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EFFECTS OF SOIL FAUNA ON DECOMPOSITION AND NUTRIENT DYNAMICS IN CONIFEROUS FOREST SOIL

Heikki Setälä

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The influence of soil fauna on decomposition and nutrient cycles in coniferous forest soil was studied at the Department of Biology, University of Jyväskylä. Experiments were conducted in the laboratory using homogenized soil, needle litter of spruce and leaf litter of birch as test materials. The study included four steps: First, litter and humus were tested separately in "microcosms"; then the complexity of the system was increased stepwise while controlled laboratory conditions were maintained (="macrocosm experiments"). Finally, birch seedlings were planted in experimental chambers with reconstructed forest floor. In an additional experiment, one animal group was present at a time, or two groups in different combinations. Depending on the experiment, the incubations lasted 20 - 98 weeks.

Before the experiments were initiated the materials were defaunated by freezing-thawing or microwave treatment and re-inoculated with microbes from the soil suspension. Soil fauna was introduced into half of the replicates. During the experiments evolution of CO_2 was monitored, and concentrations of N and P were analyzed in the water leachates drained through the test materials. At destructive samplings several soil variables were measured.

The animal populations established themselves relatively well in the experimental chambers; in the structurally most complex systems the densities approached those found in similar soil in the field. It became evident, however, that the absence of predatory fauna leads to overabundance of their potential prey, thus emphasizing the importance of biotic relationships in modifying the community structure of soil fauna.

In most cases the soil fauna increased the decomposition rate of dead organic matter. Moreover, a complex faunal community with various feeding guilds evidently enhances decomposition more than a simple system composed only of microbial feeding fauna does. In the later phases of incubation, however, the soil fauna began to influence the decomposition rate "negatively".

As a general rule, the fauna also increased the mobilization of N and P in the systems. This was generally true throughout the whole period of incubation. There were also differences in mobilization of nutrients between structurally different faunal

communities: the more diverse a system was, the greater the amounts of nutrients released.

According to the hypothesis formed in previous experiments (enhanced nutrient cycling —> more nutrients available momentarily), the birch seedlings grew faster in the presence of soil fauna. After two growing seasons the growth of leaf, stem and root biomass was 70 %, 53 % and 38 % higher, respectively, in the refaunated systems. In addition, the nitrogen content in the leaves was many times greater than that of the control with microbes only.

New techniques were developed to simulate the complexity of forest soil in the laboratory. Environmental variables can thus be controlled, allowing 1) repetition of the experiment without changes in the experimental conditions, and 2) manipulation of the desired variables at the same time. The design also renders possible the establishment of a "natural" decomposer community. This is a clear improvement on earlier microcosm studies, in which decomposition processes have been examined in systems with a radically oversimplified assemblage of soil organisms.

These results confirm the general hypothesis that the soil fauna plays a considerable role in nutrient cycling and decomposition of dead organic matter. This conclusion is also valid in systems simulating Finnish coniferous forest floor. In addition, it was shown that interrelations between faunal groups and species may exert a substantial influence on the below-ground processes, which may, in turn, reflect changes in other ecosystem levels as well. The enhanced plant growth caused by soil fauna has previously been shown by earthworms in cultivated or grassland soils, but not in other kinds of soils, nor with faunal groups other than earthworms.

Key words: Soil fauna; decomposition; nutrient dynamics; forest soil; plant growth; microcosm.

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List of original publications

This thesis is based on the following articles, which will be referred to by their Roman numerals:

I Setälä, H., Haimi, J. & Huhta, V. 1988: A microcosm study on the respiration and weight loss in birch litter and raw humus as influenced by soil fauna. Biol. Fertil. Soils 5:282-287.

II Huhta, V., Setälä, H. & Haimi, J. 1988: Leaching of N and C from birch leaf litter and raw humus with special emphasis on the influence of soil fauna. - Soil Biol. Biochem. 6:875-878.

III Huhta, V. & Setälä, H. 1990: Laboratory experiments using simulated forest floor to study the role of fauna in soil processes. - Biol. Fertil. Soils (in press)

IV Setälä, H., Martikainen, E., Tyynismaa, M. & Huhta, V. 1990: Effects of soil fauna on leaching of N and P from experimental systems simulating coniferous forest floor. - Biol. Fertil. Soils (in press).

V Setälä, H. & Huhta, V. 1990: Experiments with simulated coniferous forest soil to evaluate the impact of soil fauna in decomposition. - Biol. Fertil. Soils (in press).

VI Setälä, H., Tyynismaa, M., Martikainen, E. & Huhta, V. 1990: Mineralisation of C, N and P in relation to decopmoser community structure in coniferous forest soil. - Pedobiologia (in press).

VII Setälä, H. & Huhta, V. 1990: Soil fauna increases the growth of birch (*Betula pendula*): Laboratory experiments with coniferous forest floor. - Ecology (in press).

Contents

1. Introduction

In most terrestrial ecosystems more than 90 % of the net annual primary production enters the soil as dead organic matter (Vogt et al. 1986). Because of the large amount of this material, the saprophagic pathway in soils may account for the major part of the energy flow and nutrient turnover in various ecosystems. Thus, the decomposition of organic matter in the soils and the subsequent mineralization of organically bound nutrients are essential for the functioning of the system.

Decomposition processes are regulated by interactions between the quality of the litter, the microclimate and the soil biota (Swift et al. 1979). Of the components of the last compartment it is the microflora that is traditionally considered to be responsible for most of the heterotrophic activity through which organic material is decomposed and nutrients are mobilized (Alexander 1977). For example, soil fungi and bacteria have been estimated to cover about 99 % of the total biomass of soil organisms and about 96 % of the heterotrophic matabolism in a Scots pine forest in central Sweden. The contribution of soil fauna to biomass and respiration of soil organisms was considered to be insignificant (Persson et al. 1980). Although soil fauna contribute less to direct heterotrophy, increasing evidence has accumulated to show that soil animals can accelerate

decomposition processes either directly by modifying the physico-chemical environment or indirectly by stimulating microbial activity through grazing (see review articles by Anderson et al. 1981, Anderson & Ineson 1984, Coleman 1986). Based on efficiency quotients extrapolated from laboratory experiments, Persson et al. (1980) calculated that the soil fauna consumed 30-60 % of the annual production of microbes in the litter and humus layer in a Scots pine forest. Consequently, soil invertebrates were estimated to mineralize/excrete about 30 % of the annual mineralization of nitrogen in the forest soil (Persson 1983).

With regard to overall ecosystem dynamics, the effects of soil microfloral and faunal interactions have recently been the subject of considerable ecological research. Despite general interest in this topic, however, the contribution of various organisms participating in decomposition processes is still incompletely known. Current knowledge about the role of soil animals in decomposition is based mainly on data obtained from investigations using three different kinds of approach: 1) The traditional litter-bag method, 2) the so-called "microcosm" experiments and 3) studies in which efficiency quotients (such as consumption/assimilation/production) for the fauna measured in laboratory are applied to field populations. All three methods can be criticized for their inaccuracy and/or often marked oversimplifications in various respects. Especially the microcosm experiments, in which the diversity of both the biotic and the abiotic environments are radically

reduced, should be developed to better mimic the complexity of natural soils. This maight give a more reliable picture of the actual species interactions in the field (see Anderson 1978, Hågvar 1988). Furthermore, since the below-ground food chains are commonly long and the food webs are extremely complex (Coleman 1986), only experimental systems with a whole spectrum of microflora, fauna and an abiotic soil substrate are likely to lead to conceptual advances in ecosystem ecology (Coleman et al. 1984).

Only a few reports have been published on experiments in which the effects induced by soil microbial-faunal interactions on nutrient cycling have been studied in autotrophic systems (i.e. in systems including living plants) (see Elliott et al.1979, Bååth et al. 1981, Clarholm 1985). It is well known that due to root exudates rich in energy the soil around plant roots (the rhizosphere) is biologically more active than the surrounding bulk soil (Coleman 1976). Therefore, results of experiments in which plants have been excluded should be interpreted with care.

In the present study several laboratory experiments with different experimental designs were conducted during 1985-1989 to provide information on the role of soil fauna in decomposition and nutrient mobilization in coniferous forest soil. Most of the studies published in this field have been established in microcosms with a relatively simple structure and moreover, in a completely different type of soil.

The main objectives of the present work were:

1) To create a microcosm system in which both the biotic and the abiotic environment adequately mimics the coniferous forest floor, and in which energy flows and nutrient cycles can be monitored easily (**III,VII**).

2) To study the decomposition of different substrates over a long period of incubation, in either the presence or absence of structurally diverse soil fauna (**IV,V**).

3) To investigate whether differences in the community structure of soil organisms will cause variation in the quality and quantity of below-ground processes (**1-VII**), and whether these differences will reflect changes in other ecosystem levels (**VII**).

2. Material and methods

2.1. Experimental designs

The experiments reported in this thesis were all carried out in the laboratory at the Department of Biology, University of Jyväskylä, and can be divided into two categories according to the complexity of the experimental set-up:

1) **Microcosm** experiments (relatively simple in structure, small in size and short in duration (less than 22 weeks); **I, II** and **VI**).

2) **Macrocosm** experiments (more complex biotic and abiotic environment, larger in size and lasting longer than one "growing period"; **III, IV, V** and **VII**).

The microcosm experiments described in papers **I** and **II** will be called **preliminary experiments** (established in 1985), and the study presented in paper **VI** is referred to as an **interaction experiment**. The latter was constructed in 1988 on the basis of the hypotheses which arose during the **macrocosm experiments** (carried out in 1986-1988). The final macrocosm experiments or the **phytocosms** were established in 1987 (a preliminary study) and 1988 (the main study).

The environment of the **microcosms** consisted of raw humus and birch leaf litter, either each material alone (**I, II**) or in combination (**I,II,VI**). In order to increase the complexity of the experimental system, the **macrocosm experiments** were created with simulated floor of coniferous forest inside the chambers. In the first phase three separate experiments were conducted, two of which had alcathene granules under an organic horizon composed of raw humus, birch and spruce litter and some additional material embedded in the humus (see below) (Exps. IA and IB; **III-V**). In the third experiment (Exp. II) the alcathene beads were replaced by a layer of mineral soil. Finally, the **phytocosms** included living seedlings of silver birch (*Betula pendula*) growing inside each chamber (**VII**) (Fig. 1).

The **microcosms** were incubated in an incubation chamber at 15 + 2°C with either weak illumination (**I,II**) or in constant darkness (**VI**). The macrocosms without plants, through which a constant flow of air was maintained by means of a compresor were kept in darkness at constant temperature (16 $\pm$ 1°C). To create "winter" conditions, however, the temperature was lowered stepwise (5 °C weekly) to 1 $\pm$ 1 °C. The **phytocosms** were incubated with varying temperature and illumination regimes in order to simulate the seasonal cycles in the field (**VII**).

Note that papers I and II are based on results obtained from one experiment. The same, respectively, holds for papers III, IV and V.

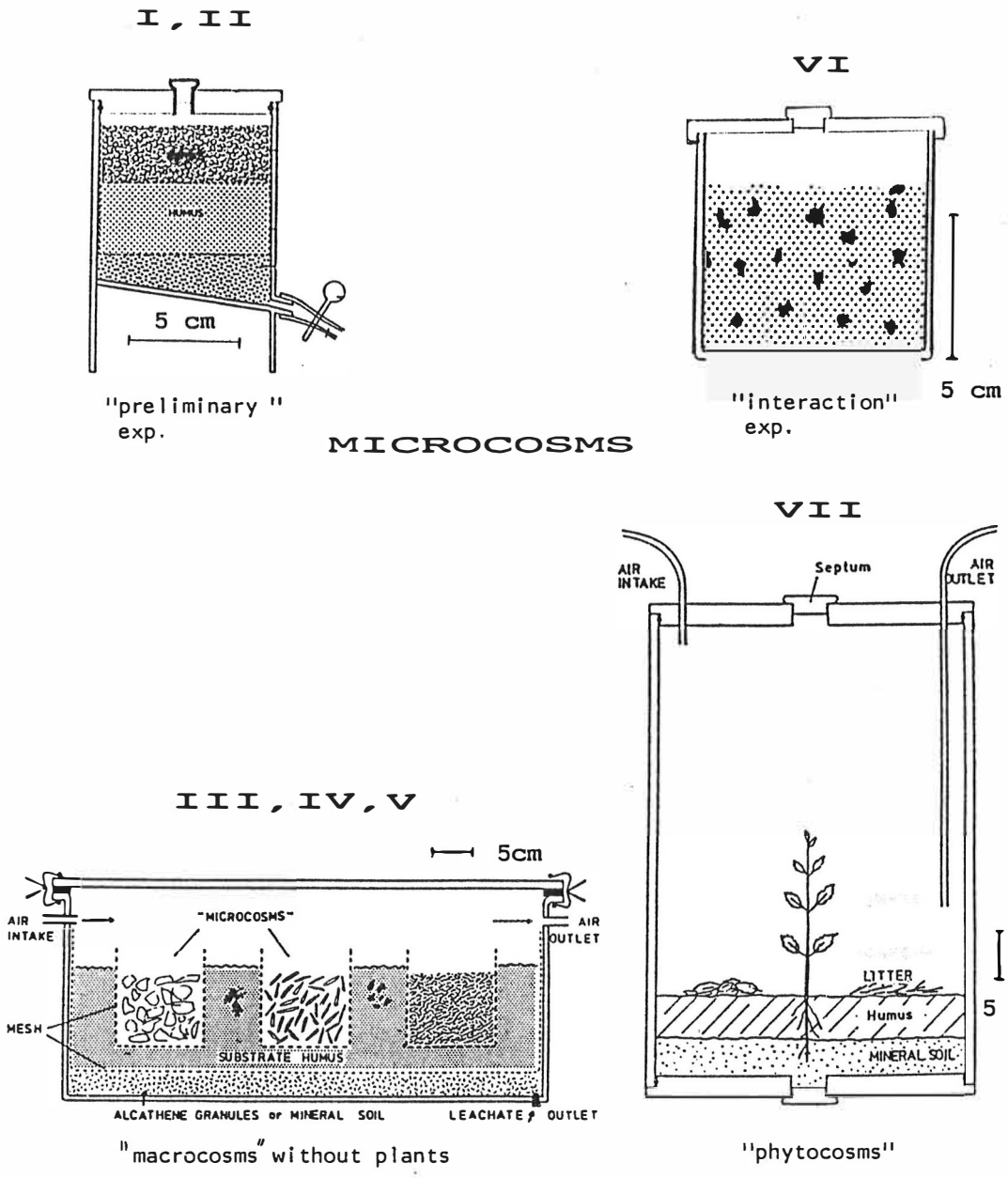

Fig. 1. Schematic presentation of the experimental systems. Roman numerals above the chambers refer to the papers in which the systems have beed applied. (Note the scales besides the figures).

2.2. Pretreatments and substrates

In the **microcosm** experiments, two kinds of test material were used: predecomposed birch (*Betula pendula*) leaf litter (cut into small pieces) and raw humus of coniferous forest (sieved through 5 mm mesh). To eliminate soil fauna, the test materials were oven-dried and then frozen (at -38 °C) (**I, II**), after which the materials were remoistened and placed in the microcosms. The materials used in the **interaction experiment** were partially sterilized by microwaving (**VI**).

The **macrocosms** received raw humus, birch (*B. pendula*) leaf litter and spruce (*Picea abies*) needle litter as test materials. These were placed into mesh-baskets embedded in the substrate humus. An additional inoculum of rotten wood, dried moss and crushed pine bark was embedded in the spaces between the mesh-baskets (**III,IV,V**) (see Fig. 1). The mineral soil (in Exp. II and the **phytocosms**) was sieved through 2 mm mesh and washed in water to remove organic debris and the finest mineral matter. Drying-freezing-thawing treatment was used to eliminate the fauna from the systems without plants (**III**), while the materials in the **phytocosms** (**VII**) were defaunated by microwaving.

2.3. Re-inoculation by microbes and animals

In every case the experimental systems were re-inoculated with microbes by spraying with diluted soil-water suspension, filtered through 5- or 10 µm mesh. Thereafter the desired assemblage of soil fauna was added by various methods to half of the replicates. A relatively diverse fauna (Enchytraeidae, Nematoda, Acari, Collembola) was introduced into the **microcosms** in the **preliminary experiment** (**I,II**). The **macrocosms** received a "normal" faunal assemblage from coniferous forest soil, excluding earthworms and large insect predators (**III,VII**). In the **interaction experiment**, in which the interactions between different representatives of soil fauna and microbes were studied, two or three groups of organisms were tested on different combinations (**VI**).

2.4. Samplings and measurements

2.4.1. Continual monitoring

Evolution of CO_2

Evolution of CO_2 in the **microcosms** was measured, using an infrared carbon analyzer URAS 7N, approximately once a week from samples taken from the air space of each microcosm (**I,**

II,VI). Respiration in the **phytocosms** was measured similarly but at irregular intervals (**VII**). Respiration in the **macrocosms** without plants was measured from the outgoing air; the air flow from each system was successivily conducted into the C analyzer, which was connected to a micro-computer programmed to measure content + production automatically at desired intervals. To measure the respiration in the "mesh-baskets" inside the macrocosms, 5-6 replicates of each test material per treatment were removed and placed in glass jars with air-tight lids. Evolution of CO_2 from the test materials was analyzed in the same manner as for the **microcosms** described above (**V**).

The contribution of the fauna to total respiration was estimated from data given by Klekowski et al. (1972), Persson & Lohm (1977) and Persson et al. (1980).

Leachate analyses

At intervals of 3-4 (**I,II**) or 4-6 (**III-V**) weeks (excluding the "winter") the microcosms and macrocosms were irrigated with distilled water (the mesh-baskets inside the macrocosms were watered separately). The **phytocosms** were irrigated only twice (**VII**). Concentrations of ammonium-N, nitrate-N, total N and ortophosphate-P in the leachates were measured photometrically from filtered samples (total N was analyzed from non-filtered samples) according to standard methods used in water analyses. After a subsample was burned at

950 °C, amounts of total C were determined using a C analyzer. Humic substances in the leachates were also analyzed occasionally (**II,V**). Nematodes and rotifers were counted in the draining waters (Exps. IB and II; **III**).

2.4.2. Destructive samplings

At the end of each experiment (**I,II,VI,VII**) or after each "growing period" (**III-V**) a destructive sampling was performed, which included e.g. the analysis of 1) mass loss, 2) number, biomass and composition of the fauna and 3) KCl-extractable NH_4^+-N, NO_3^--N, total N and PO_4^{3-}-P of the test materials (Note that in the **interaction experiment** the sample was washed with distilled water instead of KCl). In addition, the amount of fungal mycelia (total length and living hyphae) was determined by the methods of Sundman & Sivelä (1978; total fungi) and Söderström (1977; FDA-active mycelia) (I, **macrocosm experiments** without plants; not described in the articles mentioned). Metabolically active bacteria were counted once (Week 47/48; **macrocosm experiments**, not described in the articles) by the FDA-staining method (Lundgren 1981). The pH of the humus was determined in soil-water suspension (1/2, v/v). Initial contents of C and N in the litters and humus were determined with a Carlo Erba 1106 Elemental Analyzer. The net production of the above-ground and below-ground biomass of the birch seedlings was assayed twice during the 45-week

incubation (**VII**). Total N in the leaves and stems was analysed by the Soil Fertility Service (Helsinki) using the Kjeldahl procedure. Contents of P, K, Ca and Mg in the leaves were analyzed by plasma emission (ICP).

2.4.3. Statistical analyses

Differences between treatments and particular samplings were tested by Student's t-test (**I-VII**) or by ANOVA (**III-VI**). Statistical differences over long intervals were tested by ANOVA *for repeated measurements* (**III-VI**). When necessary, logarithmic transformation was used to normalize the distribution.

3. Results

3.1. Development of faunal communities

Microcosm experiments

The animal populations in the **preliminary experiments** became satisfactorily established in the microcosms (I). Some of

the taxa even reproduced to unnaturally high densities, e.g. in some replicates *Hypogastrura* spp. (Collembola) populations had increased more than 10-fold during the experiment. However, there was considerable fluctuation in animal numbers not only between various test materials but also between replicates of the same substrate. At the end of the experiment (Week 22) the animal densities were commonly somewhat lower than those found in the field in coniferous forest soils (Table 1). The controls were not contaminated by fauna during the incubation.

Microcosms in the **interaction experiment** (**VI**) reached extremely high numbers of nematodes, enchytraeids (*Cognettia sphagnetorum* Vejd.) and collembolans (*Onychiurus armatus* Tullb.) compared to natural populations in similar soils (Table 1). This was true mainly in treatments where only one animal taxon was present, but also in those where two taxa co-occurred. In the latter case the following faunal interactions were observed:

1). Predatory nematodes (*Mononchus* spp.) clearly had a negative impact on the numbers of microbial feeding nematodes throughout the experiment (3919 $\pm$ 1171) specimens without predators, and 77 + 105 when *Mononchus* were present, as calculated per g dry matter on Day 153).

2). Similarly, the presence of Collembola (*O. armatus*) significantly ($P<0.01$) reduced the numbers of microbial feeding nematodes.

3). On the contrary, enchytraeids (*C. sphagnetorum*) exerted a significant positive influence ($P<0.05$) on the number of nematodes.

Macrocosm experiments

In the macrocosm systems without plants, the animal populations established themselves well, and the numbers of organisms of several taxa (especially enchytraeids) approached or even exceeded those found in coniferous forest humus in the field. Although one of the most abundant faunal groups in the macrocosms, oribatids were quantitatively underrepresented compared to their abundance in the field. The total number of oribatid species (only adults were identified) after the first growth period was 25. On the whole, after about one year of incubation the fauna in the macrocosms was diverse enough to be considered a complex community of soil animals (III) (Table 1).

Later on, however, the populations of microarthropods begun to decrease, while the numbers of enchytraeids tended to increase. At the end of the experiment (Week 97/98), 72-86 % of the total faunal biomass was composed of enchytraeids. Nematodes appeared to be less abundant in the macrocosms than in the field, particularly towards the end of the incubation (III).

There were some differences in the development of faunal communities in Experiments IB and II, although the refaunation procedure was identical in both treatments. Perhaps the most marked difference was the establishment of an unnaturally dense population of predatory nematodes (*Mononchus* spp.) in Exp. IB. In the other treatments these predators were found only occasionally (Exp. II) or were totally absent (Exp. IA) (**III**).

The sterilization method (drying-freezing-thawing) was not effective enough to eliminate microfauna (including nematodes, rotifers and occassional tardigrades) from the control macrocosms. After some months of incubation these microbial feeders (bacterial feeding nematodes in particular) reproduced to very high densities, and their numbers clearly exceeded those in the Refaunated systems. For example, one mesh-basket containing birch leaf litter harboured more than 50 000 nematodes per gram dry mass of litter at the first destructive sampling (Week 48). The respective number in the refaunated units was generally less than 1000 (**III**).

Later on the Control systems will also be referred to as "simple communities" and the Refaunated systems as "complex communities".

In macrocosms with birch seedlings (**VII**) both the soil animal densities as well as the structure of the faunal composition resembled that of the plantless system. Some

differences between the two systems were observed, however; in the **phytocosms**, populations of Collembola and Enchytraeidae grew larger than in systems where plants were lacking, while the opposite was true for Mesostigmatid mites (Table 1).

Microwaving proved to be an effective method for eliminating microfauna from the substrate (Note that protozoans were not eliminated by microwaving and were thus included in all Controls).

Table 1. Estimated mean numbers of soil animals per square meter at the destructive samplings in the separate experiments (A-E) and in the field (F; Huhta et al. 1986). A = preliminary experiment (treatment with litter + humus; Week 22); B = interaction experiment (the figures denoting single species cultures; Week 20); C = macrocosm Exp. IB (Week 47); D = macrocosm Exp. II (Week 48); E = phytocosm (Week 45); F = annual means in a Scots pine stand of the Calluna-type.

	A	B	C	D	E	F
Nematoda x 10^{-6}	2.2	29.3	0.14	0.92	1.82	2.16
Enchytraeidae	180000	409700	14900	16360	83160	39800
Collembola	60400	162800	66300	29600	117000	81200
Oribatida	5200		44500	49500	52800	276700
Mesostigmata	1200		12300	18000	5060	16400

3.2. Carbon cycles

3.2.1. Microcosm experiments

The soil fauna had a positive influence on the evolution of CO_2 in all substrates. By the end of the **preliminary experiment** microcosms with soil fauna had respired 32.0 % (birch litter), 22.6 % (litter + humus) and 14.6 % (humus alone) more CO_2 than the Controls (with microbes only) (**I**). At the same time, the amounts of total C, as well as the concentration of humic substances, in the leachates increased significantly when the fauna was involved (**II**).

In the **interaction experiment**, respiration was always higher in Refaunated soils than in soils with microbes alone (**VI**). Moreover, more CO_2 evolved in systems with two animal taxa present than in systems with only one taxon. Of all the biotic combinations tested, the most intensive respiration was measured in units with the enchytraeid *C. sphagnetorum*. Similarly, respiration activity in the treatment with microbial-feeding nematodes was significantly enhanced when predatory nematodes were present, although the predators reduced the total biomass of fauna.

3.2.2. Macrocosm experiments

The complex faunal community in the Refaunated systems exerted a significant positive effect on respiration rate, as measured both from the litter material separately and from the total systems, particularly during the early phases of incubation (Exp. IA, **V**). At later stages of decomposition (after about one year from commencement of incubation) the influence of the complex fauna on C mineralization even turned "negative" in the litters, while in the "total systems" the positive effect of the fauna continued until the end of the experiments (Exps. IB and II). For most of the incubation time the proportion of the total respiration made up by the fauna was estimated to be less than 5 %.

For leaching of total C, there were no consistent differences between the Refaunated and Control systems when the whole 97/98 Week incubation period is considered. Leachates from the Refaunated macrocosms, however, tended to be richer in humic substances. This was also the case when the amounts of total C were lower in waters drained from the refaunated macrocosms. It should be noted that the mineral layer in Exp. II absorbed about 37 % of the carbon leached from the overlaying organic soil (**V**).

During the early stages of decomposition (0-18 Weeks incubation) there were no statistically significant differences in loss of mass between Refaunated and Control

litters (Exp. IA; V). During the middle stages (by Week 47/48), however, loss of mass was significantly greater in the presence of complex fauna. Similarly with respiration, towards the end of incubation, the rate of litter mass loss became even higher in the Controls with a simple faunal community.

In the **phytocosms (VII)** the evolution of CO_2 was almost the same in Refaunated and Control systems during the first growing period. Thereafter, the Refaunated units respired significantly more (in darkness) than the Controls did.

3.3. Release of N and P from the substrates

3.3.1. Microcosm experiments

Leaching of nitrogen (organic and inorganic forms of N) from the microcosms in the **preliminary experiment** was generally enhanced in the presence of soil fauna (II). By the end of the experiment about 50-100 % more N was leached from the Refaunated microcosms than from the Controls. However, the animals did not significantly affect any form of KCl-extractable N analyzed at the end of the experiment.

There were also differences in the forms of N liberated from the subtrates; e.g. in humus more NO_3^--N was released from the controls, whereas release of NH_4^+-N was significantly stimulated by the presence of soil fauna (**II**).

In the **interaction experiment**, the replicates in which microbial feeding nematodes occurred alone generally released the smallest amounts af NH_4^+-N. A similar trend was also recorded for the liberation of PO_4^{3-}-P. In the presence of predatory *Mononchus* the mobilization of N and P were slightly but significantly enhanced. *C. sphagnetorum* was the faunal taxon that affected the release of both nutrients from the microcosms most effectively. At times, however, the Controls (only microbes present) were even more effective in mobilizing nutrients than were any of the treatments with fauna (**VI**).

3.3.2. Macrocosm experiments

The complex faunal community significantly increased mobilization of N and P during the initial stages of decomposition, but only in the birch litter (Exp. IA, **IV**). By Week 18, Refaunated birch litters had released 27 % more PO_4^{3-}-P ($P<0.001$) and 72 % more NH_4^+-N ($P<0.05$) than the Controls had. KCl-extraction at Week 18 did not show marked differences in the amounts of soluble + exchangeable forms of N and P between Refaunated and Control systems.

During the middle stages of decomposition (until Week 47/48; Exps. IB +II) the complex fauna exerted a significant positive influence on the release of N and P from both kinds of litter and the total systems. In general, after about one year of incubation the amounts of nutrients mobilized in systems with a complex faunal community were about twice that of the Controls. When the KCl-extractable forms of nutrients are concerned, the effect of a complex fauna on nutrient mineralization was generally inconsistent (**IV**).

The positive effect of the complex biotic community on nutrient leaching from the litters continued until the end of the experiments (Week 97/98), although the differences between Refaunated and Control systems in some individual cases were insignificant. In the KCl-extraction the liberation of N and P from the substrate humus and mineral soil was significantly greater in the presence of complex fauna.

It should be noted that there were marked differences in nutrient release, not only between Refaunated and Control systems but also between the two Refaunated treatments; amounts of ammonium and ortophosphate liberated from the litters were, particularly during the late stages, clearly greater in Exp. IB than in Exp. II (**IV**).

In **phytocosms** there was a trend (often significant) towards greater amounts of total N, NH_4^+-N, PO_4^{3-}-P and NO_3^--N leaching from the control replicates. Release of

nitrate was, in contrast to the experiments without plants, greater than that of ammonium (and phosphate) at both irrigations. At the destructive samplings the amounts of KCl-extractable N and P in humus (occasionally also in mineral soil) were generally greater in the presence of soil fauna
(**VII**).

3.4. Microorganisms

In the **preliminary experiment** the amount of fungal mycelia in the test materials did not differ in replicates with or without soil fauna (as determined by microscopical counting). In the Refaunated units, however, more intensive fungal growth could alredy be seen with the naked eye after a few weeks of incubation (I).

In the macrocosms without plants (Exps. IA, IB, II) the complex animal community generally had a significant negative influence on the amounts of metabolically active fungus in birch and spruce litters. The total length of mycelia did not, however, differ in Refaunated and Control litters until the end of the incubation, when significantly more mycelia was found in Control litters (Fig.2).

The influence of fauna on metabolically active bacteria in the litters was not consistent; in spruce litter less

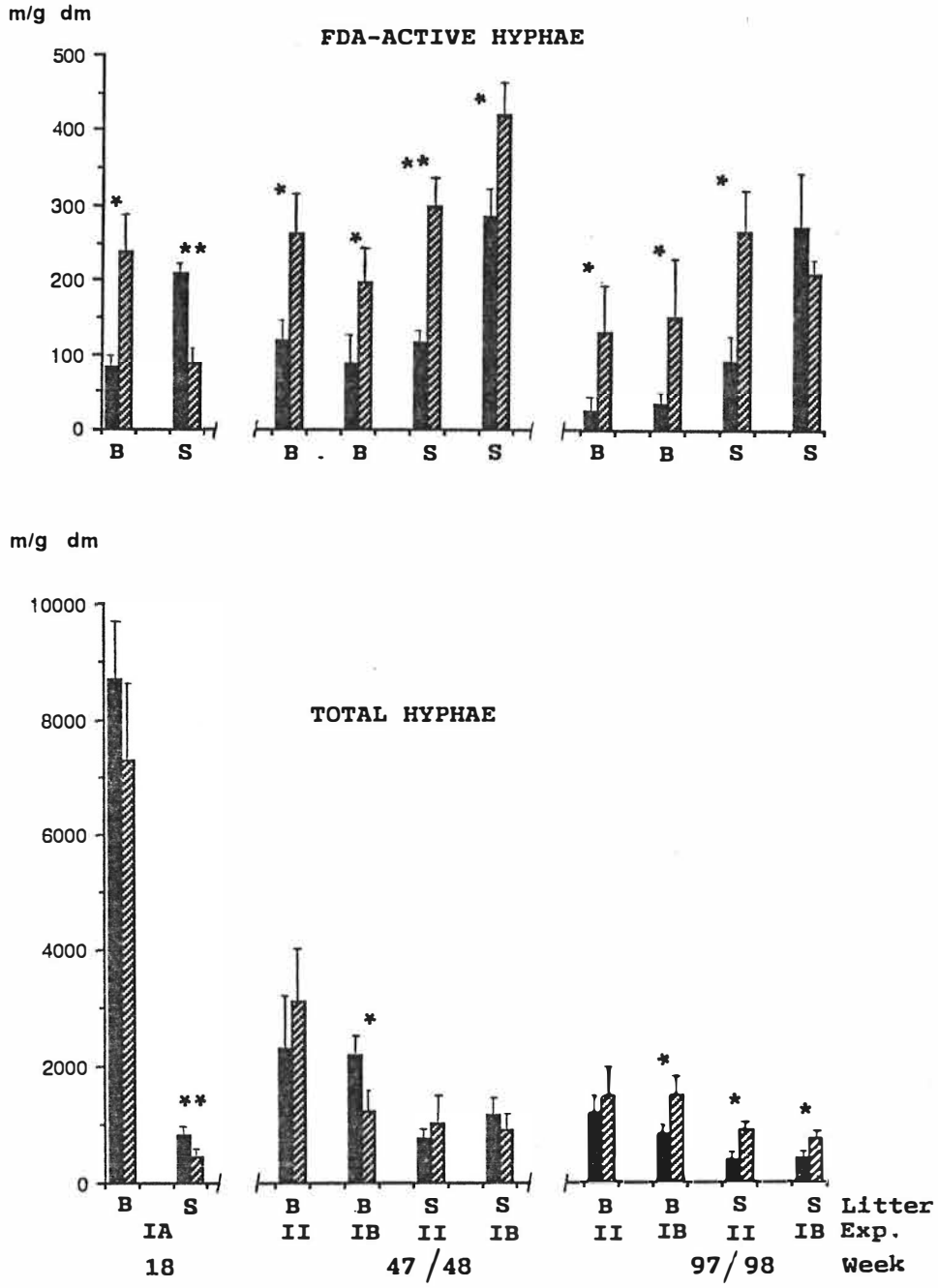

Fig. 2. Length (mean ± SE) of FDA-stained (metabolically active) fungal hyphae and total hyphae in Refaunated (black columns) and Control (shaded columns) litters of birch (=B) and spruce (=S) in the macrocosm experiments (IA, IB and II) at destructive samplings. Significant differences between Refaunated (microbes + diverse soil fauna) and Control (microbes + microbivorous fauna) are indicated with asterisks: (*=p<0.05, **=p<0.01; Student's t-test, n=5).

FDA-stained bacteria was counted in the presence of complex fauna, while in birch litter no difference was detected between the two faunal communities (Table 2).

Table 2. Numbers (mean ± SD x 10^{-8}) of metabolically active bacteria per g dry matter of Refaunated and Control litters at Week 47/48 in macrocosm Expts IB and II. Significant differences between Refaunated (microbes + diverse soil fauna) and Control (microbes + microbivorous fauna) are indicated by asterisks: (**=p<0.01; Student's t-test).

	Refaunated		Control
Exp. IB			
Birch litter	15.1 + 5.5		10.7 + 4.4
Spruce litter	18.0 + 8.8		24.3 + 12.0
Exp. II			
Birch litter	6.5 + 1.6		7.1 + 4.4
Spruce litter	11.7 + 4.7	**	25.4 + 7.4

3.5. pH

The pH in the leachate did not differ significantly between Refaunated and Control macrocosms (measured either in waters drained through the litter materials or through the "total systems" (Exps. IA, IB, II; IV). The water drained through the mineral soil layer (Exp. II) was generally about one pH unit higher (ranging between 4.7 and 5.4) than that from the systems with organic matter only (pH ranging between 3.8 and 4.4; Exp. IB). At the destructive samplings, pH in the humus

and in the mineral soil was generally slightly higher in the Refaunated systems (**IV**).

In the experiment with birch seedlings (**VII**) the pH of the water leachates ranged between 4.2 and 4.4, that of the humus between 4.5 and 4.6 and that of the mineral soil between 4.9 and 5.0. The pH did not differ significantly between Refaunated and Control systems.

3.6. Growth and nutrient contents of birch seedlings

The birch seedlings grown in the Refaunated systems produced larger and greener leaves, and stems about 3-times longer than those in the Controls. After two growing periods the growth of leaf, stem and root biomass was 70 %, 53 % and 38 % higher, respectively, in the presence of fauna (Fig. 3).

At the first harvest (Week 10) the difference in N content of green leaves between the Refaunated and Control systems was insignificant (Refaunated, 5.16 $\pm$ 0.28; Control, 5.44 + 0.60 % of dry mass, mean $\pm$ SD). However, at Week 45 the N content of leaves in the Refaunated systems was about 3 times that of the Controls. Contents of K, Ca and Mg in the leaves were almost identical in treatments, whereas the content of P was slightly greater in the presence of soil fauna. The stems also had a somewhat higher N content in the Refaunated systems (**VII**).

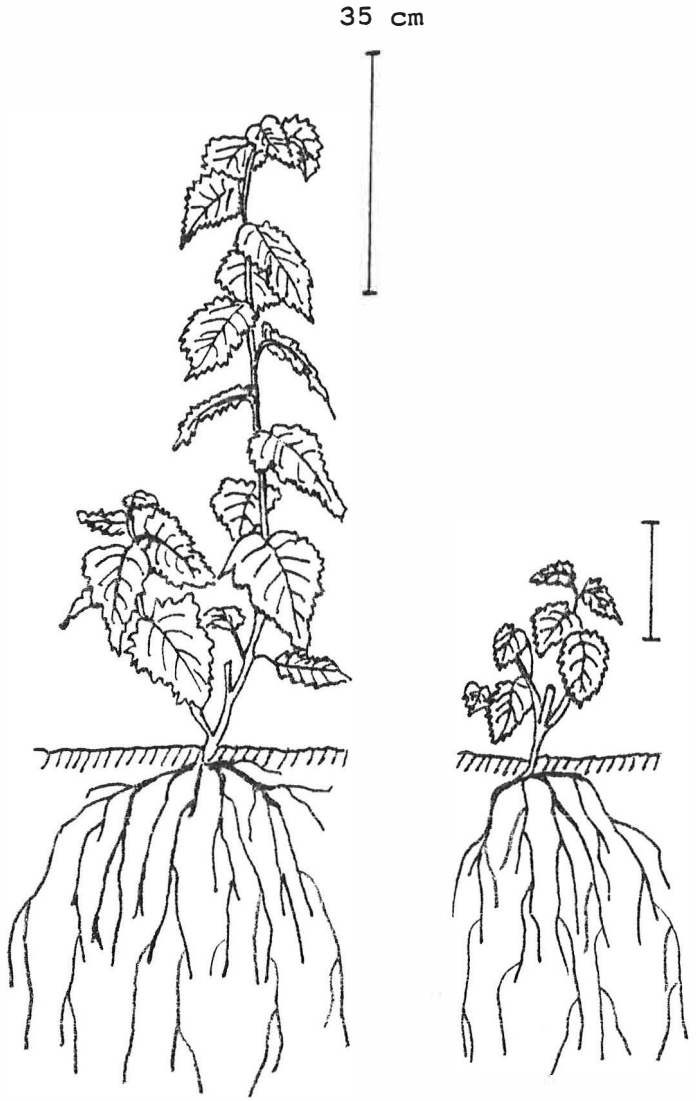

Fig.3. An illustration of typical representatives of birch seedlings (above-ground parts redrawn on the basis of a photograph) grown in experimental containers in the presence (left) or absence (right) of soil fauna after two growing periods (Week 45). The roots of the seedlings are roughly illustrated to express only the magnitude of the below-ground biomass. Vertical bars denote the minimum and maximum height of the seedlings of the separate treatments (n=10).

4. Discussion

4.1. Development of faunal communities and the use of the experimental systems in soil ecological research

The original purpose of establishing and maintaining a relatively diverse assemblage of soil animals for several months proved possible even in microcosms with a relatively simple structure (**I**). It gradually became apparent, however, that certain faunal species/- groups may grow to unnaturally high densities - even monocultures - if their predators are lacking (**I,III,VI**). These findings clearly indicate the need for biological interactions in maintaining diversity in an artificial community. At the same time the microcosm experiments emphasized that in order to satisfy the ecological demands for a fauna as diverse as possible, the physico-chemical environment of the experimental system should be much more complex. This is important because in nature detrital food chains are typically long, consisting of several trophic levels arranged in a very complex manner (Coleman 1986).

The macrocosms, being the next step in the experimental design, satisfactorily fulfilled the technical and ecological (diversified biotic and abiotic environment) demands stressed above. This is indicated by the relatively

diverse soil animal communities of the Refaunated units after an incubation of almost 2 years. Because the animals were not always identified to species or even to genus, however, one cannot be sure that the great species diversity in the field was maintained (or even achieved when the fauna was re-inoculated) in the laboratory. Moreover, the greater abundance of collembolans (as a group) than oribatids in the experimental systems is unnatural and indicates that the fauna in the laboratory incubations did not perfectly match that which occurs in the field.

It is reasonable to assume, however, that the results of the present experiments are better applicable to nature than those obtained from conventional microcosm experiments. It is worth emphasizing that the biotic component of the soil is largely responsible for the rate and amplitude of energy flows and nutrient cycles in soils, and that the pathways of these ecosystem parameters are extremely complex due to the diversity of soil organisms associated with the processes (Coleman et al. 1983). Therefore, it is understandable that such important and complex processes as energy flows and nutrient cycles cannot be studied satisfactorily unless the overall complexity of the experimental system is provided.

Although the macrocosm systems simulated the complexity of coniferous forest floor rather well, some differences between the experimental conditions and the actual situation in the field should be noted: 1) Despite the two "growing periods", no litter was added to the systems after the first

"summer". 2) The water content of the substrate humus in the macrocosms was rather stable throughout the experiment; this differs from field conditions, which have clear seasonal fluctuations in soil moisture. 3) Large-scale dispersion of the soil organisms in the experimental systems was prevented; Swift et al. (1979) emphasized the crucial role of continuous succession by fungi, bacteria and soil fauna modifying the communities of decomposer organisms and affecting the rate at which organic material is decomposed. 4) Finally, the absence of primary producers in all except one experiment (**VII**) almost surely affects the interpretation of the results.

4.2. Decomposition rate

Based on the separate laboratory experiments (**I,V,VI**), the following general conclusion can be made: The rate of decomposition of various substrates is strongly dependent on the complexity of the biotic community involved. The soil fauna exerted a positive influence on respiration and loss of mass of the birch leaf litter and raw humus compared with systems in which only microbes were present (**I,VI**). This is in accordance with a body of data from the literature emphasizing the importance of soil animals in the decomposition of various types of litters and soils (Edwards & Heath 1963, Hanlon & Andersson 1979, Seastedt 1984, Bengtsson et al. 1988). Moreover, the decomposition rate may

also differ in systems with divergent faunal communities. This was indicated by more rapid loss of mass and accelerated respiration in the Refaunated macrocosms with complex fauna present than in the Controls (simple fauna) during the early stages of decomposition (**V**). This kind of information is virtually lacking in the literature on soil ecology.

Results of the **interaction experiment** supported the previous findings according to which the decomposition rate increases as the community of soil organisms becomes more diversified (**VI**). A possible (and easy) explanation for the observations is that in biologically complex systems the wider assemblage of feeding guilds leads to more diversified substrate utilization, compared with simple systems where only microbial feeders are present.

The role of soil fauna in decomposition is generally connected with direct effects induced by the presence of fauna (processes like feeding and excretion) and with indirect effects like litter comminution and grazing on microbes (Anderson et al. 1985). Since macrofauna (capable of litter fragmentation and removal) was absent in the present experiments, it can be supposed that animal-microbial interactions affecting the decomposition rate should be more accentuated than e.g. the mechanical disintegration of the substrate by the fauna. Thus, by grazing the microbes, the complex fauna in the Refaunated systems may have increased the growth rates and activity of

the microbial populations and hence accelerated decomposition. (The contribution of the fauna to total respiration was small, particularly during the early stages of incubation) (**V,VI**).

Despite the stimulated microbial activity (measured as increased CO_2 evolution) the amount of metabolically active fungal biomass was significantly reduced in the Refaunated litters. This observation is not without exception but is compatible with those of several other studies in which it was demonstrated that grazing by soil fauna on microbes may stimulate decomposition even when the amount of microbes present remains unchanged or decreases (Coleman et al. 1977, Hanlon & Anderson 1979, Bååth et al. 1981, Bryant et al. 1982). This is, however, true only when the grazing is slight or moderate. Overgrazing by fauna on microbes has been reported to decrease total respiration (Ineson et al 1982, Anderson & Ineson 1983, Parker et al. 1984). Therefore, it is possible that the dense fauna of microbial feeders (mainly bacterivores) that developed in the absence of predators in Control macrocosms overexploited the bacterial populations. This effect may have magnified the difference in decomposition rates between the simple and complex systems (**V**).

The retardation in decomposition rates of birch and spruce litters in Refaunated units during the later stages of the experiments is of great interest, since the decomposition rate of the litters with simple fauna

continued to proceed at the same rate as before (V). The retarded decomposition in the presence of complex fauna may have been due to more effective substrate utilization and consequently, a depletion of "readily decomposable" constituents of the substrates already during the early stages of decomposition. In addition, animal-induced structural alteration of the substrate may also have been in response to the lower degradation rates. According to Harding & Stuttard (1974) and Wolters (1988), ageing faeces of soil animals are more resistant to decomposition than the parent litter is.

More evidence of the long-term effects of fauna on the decomposition rate was obtained from the water leachates; the relative amounts of humic substances in systems with diverse soil fauna were greater than those in the Controls (II,V). It has been reported that the comminution action by the fauna as well as the chemical effects of soil animals on microbial residues during their passage through gut may enhance the humification process (Kononova 1966, Babel 1975). Thus, the increased humification together with accumulation of recalcitrant mesofaunal faeces in the Refaunated systems seems gradually to turn the stimulating influence of soil fauna in decomposition processes to a retarding one. This may be considered as a positive effect since increased humification is generally associated with improved fertility.

It is evident that the main faunal-mediated response in

the enhanced decomposition rates at the early stages of experiments was indirect (i.e. stimulation of microbial activity). It is noteworthy, however, that not only animal-microbial interactions but also animal-animal relationships are of great importance in affecting the decomposition rates. The absence of predators in simple systems resulted in the development of superabundant populations of microbial feeders (**I,III,VI**), which was concluded to have affected the decomposition rate negatively (**V,VI**; see also Santos & Whitford 1981, Santos et al. 1981). In conclusion, an interactive network with multiple interspecific relationships is needed to maintain an active decomposer community.

4.3. Release of N and P

The results reported in this thesis fit well the general hypothesis that soil fauna affects the microbial-mediated mineralization-immobilization processes and amplifies the nutrient fluxes in soils (Anderson et al. 1983). The importance of faunal activities in nutrient cycles was observed not only in the litter materials (**II,IV**) but also in the total macrocosm systems. (**IV,VII**). In general, the more diverse a decomposer community was, the more N and P were released. There was an exception, however; In the **interaction experiment** there were no consistent differences in the mobilization of N and P between the simplest system

and the more complex ones (**VI**). Unexpectedly, systems with microbes + microbial feeding nematodes generally released smaller amounts of mineral nutrients than any of the other treatments (**IV,VI,VII**).

In the **preliminary experiment** (**II**), in which the mobilization of N from birch leaf litter and raw humus was compared for systems with microbes only and microbes + relatively diverse soil fauna, more N was liberated in systems where fauna was involved. This was the case in spite of the stimulated microbial respiration in the refaunated units (**I**). According to general microbiological theory (Alexander 1977), an activated microbial community should, in its growth and maintenance, effectively immobilize available nutrients. As observed with the naked eye, however, the amount of fungal mycelia was clearly reduced in the presence of fauna (**I**). Similarly in the **macrocosm experiment**, the amount of metabolically active hyphae in birch and spruce litters was significantly less in the Refaunated systems than in the Controls (see Fig. 2.). Thus, the immobilization of N should diminish with decreasing amount of microbial biomass. Ineson et al. (1982) showed that ungrazed fungal mycelia can immobilize substantial amounts of nutrients, and consequently may decisively retard nutrient cycling in leaf litter. Similar results have been reported by Coleman et al. 1977, Abrams & Mitchell 1980, Trofymow & Coleman 1982.

It is possible that the increased nutrient mineralization

in the presence of fauna is due to direct excretion of N by the animals. Based on theoretical calculations, direct excretion of NH_4^+-N by the fauna may constitute more than one third of the total N mineralization in various ecosystems (Persson 1983, Rosswall & Paustian 1984, Hunt et al. 1987). In light of the previous statements, it seems obvious that both direct (nutrient excretion by the fauna) and indirect (animal-microbial -interactions) mechanisms are needed to explain the enhanced nutrient mineralization in the Refaunated systems.

Only a few experiments have been reported in which nutrient fluxes are studied in relation to the structure of the faunal community, and most of these have been established in strongly simplified laboratory conditions (see McClellan et al. 1981, Woods et al. 1982, Griffiths 1986, Persson 1989). The present experiments conducted in macrocosms enabled comparison of nutrient mobilization between two different faunal assemblages of coniferous forest floor (**IV**). The results support the hypothesis that has arisen on the basis of the **preliminary experiment:** systems with a wide range of interactions among the biota will cycle the main nutrients (N and P) more effectively than systems in which such relationships are scarce. The same holds for the **interaction experiments:** systems with at least three trophic levels (microbes + nematodes + predatory nematodes) more effectively mobilized N and P than did those in which predators were absent (**VI**). This indicates that in the absence of the "next" link in the food chain

(predators), considerable short-term immobilization of nutrients into the biomass of microbial feeders is possible.

It is worth noting that the nutrient dynamics of the birch and spruce litters in the macrocosms also differed in the two "complex" treatments (**IV**; Exp. IB vs. II). No difference was detected in the release of nutrients between the two "simple" systems with identical fauna, which observation further confirms the idea that interactions among the fauna are important in affecting nutrient mineralization in soils.

It is generally assumed that N and P cycles are strictly involved with biological processes in soils. However, the results of the macrocosm experiments demonstrated that for phosphorus this is not necessarily the case (**IV**), as was indicated by the observations that the distinctive variation in the activity of the soil organisms (measured as CO_2 evolution) was not reflected in the pattern of release of PO_4^{3-}-P.

In conclusion, the experiments demonstrated that significant differences in nutrient flows occur not only between systems with microbes alone versus those containing both microbes and soil fauna, but also between communities with different assemblage of soil animals. A complex (=natural) decomposer community seemed to positively influence nutrient release in all test materials, regardless of their differing chemical and structural compositions.

Furthermore, this effect lasted throughout the whole period of incubation. This enhancement occurred both in separate microcosm units as well as in the total systems. Moreover, although the leaching patterns of N (supposed to be the limiting nutrient) and P (a non-limiting factor) differed, the complex faunal community exerted a positive influence on the mobilization of both nutrients. Predatory fauna were concluded to be of great importance in affecting the nutrient fluxes.

4.4. Effects of soil fauna on plant growth

Results of the previous experiments (I-VI) indisputably showed that, in general, concentrations of mineral forms of N and P in the litters and humus were significantly higher in the Refaunated systems than in systems where fauna was lacking or where the complexity of the faunal community was reduced. In practical forestry it is well-established that even a relatively small increment in N and P available to plants in the form of fertilizers in soils will considerably increase the productivity of a site. Thus, as predicted on the basis of silvicultural experience and the distinctive results of previous experiments, the presence of soil fauna in the phytocosms affected the growth and nutrient content of the birch seedlings positively. The hypothesis of the importance of the soil fauna in the soil processes became

concretisized in a visible manner (**VII**).

There have been only a few studies in which the role of soil fauna has been studied in relation to tree growth. Bååth et al. (1981) found no differences in the growth of Scots pine (*Pinus silvestris*) in microcosms with microbes alone versus microbes plus microbe-feeding fauna. The difference in the results between the present experiment (**VII**) and that of the above-mentioned Swedish group may be mainly due to differences in the plants used (fast-growing birch/slowly-growing pine). In addition, the fauna in the latter experiment was composed of microbivores only, while in the present experiment the fauna was much more complex. It should be emphasized that in neither experiment were the roots of the seedlings invaded by mycorrhizae. As most tree species growing in the field are associated with mycorrhizal fungi (Bowen & Smith 1981), the results may not be directly applicable to field conditions.

The enhanced mobilization of nutrients (mainly that of N) alone does not necessarily explain the accelerated tree growth in the refaunated systems. Undoubtedly several other faunal-mediated factors were having a positive affect at the same time: higher water content in the humus (59.3 $\pm$ 2.4 % of fresh mass in Refaunated; 46.4 + 5.6 % in Control, mean + SD) as well as somewhat greater CO_2 evolution in the presence of fauna may also be considered to be stimulative factors. Since N-content in the leaves was the most marked difference between the seedlings grown in the two separate

systems, however, the availability of that essential nutrient in the soil can be considered to be the most important factor controlling plant production.

5. Concluding remarks and relevance to general ecology

Experiments conducted in systems simulating the heterogeneity of coniferous forest floor clearly showed the positive role of soil fauna in decomposition processes. Despite the differences in the chemical and structural composition of the test materials (needles/leaves/humus; single mesh-baskets/the whole system), the positive effect of the fauna on the decomposition rate (during initial and middle phases of incubation) and N and P mineralization (throughout the almost 2-year period) was indisputable. The most marked difference between defaunated and refaunated systems in processes occurring below the soil surface could be observed even with the naked eye: the growth of birch seedlings was significantly enhanced in the presence of soil fauna.

The positive effect of the fauna on decomposition rate was largely indirect: grazing on fungi and bacteria by the animals stimulate the microbes responsible for most of the heterotrophic activity in a system. Enhanced nutrient cycling may also be associated with the indirect role of the

fauna, but the proportion of nutrient-rich compounds excreted by the fauna (=direct role) in the total mineralization can be marked.

The observations that the structure of a faunal community explains differences in nutrient mobilization between dissimilar communities lead to interesting theoretical applications. It was shown that a seemingly normal soil fauna with myriads of interrelationships among the organisms undoubtedly was the most efficient biotic assemblage for affecting soil processes. When the present data is fit into wider ecological frames, the above-mentioned observations could well be applicable to the Clementsian (Clements 1916) holistic view of ecosystems. According to this concept ecosystems can be considered to be "superorganisms" in which each unit (species or individuals) has its own task in serving the general prosperity. On the basis of this theory, the efficient nutrient cycling mediated by the fauna should also serve the functions (such as primary production) that take place above the litter layer, which in turn should induce positive feedback by nourishing the detrital food web with litter of high quality. In fact, the experiments with birch seedlings indicate clearly that a seemingly normal community of soil organisms with diverse microbial and faunal compartment is a prerequisite for keeping a system active.

It is obvious, however, that the idea of holicism is not needed and may even be incorrect for explaining the greater

productivity in systems with a complex community of soil organisms. An opposing and modern approach, the reductionist view, suggests that the prevailing conditions determine in a stochastic manner the association of organisms and their ability to survive. According to the latter view, natural selection operates on the individual level rather than on the ecosystem level. Whatever the ultimate unit of selection, however, the results of the present study emphasize that the quality and quantity of interactions among soil biota are extremely important in modifying the environment, at least in artificially created mini-ecosystems. Furthermore, as most of the soil biota (such as Collembola and Acari) possess a long history of evolution, it is reasonable to assume that not only are co-evolutionary adaptations between soil organisms reflected in the community structure but that they may also influence functional aspects of the below- and above-ground world.

Finally, data of the present experiments indicate that soil micro- and mesofauna should definitely be included in ecosystem models explaining the decomposition processes in soils. Thus, concepts, according to which only microorganisms are of importance (e.g. Bosatta & Staaf 1982) should be revised.

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Selostus

Maaperäeläinten merkitys kangasmetsämaan hajotuksessa ja ravinnekierrossa

Väitöskirjatyöni käsittelee maaperäeläinten merkitystä kangasmetsämaan hajotuksessa ja ravinnekierroissa. Tutkimukset tehtiin Jyväskylän Yliopiston Biologian laitoksessa laboratoriokokeina. Koemateriaaleiksi valittiin homogenoitu tuore kangasmetsämaa sekä kuusen neulaskarike ja koivun lehtikarike. Kokeita tehtiin neljässä vaiheessa: aluksi tutkittiin erikseen karikkeen ja humuksen hajoamista ns. mikrokosmoksissa, minkä jälkeen kokeissa pyrittiin asteittain edeten jäljittelemään metsämaan monimuotoisuutta. Viimeisellä koekierroksella koeastioihin rekonstruoituun metsämaahan istutettiin rauduskoivun taimia. Edellisten lisäksi perustettiin erillisiä koesarjoja, joissa selvitettiin eri maaperäeläinryhmien ja niiden yhdistelmien vaikutuksia hajotusprosessiin.

Ennen kokeiden alkua materiaalit steriloitiin eläinten eliminoimiseksi. Tämän jälkeen niihin palautettiin mikrobisto maauutteesta, ja joka toiseen yksikköön ympättiin maaperäeläimiä. Kokeiden kestäessä mitattiin säännöllisesti maaperän hiilidioksidituotantoa. Ajoittaisten, runsasta sadetta jäljittelevien kastelujen yhteydessä tutkittiin ravinteiden uuttumista ja valumaveden happamuutta. Kokeita purettaessa mitattiin lukuisia maaperän ominaisuuksia. Pisimmillään yhden kokeen kesto oli 98 viikkoa.

Eläinpopulaatiot menestyivät tyydyttävästi tai hyvin koeastioissa. Vielä noin kahden vuoden kuluttua kokeen perustamisesta rakenteeltaan monimuotoisimpien systeemien lajisto oli runsas ja luonnossa kangasmetsämaaperässä tavattavan kaltainen. Petojen läsnäolo osoittautui merkittäväksi saaliseläinyhteisöjen rakennetta muovaavaksi tekijäksi.

Kaikissa kokeissa maaperäeläimet lisäsivät orgaanisen aineen hajotusnopeutta hajotusprosessin alkuvaiheessa. Lisäksi ilmeni, että monimuotoinen, useasta ravinnonkäyttöryhmästä koostuva eläinyhteisö nopeuttaa hajotusta enemmän kuin yksinkertainen, pelkistä mikrobivoreista muodostunut yhteisö. Noin vuoden kuluttua kokeiden perustamisesta eläinten vaikutus hajotusnopeuteen muuttui kuitenkin päinvastaiseksi. Eläimet nopeuttivat pääsääntöisesti myös tärkeimpien ravinteiden (typpi ja fosfori) vapautumista hajoavasta karikkeesta ja humuksesta. Myös eläinyhteisön rakenteella oli merkittävä vaikutus typen ja fosforin mineralisoitumiseen.

Aiemmissa kokeissa muodostuneiden hypoteesien mukaisesti (nopeutunut ravinnekierto, enemmän hetkellisesti saatavilla olevia ravinteita) koivuntaimet kasvoivat nopeammin maaperäeläinten läsnäollessa. Kahden kasvukauden jälkeen lehti- , runko- ja juuribiomassa olivat vastaavasti 71 %, 53 % ja 38 % suurempia eläimiä sisältävissä yksiköissä. Lisäksi biomassan typpipitoisuus oli moninkertainen eläimettmään kontrolliin verrattuna.

Tutkimuksen toteuttamiseksi kehitettiin menetelmiä, joilla voidaan jäljitellä metsämaan monimuotoisuutta laboratoriossa. Tällöin ympäristöolosuhteita voidaan muunnella ha-

lutulla tavalla sekä tarvittaesa myöhemmin järjestää identtinen tai vain yhden tekijän suhteen muutettu koe. Järjestely varmistaa monimuotoisen eliöyhteisön kehittymisen koemaaperään. Aiemmissa ulkomailla tehdyissä tutkimuksissa on käytetty epäluonnollisen pieniä koeastioita, joissa on tutkittu homogeenista materiaalia, ja yleensä vain yhtä eläinlajia kerrallaan. Myös käytetty automaattinen mittaustekniikka on huomattava edistysaskel aiempiin tutkimuksiin verrattuna. Maaperän prosesseja voitiin siten tutkia pidemmälle kehitetyillä menetelmillä ja luonnonmukaisemmissa oloissa kuin muissa aikaisemmissa tutkimuksissa.

Tulokset vahvistivat yleisen otaksuman, että maaperäeläimillä on huomattava merkitys maaperän ravinnekierroissa ja eloperäisen aineen hajotuksessa. Tämä koskee myös suomalaista kangasmetsää, missä maaperäeläinten toiminnallista roolia on tähän asti pidetty merkitykseltään vähäisenä. Koivun taimet hyödynsivät tehokkaasti vapautuneet ravinteet ja kasvoivat eläinten läsnäollessa nopeammin. Kasvien nopeutunut kasvu maaperäeläinten vaikutuksesta on aikaisemmin osoitettu vain lieroilla viljely- ja ruohomaalla, mutta ei kangasmetsässä eikä muilla maaperäeläimillä kuin lieroilla. Tärkeänä voidaan pitää myös havaintoja siitä, että eläinlajien ja -ryhmien keskinäisillä vuorovaikutuksilla on suuri merkitys maaperän ravinnedynamiikassa.

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ORIGINAL PAPERS

I

A MICROCOSM STUDY ON THE RESPIRATION AND WEIGHT LOSS IN BIRCH LITTER AND RAW HUMUS AS INFLUENCED BY SOIL FAUNA

Biol. Fertil. Soils 5:282-287, 1988

by

Heikki Setälä, Jari Haimi & Veikko Huhta

https://doi.org/10.1007/BF00262132

II

LEACHING OF N AND C FROM BIRCH LEAF LITTER AND RAW HUMUS WITH SPECIAL EMPHASIS ON THE INFLUENCE OF SOIL FAUNA

Soil Biol. Biochem. 6:875-878, 1988

by

Veikko Huhta, Heikki Setälä & Jari Haimi

https://doi.org/10.1016/0038-0717(88)90096-X

III

LABORATORY EXPERIMENTS USING SIMULATED FOREST FLOOR TO STUDY THE ROLE OF FAUNA IN SOIL PROCESSES

Biol. Fertil. Soils (in press)

by

Veikko Huhta & Heikki Setälä

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IV

EFFECTS OF SOIL FAUNA ON LEACHING OF N AND P FROM EXPERIMENTAL SYSTEMS SIMULATING CONIFEROUS FOREST FLOOR

Biol. Fertil. Soils (in press)

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Heikki Setälä, Esko Martikainen, Merja Tyynismaa
& Veikko Huhta

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V

EXPERIMENTS WITH SIMULATED CONIFEROUS FOREST SOIL TO EVALUATE THE IMPACT OF SOIL FAUNA IN DECOMPOSITION

Biol. Fertil. Soils (in press)

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VI

MINERALISATION OF C,N AND P IN RELATION TO DECOMPOSER COMMUNITY STRUCTURE IN CONIFEROUS FOREST SOIL

Pedobiologia (in press)

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VII

SOIL FAUNA INCREASES THE GROWTH OF BIRCH (*Betula pendula*): LABORATORY EXPERIMENTS WITH CONIFEROUS FOREST FLOOR

Ecology (in press)

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