management activities have on this millipede and on soil processes affected by this organism.

CONCLUSION

Nitrogen mineralization was slightly enhanced by soil fauna, particularly by the millipede *H. h. haydeniana*. The effect of soil fauna on N mineralization was similar in the four soil types (tree species), and there were differences among the four tree species in rates of N mineralization in soil. Decomposition was significantly enhanced in the presence of *H. h. haydeniana* (and fauna), as was the microbial biomass of Sitka-spruce soils. Cabbage plants did not prove to be a good choice for measuring N uptake; plant
biomass was extremely variable and not related to other measures of N availability. The lack of statistical significance among treatments reflected the high variability of many of the N mineralization indices; greater replication or bulking of samples might have reduced the variability. The effects of soil fauna on N mineralization may have been underestimated due to reductions in fauna populations in the microcosms in response to fluctuating temperature and moisture conditions in the greenhouse.
LITERATURE CITED


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