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Anne Siira-Pietikäinen

Decomposer Community
in Boreal Coniferous Forest Soil
after Forest Harvesting

Mechanisms behind Responses



UNIVERSITY OF JYVÄSKYLÄ

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ABSTRACT

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Yhteenveto: Pohjoisen havumetsämaan hajottajayhteisö hakkuiden jälkeen: muutoksiin johtavat mekanismit

Diss.

Effects of different forest regeneration methods on decomposer animals in boreal coniferous forest and the mechanisms behind the responses were studied in three field experiments and a laboratory experiment. The study focused mainly on enchytraeids, collembolans and microbes. In addition, decomposition, soil nitrogen availability and primary production were measured. In the first experiment, treatments with untreated controls were selection felling, gap felling with and without harrowing, retention felling (tree patches retained) and clear felling. The other field experiments were established in untreated forest to exclude major effects of changes in microclimate. The studied factors were exclusion of mycorrhizal connections (trenching), exposure of mineral soil (sod cutting) and addition of felling residues. The functional role of enchytraeids in different soil layers was studied in the laboratory experiment. Clear felling decreased fungal biomass and increased enchytraeid numbers. Microbial respiration decreased and community structure of microbes (PLFA pattern) changed as compared with the control. In addition, some litter dwelling macroarthropods (certain beetle species, spiders, scale insects) decreased in numbers. Responses in small gaps were similar to those in clear fellings, but smaller, whereas selection felling had no influence on the studied organisms. Trenching and sod cutting induced similar changes to measured variables as observed in clear fellings. Felling residues (slash) had no effect on soil organisms. Effects of enchytraeids on nitrogen mineralisation were dependent on soil layer and resource quality. It was concluded that despite some responses, the decomposer community is well buffered against initial changes caused by forest harvesting.

Key words: Clear cutting; Collembola; Enchytraeidae; forest regeneration; microbes; soil animals.

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- II Siira-Pietikäinen, A., Haimi, J. and Siitonen J. 2002. Short-term responses of soil macroarthropod community to clear felling and alternative forest regeneration methods. *For. Ecol. Manage.* In press.
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- V Haimi, J. and Siira-Pietikäinen, A. 2002. Activity and role of enchytraeid worm *Cognettia sphagnetorum* (Vejd.) (Oligochaeta: Enchytraeidae) in organic and mineral forest soil. Manuscript.

THE AUTHOR'S CONTRIBUTION

Papers I-III

Anne Siira-Pietikäinen has planned the experimental set-up together with the co-authors and performed calculations, statistical analysis and part of the experimental work. Among the studied animal groups, collembolans were identified to species by the author. Doctor Janna Pietikäinen and Docent Hannu Fritze were responsible for the microbiological analyses. The author is responsible for writing and interpreting the results.

Paper IV

Anne Siira-Pietikäinen has planned the experimental set-up together with co-authors. She has participated in experimental work, identified collembolans to species and performed statistical analysis. She is responsible for the interpretation of the results and for writing the manuscript together with the other authors. Docent Hannu Fritze was responsible for the microbiological analyses.

Paper V

Anne Siira-Pietikäinen has planned the experimental set-up together with the co-author and performed part of the experimental work. She has participated in the preparation of the manuscript.

1 INTRODUCTION

1.1 Forest regeneration and decomposer community

Traditional clear felling, which usually involves the removal of the entire stand and site preparation for natural regeneration, planting or seeding, is the dominant forest regeneration method in many parts of the world. However, because of many environmental changes caused by clear felling, such as alterations in forest microclimate, water balance, soil and nutrient cycling as well as changes in species diversity and composition of communities (Keenan & Kimmins 1993), general concern for ecological effects of clear felling has risen. In addition, researchers are concerned about the decreases in ability of managed forest to resist external stresses, such as exposures to acid rain, ozone, climatic extremes, pests etc. (resistance), or to recover from these disturbances (resilience) (Larsen 1995). Because of these possible ecological impacts of clear felling, new forest regeneration methods have been developed (see Kimmins 1997, Kohm & Franklin 1997) and used as standard management methods (see Vanha-Majamaa & Jalonen 2001). However, although knowledge has been accumulated on the ecological effects of clear felling, those of the new regeneration methods as well as the mechanisms behind these effects are mostly unknown.

Soil decomposer organisms (microbes and soil animals) are central in forest ecosystem function due to their important role in decomposition of organic matter and nutrient cycling. Thus, they can be regarded as reasonable objects in studies concentrating on ecological effects of forest harvesting. Forest soils generally harbour a rich organism community, including many different bacteria, fungi, protozoa, nematodes, microarthropods, enchytraeids, earthworms and macroarthropods (Huhta & Koskenniemi 1975, Huhta et al. 1986). Bacteria and fungi decompose dead organic matter and release (mineralise) nutrients, whereas mycorrhizal fungi promote nutrient and water uptake of plants. Soil invertebrates, in turn, play a regulating role in decomposition processes by stimulating microbial activity (Bååth et al. 1981, Persson 1989, Teuben 1991). This is partly explained by their direct grazing on

microbes, changing soil structure through litter comminution and burrowing activities as well as depositing nutrient rich faeces (Wallwork 1976, Teuben & Verhoef 1992). Since a large part of biologically important nutrients is present in the soil as organic complexes (Killham 1994), the changes in decomposer community and soil biological processes caused by forest harvesting may affect the function of the whole forest ecosystem.

Immediately after clear felling of boreal coniferous forests, microbial biomass either increases (Entry et al. 1986, Smolander et al. 1998) or decreases (Bååth et al. 1995, Pietikäinen & Fritze 1995), and microbial community structure changes (Bååth et al. 1995). The response of the biomass is obviously related to the proportions of fungi and bacteria in the soil prior to the harvesting, since immediately after clear felling the number of bacteria (Sundman et al. 1978), bacterial biomass (Lundgren 1982) as well as the bacterial-to-fungal ratio increases (Bååth et al. 1995) whereas in the cases in which the total microbial biomass has immediately decreased, the effect seems to be due to the lowered biomass of fungi (Bååth 1980, Bååth et al. 1995). The time of recovery of microbes varies between different studies. In the study of Lundgren (1982), conducted in Scots pine forest, bacterial numbers returned to control level during the third year after the felling, while in the study of Sundman et al. (1978), conducted in Norway spruce forest, numbers were at the control level only nine years after clear felling.

Generally, soil invertebrates increase in numbers soon after clear felling mainly due to a drastic increment in numbers of enchytraeids (Huhta et al. 1967, 1969, Huhta 1976, Lundkvist 1983). Among other abundant decomposer animals, collembolans also increase whereas mites decrease in numbers after clear felling (Huhta et al. 1967, 1969, Huhta 1976). Increment has also been observed in the numbers of nematodes after clear felling of pine forest (Sohlenius 1982). However, after clear felling of spruce forest, their numbers have decreased (Huhta et al. 1969). Like microbes, some soil animals also seem to respond differently to harvesting in nutrient-poor and dry Scots pine forest and mesic and fertile Norway spruce forest. In addition, these earlier studies reveal that the responses of both microbes and soil animals are transient, i.e. numbers first increase or decrease soon after felling and then return to the control level either sharply within one to two years, or slowly within many years.

In earlier studies, the responses of microbes and decomposer animals have been examined mainly at the level of total numbers and the focus has only rarely been on species or functional groups. However, the central question is: What changes in the soil community are reflected in the decomposition and mineralisation processes, i.e. ecosystem functioning? Are the changes in single species abundances, species diversity, community structure or total biomasses important? Or is it more worthwhile to focus on functional rather than taxonomical groups? Several ecosystem processes are thought to depend on the number of species (Tilman et al. 1996 and references therein). This belief is based on the idea that each species has its own fundamental niche (*sensu*

Hutchinson 1957). When the number of species increases, the number of the niches occupied also increases. Higher number of occupied niches, in turn, results in increased resource use, i.e. increased functioning. However, no clear relationship between soil animal species diversity and decomposition has been found (Andrén et al. 1995, Laakso & Setälä 1999, Setälä 2000). Instead, it has been repeatedly shown that the biomass of single important species, such as *C. sphagnetorum* in northern coniferous forests, is more important than the diversity of species (Setälä et al. 1991, Laakso & Setälä 1999, Setälä 2000). In addition to these empirical observations, some ecological theories emphasise the central role of some single species. For example, Walker (1992) pointed out that all species in an ecosystem are not equally important to ecosystem function, i.e. the ecosystem includes both 'driver' and 'passenger' species (*sensu* Walker 1992).

The theory of driver and passenger species supposes that the biological composition of an ecosystem includes functional redundancy at the species level, and therefore even a considerable reduction in the species number or changes in community structure do not necessarily lead to effects on ecosystem function. However, if functional groups consist only of a few species, i.e. species redundancy is small within the functional group, then species identities are central (Andrén et al. 1995). In addition, as was pointed out by Andrén et al. (1995), keystone species (Bond 1994), like functional groups (Faber 1991), are not substitutable. The functional redundancy of species includes the idea of passenger species as 'reserve forces', which after major environmental disturbances or changes in environmental conditions may turn out to be drivers (Walker 1992). Therefore, in studies of ecological effects, the focus should be on responses of different levels of organisms and on both taxonomic and functional groups.

1.2 Changes in soil environment after clear felling

1.2.1 Soil moisture and temperature

Forest harvesting increases soil water content and temperature amplitude. Water content is increased due to cessation of evapotranspiration and removal of forest canopy, which increases the amount of precipitation reaching the soil (Lundin 1979, Keenan & Kimmins 1993). Tree seedlings may suffer from too high soil moisture and depletion of oxygen, especially in soils rich in fine particles (Lähde 1978). Soil temperature, in turn, increases due to the larger amount of solar radiation reaching the soil in sunny days but decreases due to heat emissions from soil in the night time and the winter time (Pritchett 1979, Keenan & Kimmins 1993). The temperature amplitude of soil is further increased by exposing mineral soil for better establishment of seedlings (Kubin

& Kemppainen 1994). On the other hand, felling residues left on site reduce sun radiation reaching the soil and consequently reduce soil warming (Bjor 1972).

Moisture and temperature are among the most important environmental variables determining biomasses and community structures of decomposers (Bååth & Söderström 1982, Sulkava et al. 1996). Generally, both microbes and animals derive benefit from increasing temperature up to +30 - +40°C, when soil moisture is not a limiting factor (review of Christiansen 1964, Nurminen 1967, Abrahamsen 1971, Pritchett 1979, Salenius 1982, review of Wardle 1992). Drying of soil usually decreases, whereas wetting increases, bacterial and fungal biomasses (review of Wardle 1992) if wetting does not cause anaerobic conditions in soil. Similarly, soil animals requiring aquatic or semi-aquatic conditions, such as enchytraeids, are sensitive to soil drying and benefit from moist conditions (Nurminen 1967, Abrahamsen 1972, Lundkvist 1982, review of Didden 1993, Sulkava et al. 1996, Yli-Olli & Huhta 2000). On the other hand, animals living in air-filled soil pores, such as microarthropods, do not necessarily respond at all to changes in soil moisture (review of Christiansen 1964, Klironomous and Kendrick 1995, Sulkava et al. 1996). Soil animals may be less directly affected by temporary drying than microbes, since they are able to move into deeper soil layers that usually retain their moisture content (Usher 1970, Pritchett 1979). However, microbes have developed means to survive during extreme soil moisture potentials. It has been proposed that part of the active microbial biomass is able to enter a dormant phase during dry periods (Wardle 1992).

1.2.2 Exclusion of mycorrhizal connections

The mycorrhizal web, consisting of tree roots and their fungal symbionts, is important not only to plants but also to soil decomposer communities. It has been estimated that fine roots turnover and rhizodeposition returns two to five times more organic matter to soil than the aerial plant biomass (Fogel & Hunt 1983, review of Grayston et al. 1996). Thus, a large part of the resources for decomposers comes from fine roots and mycorrhizal fungi. Among the decomposers, bacteria, saprophytic fungi and saprophagous animals directly utilize the easily exploitable substrate of dead fine roots, whereas fungivorous animals, like some nematodes and microarthropods, graze on living mycorrhizal mycelia. Soil microbes as well as some invertebrates compete also for the readily usable resources provided by root exudates (review of Grayston et al. 1996).

After clear felling, reduction in tree root biomass can be fairly slow; in the study of Persson (1982), total living fine-root biomass of Scots pine was reduced by 60% during two growing seasons after the harvesting. Similarly, Hagerman et al. (1999) have reported a clear reduction in numbers of active fine roots only on second and third years after felling of Engelmann spruce subalpine forest. On the other hand, most of the mycorrhizal fungi die within a year after clear felling (Dalhberg et al. 2001). The negative effect of forest regeneration on the mycorrhizal-network is increased by mechanical site preparation, since it

commonly fragments the forest floor, where most of the mycorrhizal web is found.

Decaying mycorrhizal web increases the decomposable organic matter in soil. On the other hand, the removal of the energy source of the mycorrhizal web stops energy flow into the below ground food web. These changes in soil energy and nutrient resources may affect not only the amounts of microbes, the primary decomposers, but also consumers at higher trophic levels in the decomposer food web (Scheu & Schaeffer 1998, Chen & Wise 1999). This is the case if the animal communities are controlled from the bottom level of food web through the limited amount of resources (bottom-up control). However, if top-down forces through predators or other biotic (e.g. diseases) or abiotic factors (e.g. climatic factors) are more important in structuring soil animal communities, changes in resources are not necessarily reflected in numbers of soil animals. Bottom-up and top-down controls and their relationship in forest ecosystems have received a lot of attention from researchers during the last decade (e.g. Bengtsson et al. 1998, Mikola & Setälä 1998, Scheu & Schaefer 1998, Chen & Wise 1999). However, the relationship of these two forces in forests is still poorly understood.

1.2.3 Site preparation

In boreal coniferous forest, the establishment and the survival of seedlings are usually restricted by dense ground vegetation (Munson & Timmer 1995, Jäderlund et al. 1998) and a thick humus layer, which immobilizes nutrients and makes them unavailable for plants (review of Prescott et al. 2000). In addition, the growth of seedlings may be diminished by poor soil aeration, drainage and temperature conditions (Lähde 1978). To prevent these negative impacts on tree seedlings, mechanical site preparation, such as ploughing, harrowing or scalping, is used in Finland.

Mechanical site preparation removes part of the forest floor and organisms living in these layers and, in intensive methods, ploughs organic material into the mineral soil. Although the environment of soil organisms is consequently heavily disturbed by site preparation, the physical conditions created by it accelerate biological soil processes, such as decomposition (Voss-Lagerlund 1976, Palmgren 1984, Johansson 1994, Lundmark-Thelin & Johansson 1997). This may lead to accelerated nutrient mobilisation and leaching to lower parts of the soil. On the other hand, increases in soil nutrient availability soon after felling may help seedlings, the new forest generation, to survive over the critical phase.

The evaluation of ecological impacts is complicated by different kinds of patches created by mechanical site preparation, such as residual forest floor, mixed organic-mineral soil, and exposed mineral soil patches. In these areas, both abiotic (soil temperature and moisture) and biotic conditions are different (Palmgren 1984, Johansson 1994). This means that when ecological effects of site preparations are determined, it is necessary to understand the responses of soil

organisms and their functions in different kinds of patches created by mechanical site preparation.

1.2.4 Felling residues

Felling residues left on the ground after felling increase the amount and change the quality of resources for soil decomposers. They also cause higher and more even soil moisture, lower soil temperature and daily temperature amplitude in soils, when compared with soil without these felling residues (Bjor 1972). In addition, felling residues left on site raise soil pH (Nykqvist & Rosén 1985, Staaf & Olsson 1991), which can be seen as a balancing effect during the stand rotation, since soil pH commonly decreases through ion exchange by the roots of growing trees with the age of a forest stand.

Generally, felling residues have increased the amount of decomposer organisms soon after felling. Lundgren (1982), Sohlenius (1982) and Lundkvist (1983) reported that the addition of twice the normal amount of felling residues to the ground in clear-felled boreal Scots pine forest resulted in increases in numbers of bacteria, nematodes and enchytreids. In the same study plots, fungal community was also affected by felling residues (Bååth 1981), but no responses were observed in the amount of fungal hyphae or fungal biomass (Bååth 1980). The effects of felling residues were transient, with numbers of organisms returning to the control level during the first three years after the treatment. However, long lasting positive effects have also been documented. In the same experiment, mobile animals with high trophic position, such as gamasid mites, spiders and predatory insects, were more abundant in the plots where felling residues were added than in the plots without felling residues even 15-18 years after the treatment (Bengtsson et al. 1997, 1998). On the other hand, dipteran larvae and collembolans which can be classified as microbe-detritivores and fungivores, respectively, benefited from the felling residues in a less productive pine forest, but did not respond to a treatment in Norway spruce forest (Bengtsson et al. 1997).

The earlier studies showed that felling residues have both short-term and long-term effects on the decomposer community. However, the main mechanisms which caused the observed changes are still unclear, i.e. it is not known whether the energy and nutrient resources of felling residues or the changes in soil moisture and temperature are the most important factors, or whether they all have similar effects on decomposer communities.

2 AIMS OF THE STUDY

The aim of this study was to obtain new information about the effects of different forest regeneration methods on soil decomposer communities and the reasons for changes in decomposer community during first years after forest harvesting. Effects of harvesting methods were studied in a forest stand scale experiment, repeated in different sites, while the mechanisms behind the responses were studied in two small-scale field experiments and in a laboratory experiment. The study mainly focused on enchytraeids and collembolans but also nematodes, mites and macroarthropods were studied in part of the experiments. In addition, total biomass and community structure of microbes were simultaneously studied in all field experiments. The study questions were:

- a) What are the effects of traditional clear felling on total amounts and community structures of microbes and soil animals in the years immediately following harvesting? Are the possible changes at the low level (microbial community) of the decomposer food web reflected at higher levels (microbial feeders, predators)?
- b) Do the effects of alternative forest harvesting methods differ from the effects of clear felling?
- c) How does exclusion of mycorrhizal connections attributed to forest harvesting and mechanical site preparation change decomposer community and soil biological processes? Exclusion of mycorrhizal connections results in cessation of energy flow into the below ground food web and death of the mycorrhizal web (tree roots and their symbiotic fungi).
- d) How do the decomposer community and decomposition/mineralisation processes deviate in different kind of patches created by mechanical site preparation? Are the effects of *C. sphagnetorum* on mineralisation processes related to soil layer, i.e. amount and quality of resources in the soil?
- e) How does the decomposer community respond to the energy and nutrient resources of felling residues left on the ground after harvesting?

3 MATERIALS AND METHODS

3.1 Study sites

The study questions were examined in approximately 100-year-old boreal coniferous forest stands located in central Finland. The dominant tree species was Norway spruce (*Picea abies* (L.) Karst.) with Scots pine (*Pinus sylvestris* L.) and silver and pubescent birches (*Betula pendula* Roth and *B. pubescens* Ehrh.) as co-dominants. The ground layer of the understorey vegetation consisted of a thick moss layer, while dwarf shrubs dominated the field layer.

3.2 Experimental set-ups

3.2.1 Forest stand-scale experiment (I-II)

The responses of decomposer communities to clear felling and alternative forest harvesting methods were studied in the forest stand-scale experiment carried out as a randomised block design (study questions a-b). In the experiment, four separate study sites included 23 1-ha study plots (5-6 plots in each) and their adjacent surroundings, altogether 1.5-2 ha. Within each site, the study plots were randomly assigned to the following treatments: 1) control, untreated forest, 2) selection felling, 70% dispersed retention of green trees 3) gap felling, 50% aggregated retention with three clear-cut patches (0.10-0.15 ha) per hectare 4) gap felling with site preparation, 5) retention felling, 7% retention, about 50 trees retained in three groups per hectare, 6) clear felling, 0% retention with site preparation. The site preparation method used was harrowing, which creates continuous shallow trenches and berms. The sites were felled in March 1996 and the soil was prepared in August 1996.

On each 1-ha study plot, one 200-m² subplots was placed on harvested areas about 25 m from the centre of the plot towards randomly chosen corners (on retention felled plot subplots, it was situated in one of the retention tree patches). From forest floor (=humus, F-layer, litter, ground vegetation) of each

subplot, five 25-cm²-soil corer samples were collected for collembolans, five similar samples were collected for enchytraeids and four 625-cm² square soil samples were collected for soil dwelling macroarthropods. Samples (five 40-cm² soil samples) for microbial and chemical analysis (pH, total N and C) were taken from humus in four 16-m² subplots situated 25 m from the centre of the 1-ha plot towards the corners. All twenty samples from each study plots were combined as to give one bulk sample. Sampling for microbial and chemical analysis corresponded to that of soil animals on selection felled, clear-felled and untreated forest. The soil samples were taken once before the treatments in autumn 1995 and five times after the treatments during the three subsequent growing seasons from 1996 to 1998 (the samples for microbial and chemical analysis were not collected in 1998).

3.2.2 Small-scale field experiments (III-IV)

Two smaller-scale field experiments were established in an untreated forest stand. The first of these experiments (hereafter referred to as the trenching-felling residues experiment) concentrated on effects of exclusion of the mycorrhizal connections (trenching) and the effects of resources entering soil in the form of felling residues (study questions c, d). The experiment was established on June 1997 and carried out as a factorial design of randomised blocks, in which both factors, trenching and felling residues addition had two levels (treatment done or not done). Study plots (1x1 m) were ordinated to five separate groups (=blocks) and each treatment combination was randomly assigned to study plots within each of these blocks (n=5).

Soil animals were sampled before the treatments in June 1997 and during the three successive growing seasons after the treatments from 1997 to 1999. The samples for microbial analysis were taken after the treatments on the same four sampling dates as the samples for invertebrates. On the last sampling occasion (September 1999) samples were taken also for soil chemical analyses (pH, mineral N), and the cover of field layer vegetation was estimated (area-% of each species on the study plots). Two separate soil corer samples per plot were taken for enchytraeids, nematodes and microarthropods and microbes (on the last sampling occasion only one soil sample was taken per plot for each organism group). A soil corer with a surface area of 10 cm² was used for microbes and nematodes, and 25-cm² soil corer was used for enchytraeids and microarthropods. The samples for each organism group included the whole forest floor, however green parts were removed from the samples before microbial analysis.

Another smaller-scale experiment (hereafter referred to as the sod cutting-trenching experiment) focused on disturbances caused by exposure of mineral soil (sod cutting) and trenching (study questions c, e). Similar to the trenching-felling residues experiment, this experiment was carried out as a factorial design. The factors, sod cutting and trenching had two levels (treatment done or not done) and each treatment combination had five replicates (n=5). However, this time the study plots were not grouped to blocks and the study

plots were smaller (0.25 m²). Two cellulose strips (3 × 6 cm) were also placed in the mineral soil of each study plot in order to examine decomposition of organic matter. In addition, contrary to the trenching-felling residues experiment four one-year-old Scots pine seedlings were planted on each study plot to examine primary production and nutrient availability for plants.

The soil samples were taken as in the trenching-felling residues experiment, but now one sample per organism group (microbes, collembolans and enchytraeids) was taken from each plot. In addition, surface dwelling macroarthropods were sampled with pit-fall traps during a two-week period on each sampling occasion. The soil samples for soil organisms were taken before the treatments (June 1998) and in two successive autumns after the treatments (September 1999 and 2000). The pine seedlings as well as the cellulose strips were collected on both post-treatment sampling occasions.

3.2.3 Laboratory experiment (V)

The laboratory microcosm experiment was designed to find out whether functional properties of *C. sphagnetorum* living in mineral soil are different from those in organic soil layers (study question e) and whether needles of felling residues have effects on enchytraeid numbers or function (study question d). The experiment was carried out as a factorial design with three factors and two levels: 1. humus and F-layer (=partly decayed conifer and ground layer vegetation litter and brown parts of the moss), 2. needles from 1-year old felling residues and 3. enchytraeids either added or not added on mineral soil in microcosms. This design resulted in 8 treatment combinations, which were repeated 5 times (total number of microcosms was 40). The experiment was established in semi-open (gas exchange allowed through a cotton plug at the top) transparent plastic cylinders with a bottom area of 55 cm² and height of 9 cm. The microcosms including humus with F-layer on mineral soil mimicked residual forest floor in clear-felled and harrowed areas, whereas the microcosms including only mineral soil mimicked exposed mineral soil. The soil materials were first defaunated (24h at +80°C, one week at -22°C) and then inoculated with microflora and fauna in soil water suspension. During the experiment, microcosms were kept in a climate chamber at +15°C and irrigated with de-ionised water when needed. Number of enchytraeids, their gut content, soil mineral nitrogen content, soil moisture and pH were separately analysed from mineral and organic soil layers 8 and 13 weeks after the establishment of the experiment.

3.3 Analyses of responses

3.3.1 Soil invertebrates

This study focused on total numbers and community structure of collembolans and numbers of enchytraeids. These groups were chosen since they are two of the most abundant and important decomposer animal groups in boreal forest soils. *C. sphagnetorum*, the dominant enchytraeid species can also be characterized as a 'driver species' in boreal coniferous forest soil due to its impact on decomposition activity (Standen 1978, Cole et al. 2000), nutrient mineralisation (Williams & Griffiths 1989, Abrahamsen 1990, Briones et al. 1998) and primary production (Laakso & Setälä 1999, Laakso et al. 2000). Further, these animal groups represent two types of soil animals; collembolans live in air-filled soil pores while enchytraeids are semi-aquatic. In order to get a more detailed picture of the whole decomposer animal communities in boreal forest soil, the responses of the total numbers, community structures and functional groups of macroarthropods, nematodes and mites were studied in part of the experiments.

Enchytraeids were extracted from soil samples with the standard wet funnel method. The numbers of individuals were counted and the length of each worm was measured for calculation of biomass (Abrahamsen 1973). In addition, in the laboratory experiment, gut contents of the worms were examined with a microscope. Since about 99% of individuals represented the species *C. sphagnetorum* (Vejd.) the other species were not identified further. Nematodes were extracted with the wet funnel method described by Sohlenius (1979), microarthropods were extracted with a high gradient extractor and macroarthropods were extracted with large Tullgren funnels.

Among the animal groups studied, collembolans and soil dwelling coleopterans were identified to species level whereas nematodes and mites as well as the rest of the macroarthropods were identified to higher taxonomic levels. In addition, nematodes and macroarthropods were assigned to feeding groups (Yeates et al. 1993).

3.3.2 Microbes

Soil microbes were studied in all field experiments, since they are primary decomposers and they form an important food resource for many soil invertebrates. Microbial biomass and community structure were measured by determining the phospholipid fatty acids (PLFA) present in the cell membranes of the microbes (I-IV). The PLFAs were extracted from humus using the method and nomenclature described by Frostegård et al. (1993). Twelve individual PLFAs listed by Frostegård and Bååth (1996) were regarded as having bacterial origin and 18:2 ω 6,9 was taken to represent fungal biomass. In the forest stand scale experiment microbial biomass was determined also by the substrate-

induced respiration (SIR) method as described by Priha & Smolander (1994) and based on the theory of Anderson & Domsch (1978). The SIR method takes into account the active microbial biomass having aerobic metabolism, which is able to utilize glucose. Activity of microbes was measured as CO₂ production by gas chromatography from moisture-adjusted soil samples (Pietikäinen & Fritze 1995). In addition, functionality of the bacterial community extracted from the organic soil sample was indicated using Biolog Ecoplates (www.biolog.com).

3.3.3 Vegetation, decomposition and chemical analyses

To examine the impacts of forest harvesting on function of the decomposer community, decomposition rate, nitrogen availability in soil as well as nitrogen content and growth of seedlings were determined in part of the experiments. The understorey vegetation was studied in 1-ha study plots of the forest stand scale experiment (I) by Jalonen & Vanha-Majamaa (2001). The total ground vegetation cover and proportions of single plant species were evaluated in the trenching-felling residues experiment (III) on the last sampling occasion. Decomposition was studied *in situ* using pieces of cellulose strips (3 × 6 cm) placed in the mineral soil (III). The strips were collected and their weight losses were measured 3 and 15 months after the treatments. The availability of nitrogen was evaluated by measuring amount of ammonium- (NH₄) and nitrate-nitrogen (NO₃) in soil (III-V). NH₄⁻ and NO₃⁻ ions and pH in soil were measured in a humus- or mineral soil-water suspension. Total carbon and nitrogen in humus was also analysed (I). The amount of mineral nitrogen was measured using a FIA-autoanalyser (Flow Injection Analyser) and total carbon and nitrogen in humus was measured by dry combustion with a Leco CHN-1000 analyzer. Nitrogen intake of seedlings was studied by measuring total nitrogen content of the seedling (IV). Nitrogen of seedlings was analysed by the Kjeldahl method after grinding seedlings with a mill. In addition, length of the pine seedlings and dry masses of their needles, shoots and roots were determined. Infection level of each seedling by ectomycorrhizal fungi was roughly determined under a binocular microscope by estimating the proportion of dichotomous root tips out of all the root tips (IV).

3.4 Statistical analyses

Differences between the treatments were tested with repeated measure analysis of variance using pre-treatment values as covariants (repeated measures ANCOVA). When the assumptions of normal distributions or equality of variances were not met, results were transformed with $\ln(a+1)$ or $\log(a+1)$. Pairwise comparisons were done with a Tukey's test when all pairs were compared and a Dunnett's test when the treatments were compared only to control. Effects of the treatments on collembolan, mite and nematode

community structures, as well as on microbial community structure (indicated by PLFA pattern) were analysed with non-metric multidimensional scaling (NMDS) ordination method (DECODA software, Minchin 1991 and PC-ORD software, McCune & Mefford 1999), which results in a representation of the data in few dimensions so that distances in the ordination reflect as closely as possible the similarities/dissimilarities between the community structures of the sample plots (Clarke 1993). To detect the differences between the communities after the different treatments, sample scores of NMDS were subjected to repeated measures ANCOVA, followed by Tukey's or Dunnett's test. In the ordinations, abundance data of invertebrates (the means of samples collected from each study plot/subplot) and the mol% data of PLFAs were used. The data of invertebrates were transformed to $y^{0.5}$ and the PLFA data to $y^{0.25}$ resulting in a greater contribution of rare species (see Clarke, 1993). The Sørensen (Bray Curtis) distance measure was used for mol% data of PLFAs and the relative Sørensen distance measure for abundance data of invertebrates. Total, bacterial and fungal PLFAs as well as variables formed by NMDS from the PLFA and vegetation data were used as environmental variables in NMDS ordinations of invertebrates.

4 RESULTS AND DISCUSSION

4.1 Responses to clear felling

Clear felling resulted in a 35% reduction in total microbial biomass compared with the control forest two years after the harvesting (Table 1, I). Since fungal biomass decreased (Table 1, I) the reduction in microbial biomass was most likely attributed to reduction in mycorrhizal fungi. A similar response pattern was found also in basal respiration, which decreased by 55% in the second autumn after the felling (Table 1, I). These observations supported the earlier finding that harvesting reduces the microbial biomass a few years after felling (Bååth et al. 1995, Bauhus & Barthel 1995, Pietikäinen & Fritze 1995, Bauhus 1996). However, in the present study, no changes were observed in bacterial biomass (Table 1, I), although their numbers, measured as colony forming units, have commonly increased immediately after clear felling and later have been followed by decreases to the control level or below it (Niemelä & Sundman 1977, Sundman et al. 1978, Lundgren 1982, Kauri 1983). Overall, the result of the present study supported the earlier impression that soil fungi are initially more affected by clear felling than bacteria (see Bååth et al. 1995).

The community structure of microbes responded to environmental changes caused by harvesting by the autumn of the first growing season after felling, at the time when microbial biomass was still at the control level (Table 1, I). This indicates higher sensitivity of microbial community structure to harvesting induced changes compared with total microbial biomass. Changes in microbial community structure after clear felling have been documented earlier by Niemelä & Sundman (1977) and Bååth et al. (1995). On the other hand, substrate utilisation pattern of microbes did not differ between clear-felled and mature forest suggesting that the potential degradation capacity of the microbial community did not change. This means that, in laboratory conditions, the microbial community of the clear-felled area had the same ability to decompose organic matter as the microbial community of the control forest. However, the actual function of microbes in the field is not known.

The reduction in fungal biomass was not reflected in numbers of fungal feeding collembolans: neither their total numbers nor community structure

TABLE 1 The responses of measured variables to the different treatments done in all four field experiments. '0' indicates no responses to treatment, '+' increment, '-' reduction in number/amount/content and '*' indicates change in community.

	Selection felling (I,II)	Gap felling (I,II)	Gap felling with harrowing (I,II)	Retention felling (I,II)	Clear felling (I,II)	Trenching of organic soil (III, IV)	Trenching of Exposed mineral soil (IV)	Sod cutting (IV)	Addition of felling residues (III)
Soil chemistry:									
-Ph	0				+	0	0	+	0
-C/N	0				+				
-NH ₄						+	0	-	0
-NO ₃						0	+	0	0
Seedlings:									
-Growth						0	+		
-Nitrogen content						+	0		
Decomposition rate						0	0	+	
Microbes:									
-Tot. biomass	0				-	0	0	0	0
-Basal respiration	0				-				
-Bacterial biomass	0				0	0	-	0	0
-Fungal biomass	0				-	-	0	0	0
-Community structure	0				*	*	0	0	0
Soil mesofauna:									
-Enchytraeids	0	+	0	0	+	+	0	+	0
-Nematodes						+			0
-Collembolans:	0	0	0	0	0	-	0	0	0
Community structure	0	0	0	0	0	*	*	*	0
H'	0	0	0	0	0	0	-	0	0
-Mites						-			0
Macrofauna:									
- Tot. numbers	0	0	0	0	0				
- Coleopterans:	0	0	0	0	+			-	
community structure	0	*	*	*	*				

(continues)

(TABLE 1 continues)

H'	0	0	0	0	0			
- predators:	0	0	-	0	-			
Araneae	0	0	-	-	-		+-	
Cantharidae (Coleoptera) larvae	0	0	0	0	0			
<i>O. myrmecophilus</i> (Coleoptera) larvae	0	0	0	0	0			
- Herbivores:	0	0	0	0	0			
Coccoidea	0	0	-	0	-			
Thysanoptera	0	0	0	0	0			
Aphidoidea	0	0	0	0	0			
Heteroptera	0	0	-	0	-			
Elateridae (Coleoptera)	0	0	0	0	0			
Lepidoptera larvae	0	0	0	0	0			
-Soil-dwelling fungivores:								
Aleocharinae (Coleoptera) larvae	0	0	0	0	0			
-Detritivores	0	0	0	0	0			
Brachycera (Diptera) larvae	0	0	0	0	0			
Nematocera (Diptera) larvae	0	0	+	0	0			
-Litter dwelling fungivores:								
Entomobryidae (Collembola)	0	0	0	0	0		-	

changed after clear felling (Table 1, I). The resistance of the collembolan community against environmental changes induced by harvesting is in accordance with the study of Huhta (1976) done in Norway spruce forest of the northern part of Finland. On the other hand, in the studies of Huhta et al. (1967, 1969) and Huhta (1976), done in spruce forest of the southern part of Finland, corresponding to the study sites of the present study, collembolan numbers clearly increased soon after clear felling. The different responses to clear felling may be due to different environmental conditions at the study sites or differences in food resources. While their main food source is soil fungi, collembolans have been found to feed on many kinds of organic material available in soil (Hopkin 1997). In the present study and in the studies of Huhta (1976) and Huhta et al. (1967, 1969), fungal community composition could not be analysed. Thus, the final explanation for the different responses can not be given here. However, an interpretation of the results of the present study may provide one possible reason why collembolans do not respond or increase in their numbers after clear felling. In the clear-felled areas of the present experiment, food sources of collembolans were supposed to decrease after the felling, because the total amount of fungi was reduced in the second growing season. On the other hand, Dahlberg et al. (2001) observed that mycorrhizae, a preferred food source for many collembolan species (Hopkin 1997), decrease already during the first year after felling. Thus, it is likely that saprophytic fungi increased in the plots of the present study (and those of Huhta 1976, and Huhta et al. 1967, 1969) soon after clear felling offering abundant food resources for collembolans. Collembolans were able to switch, at least partly, from mycorrhizae to other fungi, and later also to other material, as their main food source. The obvious increase in saprophytic fungi (as well as in some bacteria) in clear-felled areas during the first year after the harvesting was most likely attributed to the large amount of fresh litter available in felling residues and soil, and favourable soil conditions created by site preparation. Overall, that there were hardly any changes in collembolan community after clear felling suggests that collembolans are able to tolerate changes e.g. in their main food sources, induced by harvesting. The relation between fungi and fungal feeders was studied more closely in the small-scale experiment (see 4.4).

Number of the enchytraeid, *C. sphagnetorum*, drastically increased after clear felling (Table 1, I). The numbers in clear-felled areas were about four times higher than those in the control forest in the third year after the clear felling. A similar strong increase in number of enchytraeids has been repeatedly observed earlier, after clear felling of both Norway spruce (Huhta et al. 1967, 1969, Huhta 1976, Sundman et al 1978) and Scots pine forest (Lundkvist 1983). In the earlier studies, a strong increment in the numbers of *C. sphagnetorum* during the first few years after felling was followed by a decline to the control level. Thus, also in our study site, the responses of *C. sphagnetorum* can be expected to be transient.

Clear felling had no effect on the total numbers of soil dwelling macroarthropods (Table 1, II), but, as also observed in the study of Huhta et al.

(1967), predators (mainly spiders) and some herbivores (Coccoidea, Heteroptera) decreased, while certain detritivores (Nematocera [diptera] larvae) increased in numbers (Table 1, II). It seems that the responses of macroarthropods are, at least partly, attributed to the feeding biology of the animals, since soon after felling the food resources of herbivores (reduction in amount of living tree roots) decreased, while the food resources of detritivores increased (dying roots and shoots, felling residues).

The reduction of spiders was obviously not caused by changes in their resources, since their most evident prey taxa, microarthropods (Kajak 1997, Lawrence & Wise 2000) were not affected by the treatments (Table 1, I, II). More likely, small spiders dwelling in the uppermost soil horizons responded to the changes in litter and reduction in moss cover (Jalonen & Vanha-Majamaa 2001), because as web-builders they require suitable microhabitat structures for web construction. The reduction in numbers of spiders as well as changes in spider community after clear felling has been documented earlier. Huhta (1971), McIver et al. (1992) and Pajunen et al. (1995) observed that the catches of forest ground-living, web-building species, such as linyphiids, decreased and the catches of large hunting-spider species (Gnaphosidae, Lycosidae) increased in clear-felled areas. In the large-scale experiment of the present study, spiders were extracted from organic soil samples and only a few hunting-spiders were caught. Thus, the observed reduction in numbers of spiders was due to the reduction in small linyphiids (II). On the other hand, in the sod-cutting-trenching experiment (IV), pit fall traps were used and the spiders trapped mainly belong to the family Lycosidae (IV). In this experiment, lycosids were most active in the sod-cut plots indicating their preference for exposed mineral soil patches.

An assemblage of dominant beetle species changed almost completely after harvesting (Table 1, II): small staphylinids, *Atheta myrmecobia*, *Oxyptoda annularis* dominated the beetle community before felling and *Amischa analis*, *Sipalia circularis* and *Othius myrmecophilus* dominated after clear felling. The increases in numbers of *A. analis* and *O. myrmecophilus* after clear felling have been observed earlier by Huhta et al. (1986). However, the beetle community, as a whole, was quite resistant to changes after harvesting, since total number of beetles increased only transitionally and their species number or diversity was not affected (Table 1)(II).

4.2 Reduction in intensity of harvesting

When 30% of the stand volume was harvested by selection felling, no changes were observed in soil organisms (Table 1, I, II). Changes were expected, since selection felling and its felling residues left on site certainly, to some extent, altered the soil environment. This observation was not in agreement with the result of Huhta et al. (1967), in which numbers of enchytraeids and collembolans decreased after thinning of boreal coniferous forest.

In residual tree groups of retention-felled areas, the soil mesofauna (enchytraeids and collembolans) was not affected by harvesting when compared with those in control forest (Table 1, I). On the other hand, the macroarthropod community in the patches started to resemble communities in the clear-felled areas (Table 1, II), indicating that residual patches were too small to maintain the isolated community of mobile macroarthropods. In addition, although the patches were not mechanically prepared, the shade provided by the residual trees did not significantly prevent environmental changes in litter layer and ground vegetation, and the living environment of macroarthropods in the residual patches began to resemble the harvested surrounding. Thus, it can be concluded that the tree groups studied were hardly able to 'lifeboat' (*sensu* Franklin et al. 1997) macroarthropod species, that is to provide a refugium for them over the regeneration phase. Yet the less mobile organisms in deeper soil layers may derive benefit from the patches, since their living environment obviously was altered only slightly during the first years after felling.

4.3 Reduction in size of harvested area

Soil communities are expected to benefit from untouched forest surrounding small harvested gaps, since the mycorrhizal web and canopy shade of untouched forest reduce the environmental changes in soil caused by harvesting, such as changes in soil temperature, moisture, structure and resources ('forest influence' *sensu* Keenan & Kimmins 1993). However, in our experiment, there were no significant differences in the responses of soil organisms between the 1-ha and 0.10-0.15-ha harrowed gaps (I-II), indicating a minor role of forest influence on changes in soil communities after harvesting and site preparation. It might be that harrowing carried out after harvesting decreased the forest influence by destroying part of the mycorrhizal network and ground vegetation.

4.4 Exclusion of mycorrhizal connections

Trenching the study plots in the small-scale experiment decreased fungal biomass (Table 1, III, IV). Here the reduction was reflected in soil fungal feeders; total numbers of collembolans, abundance of some species of collembolans (*Mesaphorura yosii* and *Willemia anophtahlma*) and numbers of oribatid mites (Table 1, III, IV). The parallel changes in soil fungi and fungal feeders suggested that the exclusion of mycorrhizal connections decreases the amount of fungi preferred by microarthropods. In addition, it seemed that the food resources of euedaphic collembolan species, such as *M. yosii* and *W. anophtahlma* were most affected. Forest harvesting also eliminates the mycorrhizal connections and a similar trophic relation was therefore expected to be seen in clear-felled areas. However, as it was discussed earlier, collembolans did not respond to clear felling, although the total amount of fungi decreased significantly. The reason for these different responses may be attributed to larger natural spatial variation in numbers of fungal feeders at forest stand scale compared to that at smaller scales, exceeding the changes in numbers of microarthropods caused by the treatment. The differences between responses may also be explained by the smaller food resources of collembolans in the trenched plots compared with those in clear-felled areas: saprophytic fungi did not provide similar increasing food resources for fungal feeders in trenched plots as it might do in clear-felled areas. This is evident because ground and field layer vegetation did not die, and so no fresh organic matter was offered to decomposers and the soil organic layer remained untouched (no site preparation was applied).

C. sphagnetorum increased in numbers in trenched plots, but not until two to three years after the treatment (Table 1, III). The delayed responses might have been caused by the slowly dying and decaying roots of trees, increasing resources for enchytraeids (Persson 1982). However, we could not exclude the effect of changes in soil moisture. In earlier trenching experiments, soil moisture has commonly been observed to increase due to a lack of functioning tree roots (Gadgil & Gadgil 1974, Babel 1977, Harmer & Alexander 1985). Thus, in our experiment, enchytraeids as semi-aquatic soil animals might also have derived a benefit from the increase in soil moisture (Nurminen 1967, Abrahamsen 1971, review of Didden 1993, Yli-Olli & Huhta 2000).

The total number of nematodes increased transitionally in isolated plots, a change attributed mainly to the increase in numbers of the most abundant bacteria feeding nematode genus, *Teratocephalus* (*spp*) (Table 1, III). The reason for these increased numbers is not clear since bacterial biomass was not affected by the treatment. Yet the increment in soil ammonium nitrogen content in trenched plots obviously changed the bacterial community, which might be reflected in bacteria feeding nematodes. The positive correlation between nematodes and amount of mineral nitrogen has been observed in earlier studies (Bååth et al. 1978, Sohlenius & Wasilewska 1984, Ettema et al. 1998).

A positive effect of trenching on soil mineral nitrogen content has been observed in earlier studies (see review by Goomes & Grubb 2000). In the present experiment, increased nitrogen content in isolated soil was reflected in vegetation, as larger cover of herb species (III) and higher nitrogen content of pine seedlings in both organic soil and exposed mineral soil (IV) showing that also the nitrogen availability for plants increased (Table 1). The reason for the higher ammonium content in soil after trenching may lay both on the ceased uptake of tree roots and accelerated nitrogen mineralisation.

Overall, the responses observed after trenching of the small study plots in mature forest were very similar to those documented in clear-felled areas in earlier studies (NH₄: Smolander et al. 1998; bacteria: Lundgren 1982; fungi: Bååth 1980, Bååth et al. 1995; nematodes: Sohlenius 1982, 1996; microarthropods: Blair and Crossley 1988; enchytraeids: Huhta et al. 1967, 1969 Huhta 1976, Sundman et al. 1978, Lundkvist, 1983) and in the forest stand scale experiment of the present study (I). In the trenched study plots and in the clear-felled coniferous forest, energy flow from above to below ground stops, since the energy source of tree roots and their fungal symbionts is removed by felling and their network is fragmented by site preparation. Since the effects of the other potential causal factors in clear-felled areas (changes in soil temperature amplitude, litter fall and ground vegetation) could mainly be excluded by the experimental design, it can be concluded that the exclusion of mycorrhizal connections is one of the most important factors causing changes in decomposer community after clear felling.

4.5 Site preparation

Harrowing had no effects on enchytraeids or collembolans in residual organic soil patches of the harvested area (Table 1, I). However, the responses of some macroarthropods (spiders, Coccoidea, Nematocera larvae) were stronger in the retained forest floor of harrowed gaps than in unprepared gaps. These findings provide evidence that harrowing induced only minor changes in the retained humus layer during the first years after site preparation, while the uppermost forest floor (litter, bottom layer vegetation), the living environment of macroarthropods, was more altered.

In the sod cutting-trenching experiment the focus was on exposed mineral soil patches of harrowed areas (IV). Most decomposers live in the organic soil layer, thus a large part of them is removed by sod cutting. The re-establishment of populations after sod cutting is a relatively slow process, strongly dependent on the conditions in the new developing organic layer and the distance of exposed patches from the source population (de Goede 1996). Still, at least in some organism groups, colonization of exposed mineral soil starts immediately after sod cutting. In the present experiment, *C. sphagnetorum* increased in number already 16 months after treatment. Evidently, due to their effective

asexual reproduction, they were able to increase in number along with accumulating litter.

Microbes and collembolans showed hardly any responses in exposed mineral soil during two growing seasons after sod cutting (Table 1, IV). Only the community structure of collembolans slightly changed. The high resistance of these organisms to sod cutting was surprising, since microbes easily react to environmental changes (Wardle 1992). On the other hand, sod cutting accelerated the cellulose decomposition activity, indicating that modifications to the soil environment induced by sod cutting accelerated microbial metabolism (Table 1, IV).

Although microbial activity seemed to be accelerated in exposed mineral soil, ammonium concentrations decreased about by 45%. This reduction was reflected also in decreased nitrogen concentrations of seedlings (Table 1, IV). The reason for the reduction may lay in the increased nutrient immobilisation by soil microbes and/or the fact that sod cutting stops leaching of nitrogen from humus to lower soil layers. The relationship between sod cutting and soil ammonium nitrogen content was studied more closely in the microcosm experiment (V). In that experiment, *C. sphagnetorum* clearly increased mineralisation in bare nutrient poor mineral soil. On the other hand, the organic soil and needles on mineral soil can make the effect of enchytraeids on mineralisation negative, i.e. enchytraeids decreased soil ammonium content (V). The decreasing effect of enchytraeids on $\text{NH}_4\text{-N}$ in the mineral soil in the presence of soil organic layer and needles may be explained by enhancement of nutrient immobilisation by soil microbes induced by enchytraeid activity. This observation is consistent with the results of Liiri et al. (2001). They observed that the effect of enchytraeids on plant growth and nitrogen content turned out to be negative when the soil was treated with wood ash, which increased soil pH. They hypothesised that because ash changed the composition of the microbial community in the soil, dominating microbes in ash-treated soil may have responded differently to enchytraeid grazing compared with microbes in ash-free soils. Thus, the net impact of enchytraeids on soil nitrogen mineralization seems to be dependent on different environmental factors, such as quality of resources and microbial community structure.

Sod cutting accelerated growth of the seedlings (Table 1, IV). The explanation for this observation is obviously attributed to reduction in competition for nutrients and space with other plants as well as changes in soil physical conditions induced by exposure of mineral soil. It is, however, possible that, like in the earlier studies, sod cutting decreased acidity and amount of phenolics in soil, both of which have been observed to stimulate germination as well as development and mycorrhization of the seedlings (Baar & ter Braak 1996, Baar & Kuyper 1998,).

The sod cutting-trenching experiment gave some hints to the mechanisms behind the effects of site preparation. Since some observations made in the sod-cut plots, such as increase in decomposition activity and seedling growth, have been made earlier in clear-felled areas (Mälkönen 1976, Ritari & Lähde 1978,

Palmgren 1984, Örlander et al. 1997, Zackrisson et al. 1997), we can conclude that the modifications to the soil environment induced by removal of canopy and ceased evapotranspiration of trees have no important role in these changes. Instead, the key factor seemed to be the modifications to soil conditions created by removal of humus and ground layer vegetation.

4.6 Felling residues

The addition of felling residues to the ground of the untreated forest did not result in changes at any trophic level studied (Table 1, III). This was surprising, because, in clear-felled areas, felling residues have commonly increased the numbers of many decomposers (Lundgren 1982, Sohlenius 1982, Lundkvist 1983, Bird & Chatarpaul 1986, Sohlenius 1996, Bengtsson et al. 1997) as well as nitrogen availability in the soil (Rosén & Lundmark-Thelin 1987). This result may be explained by the fact that, under the canopy, abiotic factors such as soil temperature and moisture were different from those in clear-felled areas.

In clear-felled areas, where felling residues have been left on the ground, amplitude of soil surface temperature is lower under the felling residues layer compared to areas without felling residues. In the study of Bjor (1972), the daily temperature variations decreased by about 50% under a 30cm layer of felling residues, whereas moisture content increased, being relatively high throughout the growing season. The increment in moisture of the soil upper layers is caused by a reduction in direct evaporation under felling residues and also by the reduction of the evapotranspiration of vegetation, since plants cannot establish in the areas covered by a thick felling residues layer (Rosén & Lundmark-Thelin 1987). Both lower temperature amplitude and increased soil moisture favour soil organisms, and this could be the reason for the increased numbers of decomposers after felling residues addition in earlier studies. In the present experiment, these environmental factors were at least partly excluded, because the forest canopy decisively reduced the sun radiation reaching the soil. In addition, due to the smaller amount of felling residues added in the present experiment compared with those in the study of Bjor (1972), the field vegetation under the felling residues did not die but continued evapotranspiration. Thus, it can be concluded, that, since no responses were observed in decomposer communities, the energy and nutrients provided by felling residues were not important for decomposers during the first years after felling.

The reasons why resources of felling residues did not induce responses to decomposers are not clear. As was pointed out by Bååth (1980), the nutrients and energy that were released from felling residues could have been immobilised in the litter layer leaching only slowly to the horizons lower in the soil profile. On the other hand, energy resources added as felling residues could

be small compared to the resources already present in the northern coniferous forest humus layer.

5 CONCLUSIONS

The study suggested that the decomposer community in boreal coniferous forest soil is well buffered against initial environmental changes caused by forest regeneration. Many separate findings support this conclusion: 1) although some species were sensitive to harvesting, species richness or diversity was rarely affected, 2) changes in sensitive organism groups (microbes, mycorrhizal fungi) were not reflected at higher trophic levels, i.e. the decomposer community as a whole was able to resist the environmental changes induced by harvesting, and 3) the most intensive harvesting method, clear felling, induced only minor or moderate changes while the less intensive method did not induce any changes in the decomposer community. The study also showed that energy and nutrients in felling residues have hardly any impact on decomposer communities during the first years after felling.

One of the main mechanisms changing the decomposer community after forest harvesting is attributed to the exclusion of mycorrhizal connections. An elimination of this energy pathway to the below ground food web reduces amounts of some bacteria and soil herbivores benefiting from living roots or their exudates, and increases the number of detritivores utilizing decaying roots and fungal mycelia. In addition, cessation of root function increases soil nitrogen availability and moisture content, both of which favour many soil organisms as well as tree seedlings. The central role of the mycorrhizal web in changes of decomposer communities explains, at least partly, why no responses were observed after selection felling and why responses were minor in small residual tree groups. Due to the green trees left on site after selection felling and in retention felling, the mycorrhizal web stays alive and continues its functions also after harvesting.

Site preparation (exposing mineral soil) removes a large part of organisms with the soil organic layer. However, microbes and enchytraeids are capable of maintaining their populations, functioning in exposed mineral soil and significantly increasing their population densities along with improving conditions and accumulating organic matter.

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YHTEENVETO

Pohjoisen havumetsämaan hajottajayhteisö hakkuiden jälkeen: muutoksiin johtavat mekanismit

Metsämaassa elävä hajottajaeliöstö pilkkoo, muokkaa ja hajottaa kuollutta eloperäistä ainesta. Hajotuksen myötä siihen sitoutuneet ravinteet vapautuvat uudelleen kasvien käyttöön. Hajottajiin kuuluu bakteereja, sieniä ja monenlaisia hajottajaeläimiä. Osa metsämaan sienistä muodostaa kasvien kanssa sienijuuren, joka edesauttaa kasvien ravinteidenottoa. Sienijuuren sieniosakas liittyy kasvien juuret suureen sienijuuriverkoston, jonka kautta ravinteita ja yhteyttämisuotteita siirtyy puuyksilöstä toiseen ja jopa puulajista toiseen. Avohakkuu ja sitä seuraava maankäsittely muuttavat voimakkaasti hajottajaeliöstön elinympäristöä, eliöstön rakennetta ja toimintaa sekä rikkovat sienijuuriverkoston. Uusien metsänuudistusmenetelmien tavoitteena on osaltaan vähentää puunkorjuun aiheuttamia haitallisia muutoksia myös maaperän hajottajaeliöstössä.

Maaperäeliöstön vasteita erilaisiin metsänkäsittelyihin tutkittiin satunnaistettujen lohkojen kokeella yhden hehtaarin koelohjoilla. Tässä kokeessa käsitellyt olivat 1) harsintahakkuu, 2) pienaukkohakkuu (kolme 0.10-0.15 ha aukkoa hakattiin), 3) pienaukkohakkuu ja maan äestys, 4) uusimuotoinen avohakkuu (kolme pientä puuryhmää per hehtaari jätettiin hakkaamatta), ja 5) avohakkuu. Lisäksi osa koelohjoista jätettiin koskemattomiksi kontrollimetsiksi. Vasteisiin johtavia mekanismeja tutkittiin kahdella pienimittakaavaisella maastokokeella ja laboratorioskokeella.

Kokeissa mitattiin seuraavia maaperän biologista toimintaa kuvaavia muuttujia: humuksen pH, humuksen hiili- ja typpipitoisuus, ammoniumtyypen ($\text{NH}_4^+\text{-N}$) ja nitraattityypen ($\text{NO}_3^-\text{-N}$) pitoisuudet, maahengitys, mikrobien kokonaisbiomassa, bakteerien ja sienten biomassat (sienten biomassan muutos mittaa myös sienijuuriverkoston muutoksia), mikrobien yhteisörakenne, mikrobien kyky hajottaa eri hiilenlähteitä sekä hajottajaeläimistä änkyrimatojen biomassa ja yksilömäärä, hyppyhäntäisten yksilömäärä ja yhteisörakenne, ja makroniveljalkaisten (isokokoisten selkärangattomien) yhteisörakenne, kokonaismäärät ja yksilömäärät eri toiminnallisissa ryhmissä.

Avohakkuun jälkeen humuksen pH nousi 0,3 yksikköä, sen sijaan humuksen hiili-typpi -suhde säilyi muuttumattomana. Avohakkuun aiheuttamiin ympäristömuutoksiin reagoivat voimakkaimmin sienibiomassa, joka pieneni 30 %, ja änkyrimadot, joiden yksilömäärä kasvoi noin nelinkertaiseksi kolmantena vuonna hakkuun jälkeen. Avohakatuilla aloilla myös mikrobien hengitysaktiivisuus laski ja mikrobiyhteisö muuttui jonkin verran hakkaamattomaan metsään verrattuna. Lisäksi monet maan pintakerroksissa elävät makroniveljalkaiset kuten suljetussa kuusimetsissä yleisinä esiintyvät kovakuoriaislajit, hämähäkit (petoja) ja kilpikirvat (kasvinsyöjiä) vähenivät. Toisaalta joidenkin kovakuoriaislajien yksilömäärät kasvoivat hakkuun seurauksena. Avohakkuun

tuomilla ympäristömuutoksilla ei sen sijaan ollut selkeää vaikutusta hyppyhäntäisten yksilömääriin tai yhteisörakenteeseen, makroniveljalkaisten kokonaisuuteen tai kovakuoriaisten lajiston monimuotoisuuteen.

Harsintahakkuulla, jossa 30 % elävän puuston tilavuudesta poistettiin, ei ollut vaikutusta hajottajaeliöstöön tai sienijuuriverkoston (sienibiomassan määrään). Myöskään humuksen pH tai hiili-tyyppi-suhde eivät muuttuneet. Hakkaamattomasta metsästä pienaukkoihin ulottuvat puiden juuret ja sienirihmasto sekä puiden latvuston varjostava suojavaikutus eivät vähentäneet hakkuun vaikutusta pienaukon maaperäeläimistöön. Toisaalta myöskään pienaukoilla tai niiden äestyksellä ei ollut vaikutusta aukkojen ympärille jätetyn kasvavan metsän mikrobiyhteisöön. Pienaukon äestykseen reagoivat selvimmin maan pintakerroksissa elävät isokokoiset selkärangattomat, kun taas syvemmissä maakerroksissa elävässä eläimistössä ei havaittu eroja äestetyin ja äestämättömän pienaukon välillä. Pienissä puuryhmissä, joita jätettiin muuten avohakatuille aloille, pääosin humuksessa elävä eläimistö säilyi muuttumattomana. Muutokset maan pintakerroksessa elävissä isokokoisissa selkärangattomissa, kuten kovakuoriaisissa, olivat kuitenkin samansuuntaiset kuin avohakatuilla koealoilla, joskin pienemmät.

Yksi päämekanismeista, joka muuttaa maan hajottajaeliöstöä metsänuudistamisen jälkeen liittyy sienijuuriverkoston pirstoutumiseen hakkuualoilla. Puiden kaatamisen ja maan äestämisen jälkeen sienijuuriverkosto kuolee maaperästä vähitellen. Puiden tuottamia yhteyttämistuotteita ei enää erityisesti juuriston kautta maahan hajottajaeliöstön käyttöön. Siten monet avohakkuun aiheuttamat muutokset maaperän hajottajaeliöstössä voivat johtua juuri sienijuuriverkoston tuhoutumisesta. Asiaa tutkittiin erillisessä kokeessa, jossa puiden sienijuuriverkosto katkaistiin koealojen ympäriltä ja juurten kasvaminen takaisin koealoille estettiin lasikuitukankaalla. Toisaalta hakkuussa maanpinnalle jäävät hakkutähteet tuovat lisäresursseja hajottajille. Näiden resurssien vaikutuksia tutkittiin lisäämällä osalle koealoista havuja ja pieniä oksia. Lisäksi joitakin koealoilta poistettiin maan eloperäinen pintakerros äestystä jäljitellen. Käsittelyt tehtiin sulkeutuneessa hakkuukypsässä metsässä, jotta avohakkuuta seuraava metsikön pienilmaston äärevöityminen ja sadannan muutokset eivät vaikuttaisi tuloksiin. Koealat olivat pieniä eikä niillä kasvanut puita.

Koealojen eristäminen johti mikrobien yhteisörakenteen muutoksiin ja edelleen sieniä ravintonaan käyttävien eläinten (hyppyhäntäiset, kuoripunkit) yksilömäärien vähenemiseen. Toisaalta änkyrimadot lisääntyivät eristetyillä ruuduilla kolmantena vuonna käsittelyn jälkeen ilmeisimmin kuolleiden juurten ja niissä kasvavien mikrobien tuomien resurssien turvin. Lisäksi juurien katkaisemisesta seuraava puiden vedenoton väheneminen ja siten maan kosteuden lisääntyminen oli mahdollisesti ainakin osasyynä änkyrimatojen lisääntymiseen. Ammoniumtyypen pitoisuuden lisääntyminen eristetyillä ruuduilla ilmeisesti muutti bakteeriyhteisöä, joka näkyi myös bakteereja syövien sukku-lamatojen määrän kasvuna. Vaikka juuriverkoston katkaiseminen muutti hajottajayhteisöä, ei maan hajotustoiminta tämän seurauksena muuttunut. Hakkuutähteiden tuomilla resursseilla ei ollut merkitystä maaperän eliöille

ensimmäisinä vuosina käsittelyn jälkeen. Aikaisemmissa tutkimuksissa havaitut positiiviset vaikutukset johtunevat hakkuutähteiden aiheuttamasta maaperän lämpötilavaihtelun pienenemisestä ja maaperän kosteuden lisääntymisestä.

Toinen metsän uudistamisessa maaperän hajottajien maaraan ja yhteisö-rakenteeseen vaikuttava tekijä on maan eloperäisen pintakerroksen poistaminen puuntaimien kasvun turvaamiseksi. Eloperäisen maan poistamisen yhteydessä laikusta katoaa suuri osa sen hajottajaeliöstöstä. Tiheään pintakasvillisuuden ja humuskerroksen poistamisella oli kuitenkin positiivinen vaikutus mineraalimaan yleiseen hajotusaktiivisuuteen ja taimien kasvuun. Laboratorio kokeessa tutkittiin tarkemmin mineraalimaan poistamisen vaikutusta änkyrimatojen lukumäärään ja toimintaan. Kokeessa havaittiin, että änkyrimadot pystyvät elämään ja lisääntymään sekä vaikuttamaan typen mineralisaatioon myös paljastetussa mineraalimaassa.

Tutkimus osoitti, että hajottajayhteisö pohjoisessa havumetsämaassa kestää suhteellisen hyvin heti hakkuiden jälkeen tapahtuvia ympäristömuutoksia. Havaitut muutokset hajottajaeliöstössä ja ravinnedynamiikassa johtuvat ainakin osittain mykoritsayhteyksien katkeamisesta hakkuiden seurauksena sekä humuskerroksen ja pintakasvillisuuden aiheuttamien epäedullisten olosuhteiden paranemisesta maanmuokkauksen jälkeen.

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Original papers

I

Short-term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods

by

Anne Siira-Pietikäinen, Janna Pietikäinen, Hannu Fritze and Jari Haimi,
2001

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II

**Short-term responses of soil macroarthropod community to clear felling and
alternative forest regeneration methods**

by

Anne Siira-Pietikäinen, Jari Haimi and Juha Siitonen

Forest Ecology and Management, in press

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III

Responses of decomposer community to root-isolation and addition of slash

by

Anne Siira-Pietikäinen, Jari Haimi, Antti Kanninen, Janna Pietikäinen and
Hannu Fritze, 2001

Soil Biology & Biochemistry 33: 1993-2004

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[https://doi.org/10.1016/S0038-0717\(01\)00135-3](https://doi.org/10.1016/S0038-0717(01)00135-3)

IV

**Organisms, decomposition, and growth of pine seedlings in boreal forest soil
affected by trenching and sod cutting**

by

Anne Siira-Pietikäinen, Hannu Fritze and Jari Haimi

Manuscript

<https://doi.org/10.1007/s00374-002-0571-4>

V

**Activity and role of the enchytraeid worm *Cognettia sphagnetorum* (Vejd.)
(Oligochaeta: Enchytraeidae) in organic and mineral forest soil**

by

Jari Haimi and Anne Siira-Pietikäinen

Manuscript

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