UNIVERSITY OF CALGARY

Forest Floor Properties, Nutrient Cycling Processes, and Microarthropod Populations

in Conifer and Deciduous Stands of the Mixed-wood Boreal

Forest Following Partial and Clear-cut Harvesting.

by

Zoë Lindo

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Forest Floor Properties, Nutrient Cycling Processes, and Microarthropod Populations in Conifer and Deciduous Stands of the Mixed-Wood Boreal Forest Following Partial and Clear-cut Harvesting" submitted by Zoë Lindo in partial fulfilment of the requirements of the degree of Masters of Science.

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Abstract

The response of forest floor physical, chemical, biological properties, decomposition and nutrient cycling processes, and microarthropod populations to partial and clear-cut harvesting was examined in conifer and deciduous stands of the mixed-wood boreal forest of northern Alberta, Canada. Four treatments were studied in each stand type, 1) unharvested control, 2) selectively harvested retention patch in a partial-cut, 3) strip-cut corridor in a partial-cut, and 4) clearcut. Retention patches within partial-cuts showed less of an impact on the forest floor physical (bulk density), chemical (N and P availability), and biological (microbial biomass) properties, nutrient cycling (N and P) processes, and microarthropod communities than corridors within partial-cuts and clearcuts did. Results of a laboratory mesocosm study exploring the contribution of microarthropods to nutrient cycling processes showed that reductions in microarthropods following harvesting disturbance in the field do not affect decomposition rates, but may contribute to reduced microbial biomass and phosphate availability.

Preface

Some of the results presented in this thesis have been published, or are in review for publication in the Canadian Journal of Forest Research:

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One other paper is in preparation.

All manuscripts, published, in review, or in preparation, are the result of a collaborative effort between Zoë Lindo and Suzanne Visser. Zoë Lindo implemented the research, analysed the data, and is primary author on all manuscripts prepared from this research. Suzanne Visser did final review of these manuscripts in their final stage before submission, and as co-author of the manuscripts acknowledges and gives permission of the microfilming of this thesis.

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Chapter One: INTRODUCTION

1.1 Literature Review

1.1.1 Response of Forest Floors and Forest Floor Microarthropods to Clear-cut and Partial-cut Harvesting.

Clear-cutting is a widespread logging practice representing 80% of Canada's forest harvest (Youngblood and Titus 1996). It is generally considered a safe, cost-efficient method of timber removal and, with proper apriori site assessment, should have minimal effects on most ecological processes (Keenan and Kimmins 1993). However, many studies have shown that clear-cut harvesting disturbs the forest floor and disrupts nutrient cycling normally associated with an unharvested, closed canopy forest (Keenan and Kimmins 1993).

Canopy removal allows more solar radiation and precipitation to reach the soil surface; thereby, increasing soil temperature, diurnal temperature fluctuations and soil moisture (Keenan and Kimmins 1993). This, in conjunction with decreased evapotranspiration and root uptake, can increase water movement through the soil system and lead to increased stream flow, nutrient leaching and soil erosion (Likens *et al.* 1970). Nutrient leaching and removal of plant biomass associated with clear-cutting may have long-term effects on site fertility and productivity (Entry *et al.* 1986). The forest floor, i.e. the surface organic layer, is a vital source of labile nutrients, such as nitrogen (N), calcium (Ca), magnesium (Mg) and potassium (K) (Covington 1981, Johnson *et al.* 1991), and is more affected by the harvesting process than deeper mineral soil layers (Schmidt *et al.* 1996). One common method of removing cut timber from a site involves the use of a tracked or wheeled vehicle called a skidder to drag logs to a central area. This process can disturb the soil system through compaction of the forest floor, mixing of soil horizons, and relocation of organic matter (Carleton and MacLellan 1994).

Organic matter input to the forest system following clear-cutting is altered in quality (C:N ratios) and quantity by the large, one-time input of coarse, woody residue (slash), and the temporary cessation of annual litter inputs (Bååth 1980). The effects of clear-cutting on decomposition rates are cumulative (Trettin *et al.* 1996). Changes in the amount and type of organic matter, soil temperature, moisture and pH alter the microbial community which, in turn, affects decomposition rates and nutrient cycling processes

(Chang *et al.* 1995).

Ammonification, nitrification, and N mineralisation are often accelerated following clear-cutting (Frazer *et al.* 1990). An increase in hydrogen ions as a result of the nitrification process decreases soil pH as these ions replace essential cations on soil particles (Dahlgren and Driscoll 1994, Schmidt *et al.* 1996). Total N, nitrate (NO₃-N), ammonium (NH₄-N), available phosphate (PO₄-P), and total carbon (C) have been shown to decrease in forest floors 20 months after clear-cutting (Schmidt *et al.* 1996), while

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increasing in deeper mineral soils and in stream water. Consequently, these nutrients are believed to be leached from the forest floors after harvest (Likens *et al.* 1970).

Several studies have also reported an adverse effect of clear-cutting on forest floor microarthropods (Acari (mites) and Collembola (springtails)) and specifically oribatid mites (Acari: Oribatida) (Vlug and Borden 1973, Seastedt and Crossley 1981, Marra and Edmonds 1998, Battigelli 2000). Alterations in quality and quantity of organic matter, combined with increased temperature in the upper soil layers following clear-cutting, can adversely affect soil fauna communities (Marra and Edmonds 1998). Many studies have shown that clear-cutting and associated disturbances lead to a decrease in habitat complexity, a reduction in total abundance of soil invertebrates, and a change in species composition within soil faunal groups (Abbott *et al.* 1980, Bird and Chatarpaul 1986). Whole-tree harvesting and soil compaction associated with clear-cutting have been found to significantly reduce forest floor microarthropod density in sub-boreal spruce forests in British Columbia (Battigelli 2000), and decrease overall species richness and densities of collembola, oribatid, prostigmatid, and mesostigmatid mites (Abbott *et al.* 1980, Seastedt and Crossley 1981, Bird and Chatarpaul 1986, Marra and Edmonds 1998).

Physical, chemical and biological properties of the forest floor, decomposition, and nutrient cycling processes, and microarthropod populations are important in the functioning and sustainability of forest ecosystems. Research showing that clear-cut harvesting alters these properties, processes and populations, have prompted

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investigations into alternative, less intensive forestry practices, such as partial-cutting and selective logging (Dahlgren and Driscoll 1994, Barg and Edmonds 1999).

Partial-cutting, selective logging and retention harvesting all involve the retention of live trees within the harvest area. Harvesting is done in strips, alone or in combination with selective tree removal (thinning) in the retention areas. In either practice, areas (corridors) of 100% tree removal are created to allow machinery and equipment to access the site while various degrees of live, mature trees are left standing in the retention areas. Mechanical operations are often confined to the corridors.

In comparison with clear-cutting, partial-cutting should reduce physical disturbance to the forest floor, minimise microclimate changes in the soil, and decrease nutrient leaching through plant uptake and immobilisation, thus reducing impacts on nutrient cycling processes (Dahlgren and Driscoll 1994). Live tree and root retention areas also provide refuge for belowground organisms like mycorrhizal fungi (Barg and Edmonds 1999), provide seed banks for natural tree regeneration (Youngblood and Titus 1996), maintain soil invertebrate communities, and increase habitat complexity compared to clearcuts (Siira-Pietikäinen *et al.* 2001).

The effect of partial-cutting practices on forest floor microarthropods has not been studied in detail. Abbott *et al.* (1980) observed that communities of forest floor microarthropods in partial-cut plots were more similar to unharvested control plots than clear-cut plots. In a Finnish coniferous forest, selective thinning had similar but milder effects on forest floor microarthropods compared with clear-cutting (Huhta *et al.* 1967).

However, partial-cut and selective timber harvesting also may have significant, longlasting effects on the forest floor microarthropod community (Hoekstra *et al.* 1995). These observations suggest that partial-cut harvesting systems may be less detrimental to forest floor microarthropod populations than is clear-cutting; however, further research is required to confirm this.

1.1.2 Oribatid Mites as Indicators of Harvesting Disturbance

Oribatid mites (Acari: Oribatida) are numerically dominant among the microarthropods in forest systems (Wallwork 1983), and have high species diversity in most well developed soils (Anderson 1978, Norton 1985). There are over 7000 described species of oribatid mites worldwide from over 150 families, two-thirds of which are associated with soil systems (Balogh and Balogh 1992). Oribatid mite density is high in temperate forest soil systems, and densities can reach several hundred thousand individuals per square meter in forest floors (Petersen and Luxton 1982). Oribatid mites form stable populations in undisturbed soil systems due to long life spans, low fecundity, and overlapping generations. However, oribatid mites have low dispersal capabilities, cannot easily escape from stress or habitat perturbation, and so, often show the greatest decrease in abundance of all microarthropod groups following harvesting disturbance (Seastedt and Crossley 1981, Blair and Crossley 1988). Additionally, changes in oribatid mite community structure, specifically an increase in the relative abundance or dominance of thelytokous (parthenogenic) species or families following disturbance, suggests that oribatid mites may be a useful indicator of disturbance (Behan-Pelletier 1999). Suitable indicator species should be dominant in the community, sensitive to changes in their environment and/or reflect the effects of a disturbance regime (Lindenmayer *et al.* 2000). Oribatid mites fit this description. However, using oribatids as indicators of soil disturbance is not yet a common practice. This may be attributed to the incomplete taxonomy of oribatid mites at the species level (Behan-Pelletier 1999), and the amount of expertise and time required to identify this group of microarthropods. Clearly, more research is warranted to evaluate the use of oribatid mites as indicators of soil disturbance.

1.1.3 The Role of Forest Floor Microarthropods in Decomposition and Nutrient Cycling.

Litter and forest floor microarthropods (mites and springtails) are important components of the belowground food web and play integral roles in decomposition and nutrient cycling processes via interactions with the microbial community. While they play a minor role in the chemical degradation of organic matter, they contribute to decomposition and nutrient cycling processes by grazing microorganisms and stimulating microbial activity; by dispersing microbial propagules and spores to new substrates, and by increasing litter surface area for microbial attack through comminution of organic matter and fecal pellet deposition (Visser 1985). These activities can, in turn, affect microbial community structure (Maraun *et al.* 1998), increase rates of litter decomposition (Seastedt 1984), and alter the availability of soil nitrogen (Ineson *et al.* 1982, Bardgett and Chan 1999). Microarthropods facilitate the release of nutrients from the fungal standing crop and contribute to soil structure and humus formation (Wallwork 1983, Norton 1985). Previous studies have shown that microarthropods may contribute up to 20% of mass loss from decomposing substrates and up to 30% of nitrogen mineralisation in soils (Heneghan and Bolger 1998). Forest floor microarthropods also contribute to soil structure and humus formation via comminution of leaf litter and fecal pellet deposition (Wallwork 1983).

In boreal forest systems, microarthropods are numerous (Petersen and Luxton 1982), and often the presence of larger macrofauna (e.g. earthworms) is reduced or absent. Thus, the contribution of forest floor microarthropods to decomposition and nutrient cycling in these systems is especially important, and, as yet, relatively unquantified. In addition, many boreal forests are under anthropogenic influence which, in the case of forest harvesting practices, has been shown to significantly reduce forest floor microarthropod populations (Vlug and Borden 1973, Huhta 1976, Abbott *et al.* 1980, Blair and Crossley 1988, Marra and Edmonds 1998). Impacts on the microarthropods may persist for years. Reductions in microarthropod abundance may be detrimental to soil processes, such as decomposition and nutrient cycling, and, for this reason, preservation of forest floor microarthropods should be considered an integral

component of forest management practices (Marshall 2000). Experiments to determine the relationship between microarthropod abundance and nutrient cycling processes are necessary to elucidate the potential implications of reduced microarthropod abundance following forest harvesting on ecosystem function.

1.2 Thesis Rationale

Public pressure on Canada's forest industry to decrease unsustainable harvest rates and reduce species loss has stimulated interest in alternatives to clear-cut harvesting. Partial-cut or strip harvesting is one such alternative; however, examination of the effects of partial-cut systems on nutrient cycling processes and soil biodiversity needs to be assessed to gauge the impact and potential sustainability of these practices.

Forest ecosystem processes such as decomposition and nutrient cycling control forest productivity, which are directly related to sustainable forest management issues. Biodiversity in soil systems is crucial to these processes. Soil microarthropods are a significant component of forest floor biodiversity in boreal forests. Although their role in grazing, stimulation, and dispersal of the microbial community has been established, their contribution to decomposition and nutrient cycling requires clarification.

The present study examined the effects of different forest harvesting practices (clear-cut and partial-cut) on forest floor physical, chemical and biological properties, decomposition and nutrient cycling processes, and forest floor microarthropod

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populations in coniferous- and deciduous-dominated stands of the boreal mixed-wood forest. I asked whether partial tree harvesting would have less of an impact on forest floor properties, processes and populations than clear-cut harvesting would in a fieldbased study. In addition, I determined whether alterations in nutrient cycling processes resulting from forest harvest were related to changes in forest floor microarthropods by conducting a laboratory-based mesocosm study.

1.3 Study Objectives

The overall objective was to determine whether forest floor properties, decomposition and nutrient cycling processes, and forest floor microarthropod populations were less impacted by partial-cut harvesting than clear-cut harvesting in coniferous and deciduous stands of the mixed-wood boreal forest. The specific objectives were:

Objective #1. To evaluate the effects of clear-cutting and 50% partial-cutting relative to uncut sites on forest floor physical (bulk density, moisture, forest floor depth), chemical (pH, available N and P) and biological (microbial biomass, basal respiration, fine roots) properties in conifer and deciduous stands in a northern Alberta forest.

Objective #2. To determine the effects of clear-cut and partial-cut forest harvest on litter decomposition rates and nutrient cycling processes by conducting litter decomposition studies and analysing N and P mineralisation potentials in the laboratory. **Objective #3.** To compare the abundance and composition of the forest floor microarthropod community in clear-cut, partial-cut and uncut sites, and to examine the usefulness of oribatid mites as biological indicators of harvesting disturbance.

Objective #4. To determine the relative contribution of forest floor microarthropods to decomposition and nutrient cycling processes, as influenced by forest harvesting, and to examine the possible relationship between fauna populations and forest floor properties.

I hypothesised that those forest floor properties affected by clear-cut and partialcut harvesting would show a gradient effect related to intensity of forest removal. I expected that the effects of partial-cutting on forest floor properties would be intermediate between uncut and clear-cut treatments. I also predicted that the effects of harvesting in the strip-cut corridors and selectively harvested retention patches in the partial-cut treatment would differ; forest floors in the corridors being more impacted than forest floors in the retention patches.

This research forms one component of the Ecosystem Management Emulating Natural Disturbance (EMEND) project being conducted in the mixed-wood boreal forest of northern Alberta. EMEND is an ongoing, large-scale forest ecosystem study initiated in 1997. The overall objective of the EMEND project is to determine which forest harvest practices best maintain the natural plant and animal communities that result from natural disturbances (Sidders and Spence 2001). In addition to the research presented here, other studies at the EMEND research site include the effects of forest harvest on white spruce ectomycorrhizal biodiversity, the foraging behaviour of insectivorous bats, and the dispersal and settlement of bark beetles, to name a few.

Chapter Two: PHYSICAL, CHEMICAL, BIOLOGICAL PROPERTIES AND NITROGEN AND PHOSPHORUS PROCESSES IN CONIFER AND DECIDUOUS FOREST FLOORS FOLLOWING PARTIAL AND CLEAR-CUT HARVESTING IN A MIXED-WOOD BOREAL FOREST.

2.1 Introduction

Previous research on the effects of forest removal on the soil system has focused primarily on the impacts of clear-cut harvesting, and has shown that clear-cutting alters many soil properties, processes, and biological populations. Canopy removal associated with clear-cutting can increase the amount of solar radiation and precipitation that reaches the forest floor; thereby, increasing soil temperatures, diurnal temperature fluctuations and soil moisture (Keenan and Kimmins 1993). Decreased levels of nutrients such as total C and N, NO₃-N and PO₄-P in forest floors (Schmidt *et al.* 1996), and nutrient losses from the soil profile following clear-cutting have been documented (Dahlgren and Driscoll 1994). In addition, several studies have reported reductions in soil fungal biomass following clear-cut harvesting (Bååth 1980). How alterations in soil microclimate, nutrient levels and soil organisms relate to soil quality or 'health' has not been clearly defined; however, forest practices that minimise changes to the soil system are being sought (Youngblood and Titus 1996). Partial-cut and selective harvesting systems are gaining interest as alternative practices to clear-cutting. Compared with clear-cut harvesting, retaining live trees in partial-cut systems result in fewer alterations in soil microclimate and physical, chemical and biological properties of soil (Barg and Edmonds 1999). Partial-cutting has been shown to reduce forest floor compaction, reduce nutrient leaching, provide refuge for belowground organisms such as mycorrhizal fungi, ensure seed banks for natural tree regeneration and increase habitat complexity relative to clear-cut practices (Youngblood and Titus 1996, Barg and Edmonds 1999, Siira-Pietikäinen *et al.* 2001). However, further examination of the effect of partial-cut harvest on forest floor properties and nutrient cycling is needed to gauge the sustainability of these practices.

The present research was initiated to compare the effects of clear-cut and partialcut harvesting on forest floor physical, chemical and biological properties in conifer and deciduous dominated stands of the boreal mixed-wood forest. Specific objectives were:

1. to evaluate the effects of clear-cutting and partial-cutting on physical,

chemical and biological properties of the forest floor; and

2. to determine the effects of clear-cutting and partial-cutting on decomposition potential and N and P mineralisation processes.

The overall objective was to determine if forest floor properties in partial-cut forests were more similar to uncut forests than to clearcuts. I hypothesised that changes in forest floor properties in partial-cut sites would be intermediate between uncut and clear-cut sites.

2.2 Methods

2.2.1 Site Description and Experimental Design

The EMEND experimental area is in the Upper-Cordilleran Ecoregion of Alberta, Canada and is located approximately 90km northwest of Peace River, Alberta (56°46'13"N, 118°22'28"W). This area has a mean daily temperature of -0.6°C; and a total annual precipitation of 426.5mm (Environment Canada 2002). The elevation is 677-800m above sea level and soils are predominantly fine-textured lacustrine Luvisols.

The EMEND plots are located in 80 to 140-year-old coniferous and deciduous dominated stands. The major tree species in the deciduous stands are *Populus tremuloides* Michx. (trembling aspen) and *Populus balsamifera* L. (balsam poplar). In the conifer stand, *Picea glauca* (Moench) Voss (white spruce) is the dominant tree species. Other tree species found in limited amounts in both forest types include *Picea mariana* (Mill.) (black spruce), *Abies balsamea* (L.) Mill. (balsam fir), *Pinus contorta* Loudon (lodgepole pine) and *Betula papyrifera* Marsh. (paper birch). The most common understory shrubs are *Viburnum edule* (Michx.) Raf. (low bush cranberry), *Rosa acicularis* Lindl. (prickly rose), *Shepherdia canadensis* (L.) Nutt. (Canada buffaloberry), *Alnus crispa* (Ait.) Parsh (green alder) and *A. tenuifolia* Nutt. (river alder) (Sidders and Spence 2001).

The experimental design of EMEND is a randomised block design with two replicate conifer and deciduous stands divided at random into 10-hectare clearcut, partialcut or uncut sites. In the present study, the 50% partial-cut was separated into two treatments, the strip-cut corridors and the selectively harvested retention patches, since impacts on forest floor physical, chemical and biological properties were expected to differ between these two treatments. Thus, four treatments were considered in each block, in each stand type; 1) uncut control; 2) selectively harvested retention patches within partial-cuts (patch); 3) strip-cut corridors within partial-cuts (corridor); and 4) clearcut.

Harvesting occurred in the winter of 1998-99. Conventional full-tree harvesting using feller-bunching and direct route skidding was used in the clear-cut sites. The harvesting method within the partial-cut site was a two-pass system in which machine corridors were strip-cut on the first pass and retention patches were selectively logged on the second pass. The machine corridors were created using a feller-buncher/forwarder (skidder) full tree system, and were 5m wide and spaced at 20m intervals. All corridors are 100% tree removal and are oriented north/south, perpendicular to the prevailing wind. The retention patches were selectively cut using a feller-buncher, operating from within the adjacent corridors. Retention patches are 15m wide and have a 1:3 stem removal to total stem ratio (one of every three trees selectively removed). All harvesting and skidding was limited to the designated machine corridors (Sidders and Spence 2001). The machine corridors represent 25% of the net tree removal from the partial-cut site

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with an additional 25% tree removal from the selectively logged retention patches for a total of 50% partial-cut over the 10-hectare site.

At the time of sampling, deciduous clearcuts exhibited extensive regeneration of aspen suckers. The same degree of regeneration was not observed in the deciduous partial-cut corridors or in the conifer corridors or clearcuts.

2.2.2 Sampling Regime

Sampling was conducted in June 2001, 2.5 years post-harvest. A 50m transect was established in each treatment and soil samples were removed at 10m intervals for a total of five samples/treatment. A total of 80 samples were removed [2 stand types (conifer, deciduous) x 2 replicate stands x 4 treatments (uncut, patch, corridor, clearcut) x 5 samples per treatment]. Transects were oriented north/south to coincide with the direction of the corridors and retention patches. At each sampling point, a 25x25cm block of forest floor was excavated to a depth of 15cm for physical, chemical and biological measurements, and a 5.5cm dia. core was taken for bulk density and fine root measurements. Forest floor samples were stored at 4°C until ready for processing.

In the laboratory, the exact dimensions of each forest floor quadrat were determined and the depths of the litter and fermentation/humus (F/H) horizons were measured. Litter, slash, green vegetation and moss on the surface of the soil blocks were removed, oven-dried (80°C) and weighed; also, roots found within the quadrat sample

were collected, washed, oven-dried (80°C) and weighed. The F/H layer was separated from any underlying mineral soil and passed through a 4mm sieve. Sieved F/H materials were stored in plastic bags at 4°C until ready for analysis.

2.2.3 Measurements

2.2.3.1 Forest Floor Bulk Density

Bulk density was estimated using the core method described by Blake and Hartge (1986). Core volume was calculated using the core diameter (5.5cm), the depth of the core and the equation for the volume of a cylinder ($\pi r^2 x$ core depth). Forest floor bulk density (g/cm³) was then calculated using the oven dry weight (105°C) of the forest floor core, divided by the core volume (cm³).

2.2.3.2 Soil Moisture and Organic Matter Content

Forest floor moisture content was measured gravimetrically by drying subsamples (approx. 5g) of each sample to a constant weight at 80°C for 24h. Dried subsamples were then re-weighed and the difference in mass between fresh and dry soil was used to calculate percent moisture on a dry weight (dwt) basis (% moisture = (wwt (g)-dwt (g)/ dwt (g)) * 100).

Organic matter content was estimated using the loss-on-ignition (LOI) method, where oven dried samples used in the moisture determinations were placed in a 105°C oven for 24h, and then combusted in a muffle furnace at 400°C for 24h (Nelson and Sommers 1982). The difference in soil mass at 105°C and after combustion at 400°C was used to calculate the percent organic matter loss-on-ignition (% LOI= (dwt₁₀₅ (g)dwt₄₀₀ (g)/ dwt₁₀₅ (g)) * 100).

2.2.3.3 Forest Floor pH and Electrical Conductivity

Distilled water was added to field-moist forest floor subsamples to create a slurry of 1:10 forest floor (dwt) to deionized water (2g dwt in 20ml water). Slurry pH was measured after 1h with a glass electrode digital pH meter (Orion Research model 701A, Cambridge, USA). Forest floor slurries were then vacuum-filtered using Whatman GF/A filters. The filtrate of the slurry was used to determine the electrical conductance (EC) of the filtrate as measured in deci-Siemans/m (dS/m) using a Markson Digital conductivity meter (Amber Science Inc. model 1096, San Diego, USA).

2.2.3.4 Total N and P

Total N and P concentrations were determined by the micro-Kjeldahl procedure (no pre-treatment or catalyst) (adapted from Bremner and Mulvaney 1982). Air-dried forest floor subsamples were ground to #40 mesh (0.5mm) in a Wiley mill and further dried at 80°C for 24h. Samples (0.25g) were digested in 5ml concentrated sulphuric acid (H₂SO₄) by heating the mixtures for 30 min. at 360°C, and allowing them to cool before 0.5ml 30% hydrogen peroxide (H₂O₂) was added. After heating the samples for a further 8-10 min., another 0.5ml 30% H₂O₂ was added, and this process was repeated until the samples were clear or grey. The total amount of 30% H₂O₂ did not exceed 5ml. Once the samples were clear, they were heated for an additional 30 min. to remove all peroxide, then cooled, and made up to 75ml with deionized H₂O. Samples were stored in Nalgene bottles at 2°C until analysis. Colourimetric determinations of NH₄⁺ and PO₄³⁻ were made using a Technicon autoanalyser II (Technicon 1970) as described below.

2.2.3.5 Available N and P, and N and P Mineralisation Potential

Available N (NH₄-N and NO₃-N) was extracted from 5g (dwt) field-moist subsamples by shaking them for 1h in 40ml 2N potassium chloride (KCl) followed by filtration through Whatman GC/A filter paper. Available N was analysed using colourimetric methods on a Technicon autoanalyser II. Ammonium was measured by the indophenol-blue method and NO₃-N was measured by the cadmium reduction method (Keeney and Nelson 1982).

Phosphate-P was extracted from 5g (dwt) field-moist subsamples by shaking them for 1h in 40ml Medium Bray's Extract (dilute ammonium fluoride), followed by filtration through Whatman GC/A filter paper. Phosphate was analysed using the fluoride method on the Technicon autoanalyser II (Olsen and Sommers 1982).

N and P mineralisation potentials were determined by measuring the amount of NH₄-N, NO₃-N, and PO₄-P generated from the soil organic matter by soil microorganisms over a 6-week period in the laboratory (Hart *et al.* 1994b). Five g (dwt) field-moist forest floors were incubated in plastic chambers with vented lids to allow gas exchange. The chambers were incubated under controlled temperature and moisture conditions. The moisture content of the samples was monitored gravimetrically twice a week and maintained throughout the incubation period. After 6 weeks, the samples were extracted with KCl or Bray's extract and analysed for NH₄-N, NO₃-N and PO₄-P concentrations using the Technicon autoanalyser II. Net N and P mineralisation rates (mineralisation potentials) were estimated by comparing final N and P concentrations with the initial concentrations measured at the beginning of the incubation period (available N and P). The data were expressed as µg NH₄-N or NO₃-N mineralised/g dwt/6 weeks.

2.2.3.6 Basal Respiration and Microbial Biomass

The basal respiration rate of 5g-dwt equivalent of field-moist, sieved forest floor soil was measured as carbon dioxide (CO₂) evolution (μ l CO₂/g dwt/hour). After equilibration at room temperature for 24h each sample was transferred to a respiration

tube and attached to an Infrared gas analyser (IRGA). Carbon dioxide efflux was measured for 6h, and respiration measured in the sixth hour was used to determine basal respiration (Anderson 1982).

Following the measurement of basal respiration, each sample was evaluated for microbial biomass C (mg C_{micr}/g dwt) using the Anderson and Domsch (1978) method. In this method, sufficient glucose is added to the soil to achieve maximum substrate-induced respiration that occurs prior to microbial growth. The amount of glucose required for maximum initial respiratory response in the sieved F/H materials from the coniferous and deciduous stands was predetermined by constructing a glucose response curve using 20, 40, 60, 80, 100 and 160mg glucose/g dwt. The amount of glucose required to achieve maximum respiratory response was 60mg glucose/g dwt deciduous F/H, and 40mg glucose/g dwt conifer F/H.

After determining basal respiration, each 5g sample was amended with either 300mg (deciduous) or 200mg (conifer) glucose, and again attached to the IRGA. Carbon dioxide evolution was monitored for 12h and microbial biomass was based on the lowest respiration rate prior to the commencement of microbial growth, which often occurred at six hours after glucose supplementation. Carbon dioxide evolution rates (μ l CO₂/g dwt/h) were converted to ml CO₂/g dwt/h and the formula x=40.4y+0.37 was used to estimate microbial biomass C (where x = microbial biomass (mg C_{micr}/g soil dwt) and y = glucose induced respiration (ml CO₂/g dwt/h)) (Anderson and Domsch 1978).

2.2.3.7 Fine Root Biomass

Fine root biomass, expressed as g dwt roots/g dwt forest floor, was measured by washing roots from soil cores, separating them into size classes based on diameter (0-2mm and 2-6mm), and drying them at 80°C.

2.2.3.8 Annual Litter Input and Litter Decomposition Potential

Annual litter input (g dwt/m²) was determined by placing litter traps, consisting of 26x53cm trays, approximately 1m from each sample point along each transect in the field. Litter was collected after one year (June 2001-June 2002), separated into litter types (leaf or needle litter; coarse woody litter (<2cm dia.)), dried at 80°C and weighed.

Litter decomposition potential was estimated as percent mass loss of aspen leaves after 3-months incubation in the laboratory. For each forest floor sample, 1g (air dwt) senescent aspen leaves were placed on the surface of 10g dwt-equivalent field-moist, sieved, deciduous and conifer forest floors held in 175ml plastic containers. Samples were covered with a perforated lid and incubated under constant temperature (22-23°C) and moisture conditions for three months. Soil moisture was monitored weekly and adjusted gravimetrically to the original weight with deionized water. Mass loss of aspen leaf litter following three months decomposition was estimated as the difference in oven dry weight of leaves before and after incubation and expressed as percent mass loss (% mass loss= (g dwt aspen_{before} – g dwt aspen_{after} / g dwt aspen_{before}) * 100).

2.2.4 Statistical Analysis

Initial analyses of differences in forest floor properties between uncut conifer and deciduous stands were determined by a student's t-test using α =0.05 as the significance level. A two-factor analysis of variance (ANOVA) was performed to test for differences among the means for each parameter (forest floor depth, bulk density, moisture content, organic matter content, pH, EC, total N and P, available N and P, N and P mineralisation potential, basal respiration, microbial biomass, fine root biomass, decomposition potential, total annual litter input) and to assess variation caused by stand and treatment. For this analysis, the General Linear Model (GLM) for randomised block designs in SYSTAT 7.0 was employed. Results were considered significant at p<0.05. Further one-way ANOVA with a Tukey's HSD test was performed separately for each stand type to assess the effects of treatment on the forest floor properties listed above. Data in violation of the GLM model assumptions, in particular available NO₃-N data, were log transformed (log₁₀).

2.3 Results

2.3.1 Uncut Conifer and Deciduous Stand Comparison
Many forest floor physical, chemical and biological properties differed between the conifer and deciduous stands (Table 2.1). Bulk density, pH, and moisture content were lower in conifer stands than in deciduous stands, while forest floor depth was greater in the conifer stands. Total N, total P, NO₃-N, basal respiration, microbial biomass and root biomass (2-6mm dia.) were significantly higher in the deciduous stands. Organic matter content, fine root biomass (<2mm dia.), decomposition potential and total annual litter input were not significantly different between conifer and deciduous stands.

Initial NH₄-N concentrations in the forest floors, NH₄-N concentrations after 6 weeks incubation and net amounts of NH₄-N mineralised over 6 weeks were not significantly different between conifer and deciduous stands (Table 2.2). In contrast, initial NO₃-N levels, NO₃-N levels after 6 weeks and the net amount of NO₃-N mineralised over 6 weeks were significantly greater in the deciduous forest floors compared to the conifer forest floors. Initial total available N (NH₄-N + NO₃-N) did not differ significantly between stand types; however, total available N after 6 weeks incubation, and the net amount of total N mineralised after 6 weeks incubation were significantly greater in the deciduous F/H than in the conifer F/H. Initially, levels of available P (PO₄-P) were significantly greater in the conifer forest floors than in the deciduous forest floors, but after 6 weeks incubation, the amount of PO₄-P in conifer and deciduous F/H materials were not significantly different (Table 2.2). The net amount of PO₄-P mineralised after 6 weeks incubation in the laboratory was negative (i.e. net immobilisation) in conifer F/H materials, and significantly lower than the net amount of

Soil Property	Units	Conifer (n=10)	Deciduous (n=10)	p value
Forest floor depth	cm	8.9 (0.7)	6.3 (0.8)	0.030
Bulk density	g/cm ³	0.11 (0.01)	0.16 (0.02)	0.041
Moisture content	% dwt	168 (11.8)	249 (22.4)	0.005
Organic matter content	% LOI	82.4 (2.0)	81.5 (2.0)	ns
pH _{H2O}		5.2 (0.2)	6.2 (0.1)	0.000
Electrical conductivity	dS/m	0.18 (0.02)	0.25 (0.05)	ns
Total N	mg/g dwt	16.0 (0.43)	20.1 (0.34)	0.000
Total P	mg/g dwt	1.2 (0.05)	1.6 (0.04)	0.000
Basal respiration	µl CO ₂ /g dwt/hr	85.3 (8.1)	110.4 (8.4)	0.045
Microbial biomass	mg C/g dwt	15.9 (1.4)	21.2 (1.8)	0.033
Root biomass (<2mm dia.)	g/g dwt	0.02 (0.01)	0.06 (0.01)	ns
Root biomass (2-6mm dia.)	g/g dwt	0.05 (0.01)	0.08 (0.02)	0.016
Decomposition potential	% mass loss	43.1 (1.9)	46.6 (1.1)	ns
Total annual litter input ^a	g/m²/yr	216 (13)	228 (21)	ns

Table 2.1 Physical, chemical, and biological properties of forest floors in uncut deciduous and conifer stands. Values are means with SE in parentheses.

Note: p-values are based on students standardised t-test, ns denotes not significant (p>0.05).

^a Total annual litter input includes leaf, needle, and twig litter.

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Table 2.2 N and P availability in forest floors from uncut coniferous and deciduous stands, initially and after 6 weeks laboratory incubation, and net N and P mineralised during 6-weeks laboratory incubation. Values are means with SE in parentheses.

Nutrient (µg/g dwt)	Conifer (n=10)	Deciduous (n=10)	p value
Initial NH ₄ -N	145 (39)	233 (31)	ns
NH4-N after 6wks	44 (24)	54 (11)	ns
NH ₄ -N mineralised over 6wks	-101 (28)	-179 (35)	ns
Initial NO ₃ -N	1 (0.1)	78 (72)	0.003
NO ₃ -N after 6wks	48 (29)	537 (92)	0.000
NO ₃ -N mineralised over 6wks	47 (29)	459 (71)	0.000
Initial total N (NH ₄ -N + NO ₃ -N)	146 (39)	311 (94)	ns
Available total N after 6wks	92 (34)	590 (88)	0.000
Net N mineralised over 6wks	-54 (43)	279 (66)	0.001
Initial PO ₄ -P	121 (12)	89 (7)	0.036
PO ₄ -P after 6wks	99 (7)	139 (20)	ns
PO ₄ -P mineralised over 6wks	-22 (6)	50 (17)	0.001

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Note: p-values are based on students standardised t-test, ns denotes not significant (p>0.05).

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 PO_4 -P mineralised in the deciduous F/H materials. Net P mineralisation in the deciduous F/H was positive and increased during incubation.

2.3.2 Harvesting Effects on Soil Physical and Chemical Properties

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Brown litter, moss, and green vegetation (g dwt/m²) on the surface of the forest floor was variable, and no significant differences amongst harvesting treatments were observed for green vegetation or litter in either stand type (Table 2.3). However, the amount of moss in the conifer stands was greater in the uncut control and patch treatments than in the clear-cut treatment, and significantly greater than in the corridors. The amount of moss in the deciduous stands was negligible in all treatments. Fine roots (0-6mm dia.), coarse (>6mm dia.) and total root (fine + coarse) biomasses were also highly variable and did not differ significantly among treatments in the deciduous stands. In the conifer stands, fine root biomass (0-6mm dia.) was significantly reduced in the corridor and clear-cut treatments compared to the uncut control.

There were no significant effects of harvesting on organic matter, electrical conductivity, or decomposition potential, and harvesting effects on other physical and chemical properties were observed primarily in the conifer stands (Table 2.4). In the conifer stands, forest floor depths in the corridors were significantly reduced relative to the uncut control, patch, and clear-cut treatments. Clear-cutting in the conifer stands resulted in higher bulk density compared to the uncut treatment. Moisture contents in the conifer stands were greater in all harvested treatments (patch, corridor, and clearcut)

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Mass (g dwt/m ²)	Conifer (n=40)			
	<u>Uncut</u>	Patch	Corridor	Clearcut
Green vegetation ^a	12.3 (4) a	27.2 (9) a	42.5 (23) a	39.9 (19) a
Brown litter ^{* b}	554 (147) a	672 (198) a	627 (289) a	1105 (264) a
Moss*	634 (134) a	496 (143) a	24 (24) b	235 (124) ab
Total surface plant material*	1200 (105) a	1195 (176) a	693 (286) a	1380 (220) a
Fine Roots* (0-6mm dia.)	120 (22) a	112 (24) ab	53 (10) b	47 (11) b
Coarse Roots* (>6mm dia.)	850 (182) a	1205 (303) a	480 (133) a	701 (176) a
Total Roots ^{* °}	969 (184) a	1313 (311) a	533 (134) a	749 (179) a
	Deciduous (n=39)			
-	Uncut	Patch	Corridor	Clearcut
Green vegetation ^a	20.4 (4) a	31.0 (5) a	27.3 (3) a	47.7 (15) a
Brown litter ^{* b}	279 (25) a	257 (57) a	227 (48) a	316 (87) a
Moss*	0 a	0 a	0 a	0 a
Total surface plant material*	310 (24) a	288 (58) a	255 (48) a	386 (110) a
Fine Roots* (0-6mm dia.)	67 (14) a	63 (10) a	46 (5) a	66 (10) a
Coarse Roots* (>6mm dia.)	203 (54) a	286 (58) a	423 (103) a	390 (111) a
Total Roots* °	269 (61) a	349 (57) a	469 (105) a	456 (114) a

Table 2.3 Green vegetation, brown litter, and moss on the forest floor, and root biomass in the forest floor in uncut, patch, corridor, and clear-cut treatments in coniferous and deciduous stands. Values are means with SE in parentheses.

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Note: Within each row, values followed by the same letter are not significantly different, based on a 1-way ANOVA and Tukey's HSD test (p>0.05).

Symbols: * Values are significantly different (p<0.05) between uncut conifer and deciduous stands. ^a includes grasses and herbs. ^b includes leaf and needle litter, woody debris (<2cm dia). ^c includes fine and coarse root biomass.

Soil Property	Units	Conifer (n=40)			
	<u> </u>	Uncut	Patch	Corridor	Clearcut
Forest floor depth	cm	8.9 (0.7) a	7.3 (0.7) a	4.8 (0.5) b	8.0 (0.7) a
Soil bulk density	g/cm ³	0.11 (0.01) b	0.12 (0.01) ab	0.14 (0.01) ab	0.17 (0.02) a
Moisture content	% dwt	168 (11.8) b	274 (33.3) a	245 (27.4) ab	249 (21.9) ab
Organic matter content	% LOI	82.4 (2.0) a	82.1 (2.8) a	72.1 (4.3) a	76.9 (4.7) a
pH _(H2O)		5.2 (0.2) ab	5.0 (0.1) b	5.2 (0.1) ab	5.7 (0.1) a
Electrical conductivity	dS/m	0.18 (0.02) a	0.20 (0.02) a	0.18 (0.02) a	0.29 (0.06) a
Total N	mg/g dwt	16.0 (0.43) a	15.9 (0.55) a	13.9 (0.85) a	14.7 (0.94) a
Total P	mg/g dwt	1.2.(0.05) a	1.2 (0.06) ab	1.2 (0.07) ab	1.0 (0.06) b
Decomposition potential	% mass loss	43.1 (1.9) a	41.8 (1.0) a	41.2 (1.0) a	48.1 (3.6) a
		Deciduous (n=39)			
•	,	Uncut	Patch	Corridor	Clearcut
Forest floor depth	cm	6.3 (0.8) a	6.6 (0.5) a	7.4 (0.6) a	7.6 (0.6) a
Soil bulk density	g/cm ³	0.16 (0.02) a	0.16 (0.01) a	0.17 (0.01) a	0.17 (0.01) a
Moisture content	% dwt	249 (22.4) a	284 (21.8) a	313 (15.5) a	276 (22.7) a
Organic matter content	% LOI	81.5 (2.0) a	83.3 (1.5) a	83.1 (0.9) a	81.4 (2.2) a
pH _(H2O)		6.2 (0.1) a	6.5 (0.1) a	6.4 (0.2) a	6.3 (0.1) a
Electrical conductivity	dS/m	0.25 (0.05) a	0.20 (0.02) a	0.27 (0.03) a	0.24 (0.03) a
Total N	mg/g dwt	20.1 (.34) ab	21.9 (.77) a	20.1 (.67) ab	18.7 (.92) b
Total P	mg/g dwt	1.6 (0.04) a	1.4 (0.06) ab	1.4 (0.06) b	1.6 (0.07) ab
Decomposition potential	% mass loss	46.6 (1.1) a	46.7 (1.4) a	47.7 (1.7) a	44.9 (1.1) a

Table 2.4 Physical and chemical properties, and decomposition potential of the forest floors in uncut, patch, corridor, and clear-cut treatments in coniferous and deciduous stands. Values are means with SE in parentheses.

Note: Within each row, values followed by the same letter are not significantly different, based on a 1-way ANOVA and Tukey's HSD test (p>0.05).

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compared with the uncut control treatment. Relative to the uncut treatment, total P was significantly reduced in the clear-cut conifer stands and in the corridors of the deciduous stands. The clear-cut deciduous stands had significantly lower total N compared to the deciduous retention patches.

2.3.3 Harvesting Effects on Soil Biological Properties

Significant effects of harvesting were detected for basal respiration, microbial biomass C, fine root biomass (Fig. 2.1 a,b,c) and annual litter input (Fig. 2.2 a,b) in both stand types. In the deciduous stands, all harvest treatments (patch, corridor, and clear-cut) had lower basal respiration compared with the uncut control. In the conifer stands only clear-cutting significantly reduced basal respiration in the forest floor; patch and corridor treatments did not have significantly lower basal respiration compared to the uncut control. In the deciduous stands, the uncut control had significantly greater microbial biomass C than patch, corridor, and clear-cut treatments. In the conifer stands, microbial biomass C decreased with increasing tree removal, but only the clear-cut was significantly lower than the uncut control.

Fine root biomass (g/g dwt forest floor) in the <2mm and 2-6mm diameter size classes showed similar response patterns to forest harvesting. In the deciduous stands, fine root biomass (<2mm dia.) was significantly reduced in the patch, corridor, and clear-cut treatments compared to the uncut control (Fig. 2.1c). Fine root biomass (mean

Figure 2.1 Basal respiration (μ l CO₂/g dwt/h) (a), microbial biomass C (mg/g dwt) (b), and fine-root biomass (<2mm dia.) (g/g dwt) (c), in forest floors of uncut, patch, corridor, and clear-cut treatments in conifer and deciduous stands. Within each stand type, bars (means ± SE) superseded by different letters are significantly different, based on a 1-way ANOVA and Tukey's HSD test (p<0.05).

a) Basal Respiration







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Figure 2.2 Annual (June 2001- June 2002) litter input, including leaf litter, needle litter, and woody debris (<2cm dia.), in uncut, patch, corridor, and clear-cut treatments in a) conifer and b) deciduous stands. Within each stand type, bars (means \pm SE) superseded by different letters are significantly different, based on a 1-way ANOVA and Tukey's HSD test (p<0.05).

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g root/g dwt \pm SE) in the 2-6mm diameter size class in the deciduous stands were as follows: uncut (0.08 \pm 0.02 a) > retention patch (0.04 \pm 0.01 ab) = corridor (0.04 \pm 0.01 ab = clear-cut (0.04 \pm 0.01 b). Values in parentheses followed by the same letter are not significantly different based on a 1-way ANOVA with a Tukey's HSD test (p>0.05).

In the conifer stands, fine root biomasses (<2mm dia.) in the uncut control and patch treatments were not significantly different, but were greater than the fine root biomasses in the corridor and clear-cut treatments (Fig. 2.1c). The 2-6mm-root diameter size class followed the same pattern where: uncut $(0.05 \pm 0.01 \text{ a})$ > retention patch $(0.04 \pm 0.01 \text{ ab})$ > corridor $(0.02 \pm 0.01 \text{ b})$ = clear-cut $(0.02 \pm 0.00 \text{ b})$. Values (g root/g dwt ± SE) followed by the same letters are not significantly different based on a 1-way ANOVA with a Tukey's HSD test (p>0.05).

Annual litter input in the field was significantly lower in the patch, corridor, and clear-cut treatments than the uncut control treatments in both the deciduous and conifer stands (Fig. 2.2 a,b). Litter deposition in the patch and corridor treatments was not significantly different, and was significantly greater than annual litter input in the clearcuts of both stand types. Annual litter inputs in the conifer clearcuts were zero (g dwt/m^2) at many sample locations.

2.3.4 Harvesting Effects on Available N and P, and N and P Mineralisation Processes

2.3.4.1 Harvesting Effects on Available N and P

Initial NH₄-N levels in the forest floor were lowest in the clear-cut treatments in both stand types. Ammonium-N concentrations in the corridors were intermediate between the clear-cut and uncut treatments. Ammonium-N in the retention patches were not significantly different from those in the uncut forest (Fig. 2.3 a). Nitrate-N in F/H of the deciduous stands was variable, but tended to be higher in the corridor and clear-cut treatments (Fig. 2.3 b). The same pattern was observed in the conifer stands where NO₃-N in the corridors and clear-cuts was significantly higher than in the uncut control. Phosphate-P in the corridor and clear-cut treatments of the conifer stands was significantly reduced relative to the uncut control treatment (Fig. 2.3 c). In contrast, no impact of harvesting on PO₄-P was measured in the forest floors of the deciduous stands.

2.3.4.2 Harvesting Effects on N and P Mineralisation Processes

Net N mineralised in deciduous forest floors after 6 weeks incubation in the laboratory was highest in the uncut control and patch treatments, while net N mineralisation was negative (i.e. net N immobilisation) in the corridor and clear-cut treatments of the deciduous forest floors (Fig. 2.3 d). In the conifer treatments, net N mineralisation occurred in the patch, corridor, and clear-cut treatments, but not in the uncut treatment which exhibited net N immobilisation. However, there were no significant treatment effects on N mineralisation in the conifer stands. Figure 2.3 NH₄-N (a), NO₃-N (b), PO₄-P (c), and net N mineralisation potential (d), in forest floors of uncut, patch, corridor, and clear-cut treatments in conifer and deciduous stands. Within each stand type, bars (means \pm SE) superseded by different letters are significantly different, based on a 1-way ANOVA and Tukey's HSD test (p<0.05).

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c) Phosphate







Rates of N and P mineralisation were highly variable in the forest floors of both stand types (Table 2.5). In the conifer stands, the initial total N, final total N after 6 weeks incubation, and levels of NH₄-N and NO₃-N after 6 weeks incubation were not significantly different among treatments. The amount of PO₄-P in the conifer forest floors after 6 weeks incubation was significantly greater in the uncut and patch treatments than in the corridor and clear-cut treatments. Net NO₃-N mineralised over the incubation period was not significantly different amongst the treatments in the conifer forest floors. Also, there was no PO₄-P mineralised in this forest type, rather there was net immobilisation of P. Conversion of NH₄-N to NO₃-N was significantly greater in the patch treatment than in the clear-cut treatment in the conifer stands.

In the deciduous forest floors, initial total available N, and the amount of available NH₄-N after incubation did not differ significantly between treatments. Available N, PO₄-P and NO₃-N levels, and the amount of PO₄-P mineralised after 6 weeks of incubation in the laboratory, were all significantly greater in the uncut control than in the retention patch, corridor and clear-cut treatments. As was the case in the conifer stands, NH₄-N was converted to NO₃-N in all treatments, and was significantly greater in the uncut control forest floors than in the clearcut forest floors. The patch and corridor treatments were intermediate in terms of the amount of NH₄-N immobilised and/or mineralised to NO₃-N. Net NO₃-N mineralised was greater in the uncut control forest floors, intermediate amounts of NO₃-N were mineralised in the patch and corridor treatments.

Nutrient (µg/g dwt)	Conifer (n=40)			
	Uncut	Patch	<u>Corridor</u>	Clearcut
Initial N (NH ₄ -N + NO ₃ -N)	146 (39) a	171 (20) a	108 (21) a	83 (23) a
Final N after 6wks	92 (34) a	270 (132) a	247 (75) a	121 (37) a
NH₄-N after 6wks	44 (24) a	22 (8) a	4 (1) a	9 (3) a
NO3-N after 6wks	48 (29) a	249 (134) a	243 (74) a	112 (37) a
PO ₄ -P after 6wks	99 (7) a	94 (8) a	59 (6) b	44 (8) b
NH ₄ -N mineralised/ 6wks	-101 (28) ab	-143 (23) b	-78 (13) ab	-53 (24) a
NO ₃ -N mineralised/ 6wks	47 (29) a	242 (129) a	217 (71) a	91 (36) a
PO ₄ -P mineralised/ 6wks	-22 (6) a	-12 (15) a	-17 (12) a	-15 (4) a
	Deciduous (n=39)			
	Uncut	Patch	Corridor	Clearcut
Initial N (NH4-N + NO3-N)	311 (94) a	219 (32) a	350 (110) a	259 (130) a
Final N after 6wks	590 (88) a	314 (40) b	221 (51) b	176 (58) b
NH4-N after 6wks	54 (11) a	35 (13) a	15 (2) a	36 (15) a
NO ₃ -N after 6wks	537 (92) a	279 (49) b	206 (52) b	140 (52) b
PO ₄ -P after 6wks	139 (20) a	63 (9) b	50 (6) b	59 (8) b
NH4-N mineralised/ 6wks	-179 (35) b	-154 (31) ab	-138 (13) ab	-55 (20) a
NO ₃ -N mineralised/ 6wks	459 (71) a	250 (51) ab	8 (70) ab	-28 (102) b
PO ₄ -P mineralised/ 6wks	50 (17) a	-8 (14) b	-14 (8) b	-10 (7) b

Table 2.5 N and P availability in forest floors from uncut, patch, corridor, and clear-cut treatments in coniferous and deciduous stands, initially and after 6 weeks laboratory incubation; also, net N and P mineralised over a 6-week laboratory incubation. Values are means with SE in parentheses.

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Note: Within each row, values followed by the same letter are not significantly different, based on 1-way ANOVA and Tukey's HSD test (p>0.05)

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2.4 Discussion

2.4.1 Differences in Forest Floor Properties between Stand Types

There were significant differences in forest floor properties between deciduous and conifer stands. This would be expected since tree species influence forest floor nutrient availability as a result of differences in foliar litter chemistry, specifically C:N ratios and lignin concentrations (Paré and Bergeron 1996; Côté *et al.* 2000). Greater forest floor depth, more organic matter accumulation, lower pH, and lower rates of N mineralisation in the conifer stands than in the deciduous stands can also be attributed to differences in litter quality and foliar chemistry between deciduous and coniferous overstories (Frazer *et al.* 1990; Paré and Bergeron 1996, Côté *et al.* 2000).

Conifer systems in the boreal forest are generally regarded as being N-limited, mainly because high lignin and low N contents in conifer litter promote immobilisation of N by microbes. This reduces net N mineralisation rates, which, in turn, lowers available soil N (Côté *et al.* 2000). Low levels of NH₄-N and NO₃-N were measured in the conifer stands in this study, suggesting that these stands may, indeed, be N-poor. In contrast, higher nutrient levels (total N and P, NH₄-N, NO₃-N) and higher N and P mineralisation rates in the deciduous stands indicate that this stand type is more fertile and potentially more productive than the conifer stands.

2.4.2 Effects of Harvest on Forest Floor Physical Properties

Removal of the overstory vegetation and forest canopy by clear-cutting can affect site microclimate by decreasing thermal insulation and evapotranspiration, thereby causing an increase in soil moisture (Keenan and Kimmins 1993). Partial cutting has been shown to reduce these effects (Barg and Edmonds 1999). However, in the present study soil moisture in the retention patches and corridors was not significantly different from that in the clear-cuts, but was greater than that in the uncut controls in both stand types.

Soil disturbance was minimal due to lack of site preparation; however, compaction associated with the harvesting process was apparent in the corridors of the conifer stands, where a decrease in forest floor depth and an increase in soil bulk density were measured. The clear-cut treatments also had a thinner forest floor and greater bulk density relative to the forest floor in the uncut sites. Startsev *et al.* (1998) found trafficking by tree-removing skidders significantly increased soil bulk density after only one pass. Maximal compaction occurred after only three passes of the skidder, and this led to a negative correlation between soil respiration and bulk density. In the present study, soil compaction in the corridors and clearcuts may explain the reduction in microbial respiration and biomass observed in these treatments, since the corridors received two passes of a skidder and the clearcuts received one.

2.4.3 Effects of Harvest on Forest Floor Biological Properties

Litter and root exudates are primary resources for microbes, and roots are especially important for organisms associated with the live root biomass, such as the mycorrhizal fungi (Bååth 1980). Thus, a decrease in litter input and root biomass would be expected to reduce basal respiration and microbial biomass, as was observed in the patch, corridor, and clear-cuts in the present study. A reduction in microbial biomass following harvesting is corroborated by other studies. Bååth (1980) reported reduced microbial biomass following clear-cuttting, and Chang *et al.* (1995) found less microbial biomass in the forest floors of 3 and 10-year-old cedar plantations on northern Vancouver Island, than in the forest floors of old-growth forests. Increases in microbial biomass following harvesting also may occur (Entry *et al.* 1986; Barg and Edmonds 1999). No significant long-term changes in basal respiration and microbial biomass following harvesting have been reported also (Seastedt and Crossley 1981; Marra and Edmonds 1998).

Alterations in soil temperature and moisture due to tree removal may accelerate organic matter decomposition in the field (Covington 1981). However, many studies have reported no consistent change in overall patterns of litter decay following forest harvest (Prescott *et al.* 2000). Litter decay measurements in this study showed no harvesting effects, perhaps because moisture and temperature were standardised across all treatments during the 3-month laboratory incubation.

2.4.4 Effects of Harvest on Forest Floor Chemical Properties

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Although there was an increase in soil moisture in the patches, corridors, and clearcuts at the EMEND site, microbial biomass was reduced in these treatments and there was no effect of harvest on decomposition rates. A decline in total C, N, NO₃-N, NH₄-N, and PO₄-P in the forest floor often occurs after clear-cutting (Schmidt *et al.* 1996); yet other studies have found an increase (Vitousek and Matson 1985; Frazer *et al.* 1990), or no significant difference in these nutrients, (Maynard and MacIsaac 1998) between cut and uncut forests. The current research revealed a progressive reduction in NH₄-N from uncut to partial-cut to clear-cut sites in both stand types suggesting a gradient effect of harvesting intensity on NH₄-N. Lower NH₄-N in the corridor and clearcut treatments may be the result of increased nitrification after harvesting, as any NH₄-N that is generated has the potential to be quickly converted to NO₃-N by the nitrifying bacteria. More NO₃-N in the corridor and clear-cut treatments than in the patch and uncut control treatments supports this possibility, and suggests that there was an increase in nitrification with increased timber removal.

More NO₃-N in forest floors following clear-cutting is commonly reported and has previously been attributed to greater decomposition and nitrification rates due to increased microbial activity, as a result of improved soil moisture and temperature conditions (Frazer *et al.* 1990). An alternative hypothesis to explain the increase in NO₃-N after harvesting disturbance suggests that a decline in C input following clear-cutting reduces microbial biomass and microbial immobilisation of N, thereby increasing NO₃-N levels (Hart *et al.* 1994a; Prescott 1997). NO₃-N is susceptible to leaching which may explain the reduction in NO₃-N in forest floors of mixed northern hardwood forests following harvesting disturbance (Dahlgren and Driscoll 1994).

2.4.5 Effects of Harvest on Laboratory Nitrogen Mineralisation

Laboratory incubation studies, such as those conducted in the present study, control for temperature, moisture and plant uptake. Thus, these factors probably do not explain the lower rates of net N mineralisation measured in the forest floor deciduous sites after harvesting. Rather, a reduction in microbial biomass and/or a change in substrate quality post harvest may have induced changes in N mineralisation rates. Net N mineralisation rates in laboratory incubation studies have been shown to correlate with the C:N ratio of the forest floor (Côté *et al.* 2000, Prescott *et al.* 2000). High C:N ratios (>35:1) in forest floors tend to induce immobilisation of N by microbes. Therefore, net immobilisation of N in the corridor and clearcut deciduous forest floors at the EMEND site may be due to higher C:N ratios in the soil after harvesting, and this may be attributed to a decrease in N input resulting from lower leaf litter deposition (Prescott *et al.* 2000) combined with an input of harvesting residues high in C (Swift *et al.* 1979).

Considerable variation was measured in net N mineralisation in the conifer soil resulting in no significant treatment effects. In soil from the uncut coniferous site, there was net immobilisation of N. Net N immobilisation is not uncommon in unharvested coniferous forests, as they are often N-limited and conifer needle litter typically has high C:N ratios (>200:1). In a study of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in British Columbia that varied in N availability, the majority of the unharvested

stands showed net N immobilisation, and net N mineralisation only occurred in stands where C:N ratios were lower than 35:1 (Prescott *et al.* 2000). Net N mineralisation in the harvested treatments of the present study, is attributed to the reduced microbial biomass in these treatments, which would decrease the amount of N immobilised by the microbial community.

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2.5 Conclusions

- Overall, the effects of partial-cut harvesting on many forest floor properties were less pronounced than the effects of clear-cut harvesting in the EMEND mixed-wood boreal forest. However, in many cases, within the partial-cut harvesting sites, patch and corridor treatments differed in their forest floor properties. The retention patches were more likely to retain forest floor properties similar to the uncut treatments, whereas forest floors in the strip-cut corridors tended to be more similar to those in the clear-cuts.
- 2. An increase in soil moisture and bulk density, and a decrease in forest floor depth following partial and clear-cut harvest of the conifer stands, can all be attributed to soil compaction during the harvesting process. These effects were not as apparent in the deciduous stands where rapid re-establishment of the overstory vegetation may have mitigated the effects of compaction.
- 3. Available NH₄-N, NO₃-N and PO₄-P concentrations in the partial-cut treatments were intermediate between the clear-cut and uncut treatments. Harvesting caused a decline

in NH₄-N and PO₄-P concentrations, while NO₃-N concentrations increased. Changes in nutrient concentrations after harvest are attributed primarily to decreases in microbial biomass and litter input.

- 4. Biological properties of the conifer and deciduous forest floors, in particular soil respiration, microbial biomass C, annual litter input and fine root biomass, were lower in the partial-cut and clear-cut harvesting treatments than in the uncut control treatments. Decomposition potential as measured in a laboratory incubation study showed no effect of harvest treatment.
- 5. Rates of net N mineralisation (and N immobilisation) in laboratory incubations of conifer and deciduous forest floors suggest that reduced microbial biomass, decreased litter inputs and/or changes in forest floor C:N ratios following forest harvesting alter N mineralisation potentials.

Chapter Three: FOREST FLOOR MICROARTHROPODS AND ORIBATID MITE (ACARI: ORIBATIDA) COMMUNITY COMPOSITION IN HARVESTED CONIFER AND DECIDUOUS STANDS.

3.1 Introduction

Microarthropods range in size from 0.1-2mm in length and in soil, include primarily Acari (mites) and Collembola (springtails). These microarthropods play an important role in regulating rates of decomposition and nutrient cycling via interactions with the microbial community (Seastedt 1984). Microarthropods influence microbial populations by stimulating microbial growth through grazing, introducing microbial propagules to new substrates, and increasing litter surface area for microbial attack through comminution of organic matter and fecal pellet deposition (Visser 1985). Microarthropods also release nutrients held within fungal standing crops and contribute to soil structure and humus formation (Wallwork 1983, Norton 1985). While the relative contributions of microarthropods to decomposition and nutrient cycling have not been specifically quantified, reductions in microarthropod abundance may be detrimental to soil processes. For this reason, preservation of soil biodiversity should be considered an integral component of forest management practices (Marshall 2000).

Numerous studies have reported a reduction in soil microarthropods following forest clear-cutting (Vlug and Borden 1973, Huhta 1976, Abbott *et al.* 1980, Blair and Crossley 1988, Marra and Edmonds 1998). However, the effect of forest harvesting at reduced intensities, such as that practised in residual-leave or partial-cut systems, on forest floor microarthropods has not been studied in detail. Green tree retention within harvested sites is thought to reduce overall soil disturbance, maintain organic matter inputs and nutrient cycles, reduce nutrient losses (Dahlgren and Driscoll 1994), provide refuge for belowground organisms like mycorrhizal fungi (Barg and Edmonds 1999), and help maintain soil invertebrate communities (Siira-Pietikäinen *et al.* 2001). Abbott *et al.* (1980), observed that communities of soil microarthropods in partial-cut sites were more similar to those in uncut sites than those in clearcuts. Huhta *et al.* (1967) found that forest thinning reduced soil microarthropod abundance in a Finnish coniferous forest, but reductions were less than in clear-cut sites. Other research has shown that partial-cut and selective timber harvesting may have significant, long-lasting effects on the soil arthropod community (Hoekstra *et al.* 1995). These observations suggest that partial-cut harvesting may be less detrimental to forest floor microarthropod communities than is clear-cutting, but further research is required to confirm this.

Oribatid mites (Acari: Oribatida) are the numerically dominant microarthropods in forest systems (Wallwork 1983), and often show the greatest decrease in abundance following harvesting disturbance (Seastedt and Crossley 1981, Blair and Crossley 1988). The diversity of oribatid species is high compared with other microarthropod groups and changes within oribatid mite community structure may be a useful indicator of disturbance (Behan-Pelletier 1999).

Oribatid mites generally have low dispersal capabilities and cannot easily escape from the stress of disturbance or recolonise disturbed habitats. Oribatid mites are considered k-selected organisms (low fecundity, iteroparous, slow developmental times, and metabolic rates, long lifespans); thus, they do not recover quickly from reduced population numbers (Norton 1990). However, some families and species of oribatid mites are known to be thelytokous (parthenogenic) and may have an advantage over other species to increase numerically following disturbance. It is suggested then, that in disturbed soil systems, measurable changes in community composition as a result of an increased dominance of thelytokous families or species will be observed (Behan-Pelletier 1999). The use of oribatids as indicators of soil disturbance is not yet a common practise. This may be the result of incomplete taxonomy of oribatid mites at the species level and/or the amount of expertise and time required to identify this group of microarthropods.

The present study examined the effects of clear-cut and 50% partial-cut harvesting on forest floor microarthropods in coniferous and deciduous dominated stands of the boreal mixed-wood forest. The overall objective was to determine whether a 50% partial-cut harvest had less of an impact on forest floor microarthropods than a clear-cut harvest did. In addition, oribatid diversity and community composition were assessed to evaluate the usefulness of oribatid mites as biological indicators of harvesting disturbance. I hypothesised that forest floor microarthropod populations would be reduced by partial-cut harvesting compared with uncut sites, but that microarthropod numbers would be higher in partial-cut than clear-cut sites. Within the partial-cut sites, I predicted that there would be differences in microarthropod numbers, since strip-cut corridors and selectively harvested retention patches within the partial-cut differ in the degree of forest floor disturbance. Changes in oribatid mite community composition, and shifts in the dominance or relative abundance of certain oribatid species would be expected as a result of harvesting disturbance.

3.2 Methods

3.2.1 Site Description and Experimental Design

The study site and experimental design have been described previously (chapter 2).

The treatments used to determine harvesting impacts on the microarthropod communities were: 1) uncut control, 2) selectively harvested retention patches within partial-cuts (patch), 3) strip-cut corridors within partial-cuts (corridor), and 4) clearcut.

3.2.2 Sampling Regime and Sample Processing

Forest floor microarthropod sampling was conducted in June 2001, 2.5 years after harvest. A total of 80 forest floor cores (to mineral soil depth) were removed along 50m transects in each treatment [2 stand types (conifer, deciduous) x 2 replicate stands x 4 treatments (uncut, patch, corridor, clearcut) x 5 samples per treatment]. Transects were oriented north/south to coincide with the direction of the patch and corridors. Individual 5.5cm diameter PVC soil corers were used for each sample, and samples were stored in the corer at 4°C until just prior to microarthropod extraction. Intact forest floor cores were extruded from the plastic corers, divided into 4cm sections and placed in a Macfadyen extractor (Macfadyen 1961), where a temperature and moisture gradient forced soil fauna to move down the core into a picric acid fixative over a period of 10 days. Microarthropods extracted from the cores were filtered from the picric acid and preserved in 70% ethanol. The total number of microarthropods and total numbers of individuals within major microarthropod groups (Collembola and Acari) were evaluated using a dissecting microscope at 12X magnification. Collembola (springtails) were identified to suborder (Arthroplèona and Symphyplèona), as were the Acari (Oribatida, Prostigmata, Astigmata, and Mesostigmata). Oribatid mites from the uncut and clear-cut treatments were classified to genus and species where possible using a compound microscope (100X-400X magnification) and keys produced by Norton (1990, unpublished key), Balogh and Balogh (1992), Balogh and Mahunka (1983) and Gilyarov (1975).

3.2.3 Microarthropod and Oribatid Mite Abundance, and Community Composition

Microarthropod abundance expressed as the number of individuals per 100g dwt forest floor, was used to estimate abundance at various taxonomic levels, and to determine changes in absolute abundance (density) of microarthropods between treatments.

Changes in microarthropod community composition were explored using percent relative abundance of microarthropod suborders (number individuals in a suborder / total number individuals * 100). Relative abundances are useful for comparing the structure of microarthropod assemblages, and to identify groups (suborders) most impacted by forest harvest. Taxonomic groupings at the suborder level for oribatid mites, and mesostigmatid mites are roughly equivalent to functional groups (organisms which share similar functional roles in the community), based on characteristics such as primary food source, feeding mode, reproductive rate and defence against predators (Moore *et al.* 1988). Any changes in the relative abundance of microarthropod functional groups (community composition) can affect energy and nutrient pathways in the belowground foodweb (Seastedt and Crossley 1984).

Oribatid mite community composition and diversity were examined by applying non-parametric diversity indices including species richness, diversity, evenness, and dominance (Magurran 1988). Species richness (N) measures the total number of species recorded for a given sampling unit. The species richness index is very simple to calculate and is widely used; however, it is very sensitive to sampling effort, thus a cumulative species curve for oribatid mites was constructed to test whether the oribatid sampling effort was intensive enough to find all oribatid mite species present in conifer and deciduous stands of this mixed-wood boreal system.

The diversity index, inverse of Simpson's, was calculated using the formula $1/D = 1/\Sigma p_i^2$, where D is Simpson's index and p_i is the proportion of individuals found in the *i*th species. Simpson's index has low sensitivity to sample size and is widely used (Magurran 1988). The Shannon-Wiener index of evenness was calculated using the formula $H' = -\Sigma p_i \ln p_i$, where H' is Shannon's index and p_i is the proportion of

individuals found in the *i*th species. The Shannon-Wiener index has average discrimination ability, is widely used, but is moderately sensitive to sampling effort (Magurran 1988). The Berger-Parker index, calculated as the inverse of $d = N_{max}/N$, where N_{max} is the number of individuals in the most abundant species and N is the total number of individuals, is not as widely used as other indices, but provides a simple calculation of the inverse dominance of a community independent of species richness (Magurran 1988).

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3.2.4 Statistical Analysis

The General Linear Model (GLM) for randomised block designs in SYSTAT 7.0 was used to analyse the abundance data. A two-factor ANOVA was performed to test for stand and treatment effects on absolute and relative abundance means for total microarthropods, total Acari, total Collembola, and suborder level data. Results were considered significant when p<0.05. Within each of the conifer and deciduous stand types, additional 1-way ANOVAs with Tukey's HSD tests were performed to assess the effects of harvesting treatments on total microarthropod abundance, total Acari, total Collembola, and microarthropod suborder abundance. Microarthropod abundances were log transformed (log₁₀) to normalise the data and to minimise the effects of rare species and aggregated population distributions (Krebs 1989).

Pearson's correlation coefficients were used to determine relationships between total microarthropod, total Acari and total Collembola absolute abundance, and forest floor moisture, bulk density, fine root biomass, microbial biomass, and total and available N and P in each stand type. Hierarchical cluster analysis was used to group the most similar treatments in each stand type based on the absolute abundance patterns of microarthropod suborders. Where possible, oribatid species in uncut and clear-cut treatments in each stand type were compared using a one-way ANOVA.

3.3 Results

3.3.1 Harvesting Effects on Total Microarthropod, Acari and Collembola Abundance

Acari and Collembola accounted for 98% (70% and 28%, respectively) of the total microarthropods enumerated in this study. The remaining 2% of fauna collected from the forest floors included various other taxa, predominantly insect larvae and small arachnids. Therefore, patterns of total microarthropod abundance were influenced primarily by Acari abundance. Forest floors from uncut conifer stands had significantly greater total microarthropod (p=0.031) and Acari abundance (p=0.017) than did uncut deciduous forest floors (Fig. 3.1 a, b). Collembola were also more abundant in uncut conifer forest floors than in uncut deciduous forest floors, but the difference was not significant (Fig. 3.1 c).

Acari, Collembola, and total microarthropod numbers were significantly reduced in the corridors of the deciduous stands (Fig. 3.1 a, b, c). Total microarthropod and total Acari numbers were also significantly reduced in the clear-cut treatments of the conifer Figure 3.1 Average abundance of a) total microarthropods, b) total Acari (mites), and c) total Collembola (springtails) in forest floors of uncut, patch, corridor, and clear-cut treatments in conifer and deciduous stands. Within each stand type, data points (means \pm SE) accompanied by different letters are significantly different (p<0.05) based on a 1-way ANOVA with Tukey's HSD test.

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c) Total Collembola



stands relative to the uncut control treatment. There was no significant treatment effect on Collembola abundance in the conifer forests, where springtail abundances were highly variable.

Correlation analysis of total microarthropod, total Acari and total Collembola abundances with selected forest floor properties suggests that microarthropod communities differ between conifer and deciduous stands (Table 3.1). In the conifer stands, total microarthropod, total Acari and total Collembola numbers were significantly positively correlated with microbial biomass, total P, NH₄-N and PO₄-P. Acari abundance was also positively correlated with fine root biomass (<2mm dia.). In contrast, Acari abundance and consequently, total microarthropod numbers, were significantly negatively correlated with bulk density in the conifer stands. In the deciduous stands total microarthropod and total Collembola numbers were negatively correlated with moisture content. Acari and Collembola abundances were negatively correlated with pH. Total microarthropods were significantly correlated with fine root biomass (<2mm dia.) in the deciduous stands.

3.3.2 Harvesting Effects on Acari and Collembola Suborders

Forest harvest had a significant effect on the absolute abundances of oribatid mites and prostigmatid mites in both conifer and deciduous stands (Fig. 3.2 a, b). Oribatid and prostigmatid mite numbers were significantly lower in the strip-cut corridors of the deciduous stands, and in the corridors and clear-cuts of the conifer stands than in

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		Conifer (n=40)	
	Total microarthropods	Total Acari	Total Collembola
Moisture content	0.016	-0.168	0.301
pH _(H2O)	0.108	0.086	0.109
Soil bulk density	-0.501**	-0.543**	-0.307
Microbial biomass C	0.569**	0.626**	0.346*
Total N	0.289	0.253	0.271
Total P	0.434*	0.382*	0.417*
Available NH4-N	0.429*	0.367*	0.438*
Available NO3-N	0.000	-0.036	0.000
Available PO ₄ -P	0.446*	0.433*	0.373*
Fine root biomass (<2mm dia.)	0.272	0.338*	0.117
	Deciduous (n=39)		
	Total microarthropods	Total Acari	Total Collembola
Moisture content	-0.493**	-0.142	-0.426*
pH _(H2O)	-0.259	-0.345*	-0.316*
Soil bulk density	-0.205	-0.194	-0.218
Microbial biomass C	0.262	0.261	0.276
Total N	-0.017	-0.277	-0.083
Total P	0.268	0.158	0.251
Available NH4-N	0.261	-0.019	0.207
Available NO ₃ -N	0.135	0.058	0.142
Available PO ₄ -P	0.129	-0.017	0.098
Fine root biomass (<2mm dia.)	0.335*	0.122	0.296

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Table 3.1 Pearson's correlation coefficients for forest floor microarthropod abundances and selected forest floor properties in conifer and deciduous stands. _____

Fine root biomass (<2mm dia.)</th>0.33* Correlation is significant at the 0.05 level (2-tailed).** Correlation is significant at the 0.01 level (2-tailed).
Figure 3.2 Abundance of a) oribatid mites, b) prostigmatid mites, c) astigmatid mites, d) mesostigmatid mites, e) arthropleonid collembola, and f) symphypleonid collembola in forest floors of uncut, patch, corridor, and clear-cut treatments in conifer and deciduous stands. Within each stand type, bars (means \pm SE) superseded by different letters are significantly different, based on a 1-way ANOVA and Tukey's HSD test (p<0.05).

















the uncut controls. Numbers of astigmatid mites, mesostigmatid mites and arthropleonid collembola were lower in the retention patches and significantly lower in the corridors of the deciduous stands compared to the uncut control (Fig. 3.2 c, d, e). However, numbers of astigmatid mites, mesostigmatid mites, and arthropleonid collembola in the deciduous clearcuts were not significantly different from those in the uncut controls. No significant effect of harvest on astigmatid and mesostigmatid mites and arthropleonid collembola was detected in the conifer stands. Symphypleonid collembola were not affected by forest harvest treatment in either stand type (Fig. 3.2 f).

Hierarchical cluster analyses (Fig. 3.3) showed that patterns of absolute abundance (density) within the microarthropod suborders in the conifer stands were similar between the strip-cut corridors and the clear-cut treatments, while abundances in suborders in the retention patches were more similar to those in the uncut control forest. In the deciduous stands, the numbers and types of microarthropods in the retention patches and the clear-cut treatments were most similar, and resembled the pattern in the strip-cut corridors. The uncut control treatment was dissimilar to the patch, corridor, and clear-cut treatments in the deciduous stands.

Harvesting decreased the relative abundance (% of total) of oribatid mites, with numbers in the corridor and clear-cut treatments in the conifer stands being significantly less than those in the uncut control (Table 3.2). The relative abundance of prostigmatid mites was lower in both conifer and deciduous clearcuts than in their respective controls. In the deciduous stands, the relative abundance of mesostigmatid mites was lowest in the strip-cut corridors, but no significant shifts in Figure 3.3 Hierarchical cluster analysis (based on percent similarity measures) of forest harvest treatments using absolute abundance patterns of forest floor microarthropod suborders in a) conifer and b) deciduous stands. Low distance scores denote the most similarity between treatments.



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Suborder	Conifer (n=40)					
	Uncut	Patch	Corridor	Clearcut		
Oribatida	67.8 (3.2) a	52.2 (6.8) ab	46.4 (3.0) b	46.3 (6.8) b		
Prostigmata	5.2 (0.5) a	4.4 (0.8) ab	5.2 (0.5) a	3.0 (0.7) b		
Astigmata	3.4 (1.2) a	6.0 (3.3) a	9.5 (2.4) a	6.6 (2.8) a		
Mesostigmata	4.4 (0.8) a	4.7 (0.9) a	8.2 (1.3) a	5.8 (1.3) a		
Arthropleona	17.9 (2.1) a	29.8 (5.0) a	23.8 (3.0) a	30.4 (4.7) a		
Symphypleona	0.5 (0.1) a	0.3 (0.2) a	1.2 (0.4) a	1.5 (0.6) a		
	Deciduous (n=40)					
	Uncut	Patch	Corridor	Clearcut		
Oribatida	48.9 (2.5) a	48.1 (2.4) a	46.2 (4.8) a	36.8 (4.7) a		
Prostigmata	17.6 (2.4) a	16.0 (1.4) ab	13.6 (1.0) ab	9.9 (1.3) b		
Astigmata	2.1 (0.6) a	0.5 (0.2) a	0.8 (0.5) a	2.4 (0.9) a		
Mesostigmata	8.4 (1.4) ab	6.1 (0.9) ab	5.0 (1.1) b	10.0 (0.9) a		
Arthropleona	20.3 (2.3) b	24.2 (2.2) ab	25.3 (3.6) ab	34.6 (4.2) a		
Symphypleona	1.0 (0.3) a	2.0 (1.0) a	1.4 (0.8) a	2.8 (1.2) a		

Table 3.2 Relative abundance (% of total abundance) of forest floor microarthropod (Acari and Collembola) suborders in uncut, patch, corridor, and clear-cut treatments of conifer and deciduous stands. Values are means with SE given in parentheses.

Note: Within each row, values followed by the same letter are not significantly different, based on a 1-way ANOVA and Tukey's HSD test (p>0.05).

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mesostigmatid relative abundance were evident in the conifer stands following harvesting. Arthropleonid collembola increased in relative abundance as harvest intensity increased, so that numbers in the clear-cut treatment of the deciduous stands were significantly greater than numbers in the uncut deciduous control treatment. A similar trend was seen in the conifer stands, but this was not significant. Astigmatid mites and symphypleonid collembola showed no significant shifts in relative abundance as a result of harvesting disturbance, and were consistently less abundant than the other groups of microarthropods.

3.3.3 Clear-cut Harvesting Effects on Oribatid Mites

Over 3900 adult oribatid mites from 19 families were identified to species from the uncut and clear-cut treatments (Table 3.3). Individuals from the family Oppiidae (2 species) were the most abundant, followed by Suctobelbidae (4 species) and Brachychthoniidae (11 species). Individuals from these three families accounted for >85% of all oribatid mites observed in the uncut and clear-cut treatments. A total of 39 species of oribatid mites were identified; 33 species inhabited the conifer forest floor and 25 species occurred in the deciduous forest floor, while 19 species were common to both stand types. The most abundant species in both conifer and deciduous stands was *Oppiella nova* (Oudemanns) in the family Oppiidae.

There was a significant decline in the absolute abundance of O. *nova* as a result of clear-cutting in both stand types (deciduous p=0.004, conifer p=0.000) (Table 3.3). Also,

Table 3.3 Mean densities (# individuals/100g dwt \pm SE) of oribatid species found in the forest floors of uncut and clearcut conifer and deciduous stands.

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	Conifer (n=20)		Deciduor	us (n=20)
	<u>Uncut</u>	<u>Clearcut</u>	Uncut	Clearcut
Family Brachychthoniidae				
Brachychthonius sp. nr. berlesei Willmann	0.0	0.0	0.0 a	0.6 (0.6) a
Liochthonius sellnicki (Thor)	9.2 (4.6) a	12.3 (5.5) a	0.0	0.0
L. sp. nr. brevis (Michael)	102.2 (42.6) a	89.6 (30.3) a	6.2 (4.2) a	1.3 (0.9) a
L. sp. nr. clavatus (Forsslund)	0.8 (0.8) a	0.5 (0.5) a	0.0	0.0
L. sp. nr. muscorum Forsslund	12.5 (5.0) a	1.6 (1.1) b	0.0 a	0.7 (0.6) a
L. sp. nr. <i>simplex</i> (Forsslund)	72.7 (25.4) a	40.7 (17.8) a	0.0	0.0
Mixochthonius sp. nr. concavus (Chinone)	7.9 (4.8) a	2.6 (2.0) a	0.0	. 0.0
Paraliochthonius sp. nr. occultus (Niedbala)	0.8 (0.8) a	0.5 (0.5) a	0.0	0.0
Poecilochthonius sp. nr. spiciger (Berlese)	0.0	0.0	0.0 a	1.1 (1.1) a
Sellnickochthonius rostratus (Jacot)	1.0 (0.6) a	0.0 a	0.0	0.0
S. suecica Forsslund	85.7 (36.5) a	2.5 (1.4) b	0.0 a	0.6 (0.6) a
Family Pterochthoniidae				
Pterochthonius angelus (Berlese)	0.0	0.0	0.0 a	0.6 (0.6) a
Family Phthiracaridae				
Phthiracarus sp. nr. borealis (Trägårdh)	0.0	0.0	0.3 (0.3) a	0.0 a
Family Oribotritiidae				
Protoribotritia sp.	0.0	· 0.0	0.2 (0.2) a	0.0 a
Family Camisiidae				
Heminothrus minor Aoki	1.4 (1.0) a	1.8 (1.0) a	0.0	0.0
Platynothrus peltifer (C.L. Koch)	0.0 a	0.6 (0.6) a	0.0	0.0
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Table 3.3 cont.

	Conifer (n=20)		Deciduous (n=20)	
	Uncut	Clearcut	Uncut	<u>Clearcut</u>
Family Trhypochthoniidae	•			
Trhypochthonius tectorum (Berlese)	0.7 (0.7) b	12.2 (5.5) a	1.0 (1.0) a	0.0 a
Family Damaeidae				
<i>Epidamaeus</i> sp. 1	5.9 (2.5) a	2.1 (1.1) a	1.2 (0.7) a	1.1 (1.1) a
<i>E</i> . sp. 2	1.4 (1.0) a	0.0 a	0.0	0.0
<i>E</i> . sp. 3	0.8 (0.8) a	0.9 (0.9) a	0.0 a	5.2 (3.2) a
Family Cepheidae				
Cepheus corae Jacot	2.7 (1.5) a	0.0 a	0.0	0.0
C. latus C.L. Koch	0.7 (0.7) a	0.0 a	0.0	0.0
Family Eremaeidae				
Eremaeus tramslamellatus Hammer	1.4 (0.9) a	1.1 (1.1) a	0.0 a	0.5 (0.5) a
Eueremaeus marshalli Behan-Pelletier	0.0 a	1.3 (0.9) a	0.0	0.0
Family Astegistidae	·			
Astegistes sp.	0.0	0.0	0.2 (0.2) a	0.9 (0.9) a
Family Peloppiidae				
<i>Ceratoppia quadridentata (arctica)</i> Hammer	1.2 (0.8) a	0.0 a	0.3 (0.3) a	0.7 (0.7) a
Family Tectocepheidae				
Tectocepheus velatus (Michael)	2.8 (2.1) a	10.2 (5.2) a	3.4 (1.4) a	8.6 (5.3) a
Family Oppiidae				
Moritzoppia clavigera (Hammer)	37.9 (17.5) a	5.4 (3.0) a	3.3 (2.6) a	0.0 a

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Table 3.3 cont.

	Conifer (n=20)		Deciduous (n=20)	
	<u>Uncut</u>	<u>Clearcut</u>	Uncut	<u>Clearcut</u>
Oppiella nova (Oudemanns)	720 (154) a	177 (67) b	203 (50) a	35.1 (6.8) b
Family Quadroppiidae				
Quadroppia quadricarinata (Michael)	11.2 (4.4) a	9.0 (3.4) a	32.2 (7.6) a	20.0 (7.2) a
Family Suctobelbidae				
Suctobelba sp.	0.0 a	1.9 (1.4) a	0.0 a	0.7 (0.7) a
Suctobelbella sp. nr. acutidens (Forsslund)	79.8 (19.9) a	73.8 (26.4) a	25.9 (7.2) a	24.3 (7.0) a
Suctobelbella sp. 1	161.1 (32.4) a	90.0 (41.8) a	63.1 (10.7) a	30.5 (6.5) b
Suctobelbella sp. 2	15.6 (3.4) a	14.8 (8.1) a	36.1 (10.8) b	126 (37.1) a
Family Protoribatidae				
Liebstadia sp. nr. similis (Michael)	0.0 a	0.7 (0.7) a	0.0	0.0
Family Ceratozetidae				
Ceratozetes gracilis (Michael)	37.3 (16.4) a	6.4 (4.3) a	2.8 (2.4) a	0.0 a
Family Mycobatidae				
Mycobates conitus Hammer	15.2 (9.7) a	0.3 (0.3) a	0.0	0.0
M. incurvatus Hammer	2.7 (1.1) a	1.0 (0.7) a	5.3 (2.3) a	6.2 (3.2) a
Family Galumnidae				
Pilogalumna sp.	0.0 a	3.0 (7.9) a	0.9 (2.7) a	1.4 (3.5) a
Average total adult oribatids	1393 (235) a	564 (186) b	386 (65) a	266 (60) a

Note: Values are means with SE given in parentheses. Within each row, within each stand type, values followed by different letters are significantly different, based on a 1-way ANOVA (p<0.05).

Suctobelbella sp. 1 was reduced in the clearcuts of the deciduous stands relative to uncut deciduous stands (p=0.020). While numbers of *Liochthonius* sp. nr. *muscorum* (Forsslund) and *Sellnickochthonius suecica* Forsslund in the conifer stands decreased significantly following clear-cutting (p=0.050 and p=0.019, respectively), *Trhypochthonius tectorum* (Berlese) increased in absolute abundance after harvesting the conifer stands (p=0.029). In the deciduous stands, absolute abundance of *Suctobelbella* sp. 2 increased significantly after clear-cutting (p=0.035). No other oribatid species showed significant changes in abundance as a result of clear-cutting.

Twenty-eight species of oribatids were identified in both the uncut and clear-cut treatments in the conifer stands, but in the deciduous stands species richness increased from 17 species in the uncut treatments to 20 species in the clear-cut treatments (Table 3.4). Shannon-Wiener, inverse Simpson's, and Berger-Parker indices were all higher in conifer stands than in deciduous stands, and all indices were higher in clearcut than uncut treatments. A cumulative species curve constructed for oribatid mites from both conifer and deciduous stands showed that the number of oribatid mite species observed in this study may be slightly underestimated since the cumulative number of species did not attain a plateau with the maximum number of samples processed (n=40) (Fig. 3.4). Some species showed a preference for one stand type over another. *Quadroppia quadricarinata* (Michael) and *Suctobelbella* sp. 2 were more abundant in the deciduous stands, while *Suctobelbella* nr. *acutidens, Suctobelbella* sp. 1, *Moritzoppia clavigera* (Hammer), and members of the genus *Liochthonius* were more abundant in the conifer stands.

	. Conifer		Deciduous	
Indices	Uncut	Clearcut	Uncut	Clearcut
Species richness (Number)	28	28	17	20
Evenness (Shannon-Wiener)	1.82	2.13	1.56	1.78
Diversity (1/Simpson's)	3.36	5.73	3.08	3.70
inverse Dominance (Berger-Parker)	1.93	3.18	1.90	2.12

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Table 3.4 Species diversity indices calculated for forest floor oribatid mites in uncut and clear-cut conifer and deciduous stands.

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Figure 3.4 Cumulative number of forest floor oribatid species collected with increasing number of soil samples removed from uncut and clear-cut treatments in conifer and deciduous stands of the EMEND research area.

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3.4 Discussion

3.4.1 Effects of Harvest on Microarthropods and Major Microarthropod Suborders

Total microarthropod densities in the uncut deciduous and conifer forest floors compared favourably with densities of 262,000 total microarthropods/m² found in subboreal spruce forests in British Columbia (Battigelli 2000), and 278,000 total microarthropods/m² in aspen stands of the Kananaskis valley in Alberta (Mitchell 1974). However, partial and clear-cut harvesting had an adverse effect on the forest floor microarthropods, with oribatid and prostigmatid mites being the groups most affected. A negative clear-cutting effect on oribatid mites, which are the numerically dominant microarthropod suborder in these systems, created a carry-through effect to higher taxonomic levels, and thus, significant reductions were seen in total Acari and total microarthropod numbers following forest harvesting.

Overall, trends in microarthropod abundance were reflected in the cluster analyses. Using a cluster analysis, it became clear that harvesting disturbance in the corridors and clearcuts of the conifer stands caused similar reductions in microarthropod densities at the suborder level, whereas densities in the retention patches were less altered and not significantly different from those in the conifer control. The cluster analysis pattern was different in the deciduous stands, where microarthropod suborder densities were most reduced in the corridors. Microarthropod suborder densities in the deciduous patch and clear-cut treatments also showed decreases, but these decreases in abundance were usually not significant compared with the uncut control treatment.

The reduction in forest floor microarthropods following forest harvest has been attributed to decreases in organic matter, litter input, microbial biomass, (Huhta *et al.* 1967, Bird and Chatarpaul 1986, Marra and Edmonds1998) and soil pore space (Vlug and Borden 1973, Battigelli 2000), and to changes in microclimate (Abbott *et al.* 1980, Seastedt and Crossley 1981, Marra and Edmonds 1998) that occur following harvesting disturbance. In the present study, the reduction in forest floor microarthropods and the alteration of microarthropod and oribatid mite community structure are probably a result of some, or all, of these factors. That total Acari and total Collembola numbers correlated positively with microbial and fine root biomass in both stand types, supports the idea that microarthropod densities are related to food availability, and that any alterations in these food sources will have repercussions on the microarthropod communities

A decline in microarthropods following harvesting in the corridors and clearcuts may be directly related to physical disturbance (compaction) of the forest floor. Compaction associated with the harvesting process can significantly increase soil bulk density and reduce the soil pore space that is inhabited by microarthropods (Startsev *et al.* 1998). Battigelli (2000) found that heavy compaction (4 cm) of the forest floor associated with stem-only and whole-tree harvesting significantly reduced total microarthropod density by 50% or more versus uncut forests in sites in British Columbia. Compaction was apparent in the corridors and clear-cut treatments in this study, where a decrease in forest floor depth and an increase in soil bulk density were observed (chapter 2). Pearson's correlation coefficients also showed a significant negative relationship between microarthropod abundance and soil bulk density, particularly in the conifer sites.

Clear-cut areas within the deciduous stands demonstrated extensive regeneration of aspen suckers 2.5 years following clear-cutting, that were approximately 4 feet high at the time of sampling. This may have mitigated any reductions in microarthropod numbers that may have occurred immediately following clear-cutting in this stand type. In general, removal of overstory vegetation results in reduced organic matter and leaf litter input, which can affect microbial populations (Bååth 1980). Also, canopy removal allows more solar radiation and precipitation to reach the soil surface; thereby altering temperature and moisture regimes (Keenan and Kimmins 1993). Thus, the rapid reestablishment of overstory vegetation in the deciduous clearcuts may have stabilised the forest floor microclimate and litter inputs more quickly in the deciduous than conifer clearcuts. Recovery of habitats for microarthropod colonisation may allow microarthropod densities to return to pre-disturbed levels more quickly in deciduous clearcuts than in conifer clearcuts or corridors where tree regeneration occurs more slowly.

Increases in relative abundance of arthropleonid collembola, which was most apparent in the deciduous stands, corroborate results found in other studies (Bird and Chatarpaul 1986, Blair and Crossley 1988). These increases have been attributed to the r-selected life history of the collembolans (i.e. high fecundity, fast developmental times and generation turnover rates) (Marshall 2000). An increase in absolute abundance of Collembola following harvest has been observed also (Huhta *et al.* 1967; Bird and Chatarpaul 1986; Marra and Edmonds 1998), but this was not the case in the present study.

Oribatid mites have long been identified as the microarthropod group most sensitive to forest harvest (Seastedt and Crossley 1981, Bird and Chatarpaul 1986). This is supported by the present study, since oribatid mites, along with the prostigmatid mites, were found to be most negatively affected by harvesting disturbance. Reductions in the absolute and relative abundances of oribatid mites were observed in both deciduous and coniferous stands, while prostigmatid mites decreased in relative abundance only in the deciduous stands.

3.4.2 Clear-cutting Effects on Oribatid Mites

The majority of oribatids are fungivores and/or detritivores. Partial and clear-cut harvesting reduced microbial biomass, fine-root biomass and annual litter input in both stand types (chapter 2); thereby, decreasing resource availability and causing a decline in forest floor oribatids. Maximum surface soil temperatures were not available for this study; however, surface temperatures near or exceeding 40°C following clear-cutting have been documented in other investigations (Vlug and Borden 1973, Abbott *et al.* 1980, Seastedt and Crossley 1981, Bird and Chatarpaul 1986). Temperatures above 40°C exceed the thermal death point (TDP) for oribatid mites and may contribute to reductions in oribatid mite populations following forest harvest (Madge 1965).

Oribatid mites may take longer than other microarthropod groups to recover from a reduction in density following forest harvest due to low fecundity, slow developmental times, low metabolic rates and long generation times (Norton 1990). In thelytoky, all reproduction is parthenogenic and males are absent in the population. Oribatid species that exhibit this reproductive strategy may have a greater ability to recolonise disturbed habitats compared to other oribatids. In this study, *Trhypochthonius tectorum* and *Suctobelbella* sp. 2, both suspected parthenogenic species, increased in abundance after harvesting, but other species known to be parthenogenic, such as *Oppiella nova*, did not.

Diversity indices of oribatid mite species were higher in clear-cut treatments of both stand types compared with those in the uncut control treatments. This contradicts Marra and Edmonds (1998), who found that oribatid mite communities in undisturbed sites had higher species richness and diversity than communities in clear-cut sites. Diversity indices are a measure of community structure based on the number and relative abundance of species within the community. The increase in evenness (Shannon's index) and diversity (inverse Simpson's index) in the clear-cut treatments in this study is likely related to the relative abundance of the most dominant species, *O. nova*. The reduction of *O. nova* in clear-cut sites was proportionally greater than any other oribatid mite species, thus leading to greater evenness of species within the oribatid community, and a reduction in the dominance of any particular oribatid species in the clear-cut treatments. Changes in the oribatid mite community following partial and clear-cut forest harvest were more quantitative (absolute abundance) than qualitative (relative abundance, community composition). Oribatid mites, in general, may be useful as biological indicators of harvesting disturbance as they are sensitive to changes in their environment and show measurable decreases in abundance when their habitat is disturbed.

The cumulative species curve for oribatid mite species as a function of sampling effort suggests that additional sampling is required to obtain a complete inventory of oribatid mite species for this region. However, compiling an oribatid species list was not an objective of this study, and does not appear to be necessary for observing the effects of forest harvest on the forest floor microarthropod community. Significant reductions in microarthropods following forest harvest were observed at all levels of taxonomic resolution and seem to be associated with the numerically dominant species, *O. nova*.

3.5 Conclusions

- Densities of forest floor microarthropods were reduced 2.5 years following partial and clear-cut harvesting, and oribatid and prostigmatid mite populations were the most adversely affected by forest harvest in both conifer and deciduous forests; arthropleonid collembola were also adversely affected in the deciduous corridor treatments.
- 2. In general, partial-cut harvesting impacted the forest floor microarthropods less than clear-cut harvesting did; however, the two components of the partial-cut system,

patch and corridor, differed in their degree of impact. In both conifer and deciduous stands, microarthropod numbers in the retention patches were not significantly lower than in the controls, whereas significant reductions in microarthropods were observed in the corridors. Reductions in microarthropod densities associated with the corridors are attributed to compaction of the forest floor during the harvesting process.

- 3. Lower densities of forest floor microarthropods following harvesting are likely due to different factors such as decreases in food (organic matter, root and microbial biomass) and habitat (organic matter, pore space), but changes in forest floor microclimate conditions may also have contributed. Minimising or mitigating harvesting disturbance of the forest floor may be helpful in the maintenance or recovery of forest floor microarthropod populations.
- 4. The reduction in the numerically dominant oribatid species, O. nova, following forest harvesting created a carry-through effect to higher taxonomic levels. Significant reductions in O. nova were translated into significant reductions in total oribatids, total Acari and total microarthropod numbers in clearcuts of conifer stands. Total oribatids, total Acari and total microarthropod numbers were also lower in the corridors than in the controls of both coniferous and deciduous forests. Decreased abundance of O. nova following clear-cutting also led to greater evenness of species within the oribatid community, thereby increasing diversity indices in this treatment. No overall trend in the response of parthenogenic oribatid mite species following harvesting disturbance was observed.

Chapter Four: THE CONTRIBUTION OF MICROARTHROPODS TO DECOMPOSITION AND NUTRIENT CYCLING IN HARVESTED AND UNHARVESTED CONIFEROUS AND DECIDUOUS FOREST FLOORS: A MESOCOSM STUDY.

4.1 Introduction

The importance of the soil microarthropods in belowground food webs and in soil processes such as decomposition and nutrient cycling is well documented (Seastedt 1984, Moore *et al.* 1988). However, their participation in soil processes is mostly indirect via their interactions with the microbial community. Microarthropod feeding activities disperse microbial propagules and spores, and have been shown to alter microbial community structure (Maraun *et al.* 1998). Also, grazing by microarthropods can increase basal soil respiration rates (Persson 1989), stimulate microbial growth, and increase microbial biomass (Bardgett and Chan 1999).

In general, investigations of the role of microarthropods in soil processes have shown that soil fauna accelerate decomposition and increase nutrient release. In an extensive review of the literature that included 11 studies on litter decomposition in the presence and absence of microarthropods, Seastedt (1984) found that microarthropods contributed an average of 23% to litter decomposition (mass loss). Rates of net N mineralisation can be increased by 10-49% (average 30%) in the presence of microarthropods (Persson 1989). Heneghan and Bolger (1998) and Bardgett and Chan (1999) measured higher levels of NH_4 -N, NO_3 -N, and PO_4 -P in soil with microarthropods than in defaunated soils.

Because the role of microarthropods in decomposition and nutrient cycling processes may be primarily indirect through their interactions with the microbial community, any direct involvement in these processes may not be measurable, or difficult to separate from indirect effects (Moore *et al.* 1988). Many studies exploring the contribution of microarthropods to soil processes have found no measurable results (Faber and Verhoef 1991, Cárcamo *et al.* 2001). In addition, soil physical and chemical properties may confound the measurement of microarthropod participation in the litter decay process (Brussaard *et al.* 1995).

Studies attempting to measure the relative contribution of microarthropods to decomposition and nutrient cycling are conducted in field or using laboratory-based mesocosms. Field studies typically involve exclusion of the microarthropods using litterbags of different mesh sizes and/or naphthalene treated soils (Anderson 1978, Douce and Crossley 1982). In the laboratory, the effects of specific numbers of certain types of microarthropods introduced to litter/soil held in mesocosms is the usual approach (Hanlon and Anderson 1979, Ineson *et al.* 1982, Brussaard *et al.* 1995, Bardgett and Chan 1999), or studies are conducted in the presence/absence of the microarthropods, regardless of their density (Persson 1989). Experiments in which the full complement of microarthropods is introduced to defaunated soil in mesocosms at field densities are rare.

The overall objective of the present research was to determine the contribution of forest floor microarthropods to decomposition and nutrient cycling processes in conifer

and deciduous forest floors of the mixed-wood boreal forest. Given reductions in microarthropod abundance following forest harvesting (chapter 3), I asked whether fewer mites and collembola in clear-cut sites would make a difference to decomposition and nutrient cycling processes. The specific objectives of my study were:

- to determine the effect of reduced microarthropod numbers on basal respiration and microbial biomass;
- 2. to determine the effect of reduced microarthropod numbers on decomposition potential as measured by mass loss of senesced aspen leaves; and
- to determine the effect of reduced microarthropod abundances on available NH₄-N, NO₃-N, and PO₄-P.

I hypothesised that lower densities of forest floor microarthropods would result in lower basal respiration, microbial biomass, decomposition potential and N and P availability.

The present mesocosm study used a more realistic approach because natural communities of microarthropods were used versus the more common single species experiments. Microarthropod populations were quantified at the beginning, middle, and end of the experiment, and data were analysed by regression analysis. This approach allowed me to test a natural range of microarthropod densities, rather than determine the effects of specific numbers of fauna- the approach usually used in these types of studies.

4.2 Methods

4.2.1 Sampling Regime and Site Description

Soil sampling for the mesocosm experiment occurred in June 2002, at the EMEND research site in the mixed-wood boreal forest, near Peace River, Alberta, Canada (56°46'13"N, 118°22'28"W). The EMEND research site has replicate 10ha uncut and clear-cut sites within conifer and deciduous stands. Harvesting of the stands occurred in the winter of 1998-99. Refer to chapter 2 for further details of the EMEND experimental design, site descriptions and harvesting methods. Of the four treatments studied in this project, only the uncut and clear-cut treatments were addressed in the mesocosm study.

A 50m transect was established in uncut conifer and deciduous stands, and soil samples were removed at 10m intervals for a total of 5 samples/stand. At each sampling point, intact forest floor soil blocks (25 x 25cm) were excavated to a depth of 15cm, and a 5.5cm dia. core was taken. In addition, 10 core samples (5 conifer, 5 deciduous) were removed from the 3.5 year-old clear-cut sites. A separate PVC soil corer was used for each soil core to minimise disturbance during transport from the field to the laboratory. All samples were stored at 4°C until ready for processing.

Litter and mineral soil were removed from each forest floor quadrat and the remaining F/H layers were passed through a 4mm sieve to produce homogeneous conifer or deciduous F/H soil for use in the mesocosms. The moisture contents (determined gravimetrically on a % dwt basis) of the F/H soil were 100% in conifer and 204% in deciduous stands, while organic matter contents (% LOI) were 72.5% and 69.5% in

conifer and deciduous samples, respectively. The pH (in water) of the F/H matrix was 4.6 in conifer soil and 5.8 in deciduous soil.

4.2.2 Mesocosm Experimental Design

All fauna in the sieved conifer and deciduous F/H soil were eliminated by extracting multiple 10g dwt-equivalent, field moist, F/H samples in a Macfadyen high gradient extractor. In the extractor, a temperature and moisture gradient established in each soil sample, forced fauna down through the soil into a picric acid fixative over a period of 10 days (Macfadyen 1961). Extracted fauna were filtered from the picric acid and preserved in 70% ethanol.

Four mesocosm treatments were tested in each of the conifer and deciduous stand types:

- 1) no-fauna- defaunated F/H material with no fauna added;
- low-density (clearcut) fauna- defaunated F/H material, refaunated with microarthropods extracted from clearcut soil cores;
- high-density (uncut) fauna- defaunated F/H material, refaunated with microarthropods extracted from uncut forest soil cores;
- 4) unextracted control- unextracted F/H material with no additional fauna added.
 The unextracted control treatment was used as a reference to gauge the effect of the extraction process on the F/H soil.

There were five replicates /treatment /sampling time (0, 30, 60 days)/stand type (conifer, deciduous) for a total of 100 mesocosms.

The mesocosms consisted of 500ml glass mason jars with vented lids. Mesocosms were prepared by placing 20g (dwt) extracted (defaunated) F/H material into each of 70 mesocosm jars (35 conifer, 35 deciduous) and 20g (dwt) unextracted F/H material into each of 30 control mesocosm jars (15 conifer, 15 deciduous). All mesocosms were re-moistened to 200% moisture content (dwt basis) with deionized water and allowed to equilibrate for 10 days after re-moistening before commencement of the experiment. Moisture was maintained gravimetrically throughout the experiment. Prior to the start of the experiment, (Day 0), senesced aspen leaves (0.5g dwt) were placed on the surface of the F/H in each mesocosm.

4.2.3 The Refaunation Process

Refaunation of the low and high-density fauna treatments started on Day 1 of the experiment and was completed by Day 10, with most fauna added by Day 5. Mesocosms were refaunated using microarthropods extracted from either clear-cut or uncut deciduous and coniferous forest floor core samples. Intact core samples were removed from their plastic corer sleeves, the litter layer was removed, and the upper 4cm of F/H material (~20g dwt) was placed on the Macfadyen extractor. Fauna were extracted over 10 days and collected in water. Each day, the extracted microarthropods were handpicked from the collection cups using a fine-tipped paintbrush and placed into the appropriate

mesocosms (i.e. fauna extracted from the uncut sites were placed into high-density fauna mesocosms and fauna extracted from clear-cut sites were placed into low-density fauna mesocosms).

During the refaunation process the total number of forest floor mites and springtails, and the total numbers of individuals within the major microarthropod groups were enumerated using a dissecting microscope at 25X magnification. Collembola were identified to suborder (Arthroplèona and Symphyplèona), and Acari to suborder (Oribatida, Prostigmata, Astigmata, Mesostigmata). Other fauna extracted from the cores, primarily insect larvae and small arachnids, comprised a small proportion of the total microarthropod numbers (<2%) and were not added to the mesocosms.

4.2.4 Mesocosm Sampling and Measurements

Ten unextracted control mesocosms (5 of each stand type) and 10 extracted (defaunated) mesocosms (5 of each stand type) were destructively sampled initially, at Day 0, and analysed for microarthropod abundance, microbial biomass C, basal soil respiration, available NH₄-N, NO₃-N and PO₄-P. Further sampling occurred at 30 and 60 days after the introduction of the fauna. At each sample time, 5 mesocosms in each of the 4 treatments/stand type were destructively sampled and analysed for microarthropod abundance, microbial biomass C, basal soil respiration, decomposition potential, available NH₄-N, NO₃-N and PO₄-P.

4.2.4.1 Microarthropod Abundance

Microarthropod abundance (#/g dwt) at each sample time (Day 0, 30, 60) was measured by extracting microarthropods from 10g (dwt) F/H material (50% of the soil in each mesocosm) using the Macfadyen high gradient extractor as described previously. Extracted microarthropods were preserved in 70% ethanol, and the total number of individuals within each major mite or springtail group (suborder) was determined using a dissecting microscope at 25X magnification.

4.2.4.2 Basal Respiration, Microbial Biomass and Decomposition Potential

Basal respiration (μ g CO₂/hr/g dwt) was monitored by non-destructive sampling techniques and was measured repeatedly every 5 days over the 60-day duration of the experiment. Every 5 days each mesocosm jar was sealed and the amount of CO₂ in the headspace was measured initially and following 1h incubation. A GasHound infrared CO₂ analyser, model LI-800 (LI-COR Inc. 1998) was used to measure CO₂ in parts per million (ppm). The amount of CO₂ accumulated in the headspace after 1h incubation was converted to μ g CO₂/hr/g dwt by applying the following equation: change in ppm (per minute) x volume of headspace in the mesocosm (0.44 litres) x standard temperature and pressure at 22°C (0.813) x constant (0.5371) x 1/g dwt soil (20) x 60 minutes (LI-COR Inc. 1998).

At each sample time (0, 30, 60 days) microbial biomass C (mg C_{micr}/g dwt) was estimated using the substrate-induced respiration method (Anderson and Domsch 1978)

as described in chapter 2. Five g dwt F/H from each mesocosm was amended with 300mg glucose in the case of the deciduous F/H and 200mg in the case of the conifer F/H, placed in glass tubes and attached to the IRGA. CO₂ evolution was monitored for 12 hours and microbial biomass was determined on the basis of the lowest respiration rate prior to the commencement of microbial growth, usually within six hours after glucose addition. CO₂ evolution rates (μ l CO₂/g dwt/h) were converted to ml CO₂/g dwt/h and the formula x=40.4y+0.37 was used to estimate microbial biomass C (where x= microbial biomass (mg C_{micr}/g soil dwt) and y= glucose induced respiration (ml CO₂/g dwt/h)) (Anderson and Domsch 1978).

Litter decomposition potential was estimated as percent mass loss of senesced aspen leaves after 30 and 60 days incubation. Mass loss was calculated as the difference in dry weight of leaves before and after incubation and corrected to oven dwt (80°C) (% mass loss = (g dwt aspen_{before} - g dwt aspen_{after} / g dwt aspen_{before}) * 100).

4.2.4.3 Available N and P

At each sample time, available N (µgNH₄-N and µgNO₃-N per g dwt) and available P (µgPO₄-P per g dwt) were extracted from 2.5g dwt F/H material from each mesocosm. Available N and P were extracted from soils with KCl (Keeney and Nelson 1982) and Medium Bray's Extract (Olsen and Sommers 1982), respectively, and analysed using a Technicon Autoanalyser II (Technicon 1970) as described in chapter 2. N and P extracts were frozen at -20°C until the end of the experiment so all samples could be analysed together.

4.2.5 Statistical Analysis

The effects of faunal extraction on microarthropod numbers, basal respiration, microbial biomass, available NH₄-N, NO₃-N and PO₄-P at Day 0 were determined by comparing data from extracted (defaunated) mesocosms and unextracted control mesocosms using a two-sample t-test. Initial microarthropod numbers in the defaunated no-fauna, refaunated low-density fauna, refaunated high-density fauna, and unextracted control treatments were compared using a 1-way ANOVA with Tukey's HSD test to detect differences amongst means. Microarthropod numbers following the refaunation process in low and high-density fauna treatments were considered equivalent to Day 0 densities. The statistical program used for the analysis was SYSTAT 7.0, and the level of significance was p<0.05. For all variables measured, conifer and deciduous mesocosms were analysed separately.

A repeated measure ANOVA (RM-ANOVA) was performed on basal respiration measurements to test differences among treatments over time. Regression analysis was used to explore the effect of microarthropod density on microbial biomass C, basal respiration, decomposition potential, available NH₄-N, NO₃-N, and PO₄-P at 30 and 60 days. Total microarthropod abundance at each sample time was used as the independent variable for the analyses. Regression analyses were performed with and without the unextracted control mesocosms, but because of the effect of defaunation on the F/H material, only results from regression analysis without control mesocosms are considered relevant.

The effects of microarthropod density within each suborder and microarthropod biomass on the experimental variables were determined also using regression analysis. Microarthropod biomass estimates were calculated using a range of biomass values for mites and springtails suggested by Petersen and Luxton (1982). Regression analysis using total microarthropod biomass in all cases matched the regression analysis results obtained using total microarthropod abundance; therefore, data based on biomass estimates are not included. Effects of microarthropod density in each mite and springtail suborder are noted only where there was a significant (p<0.05) regression relationship. Microarthropod community structure within the mesocosms was examined using the relative abundance (% of total abundance) in each microarthropod suborder.

4.3 Results

4.3.1 Initial Effects of the Defaunation Process

The defaunation process (high gradient extraction) effectively removed >95% of all microarthropods (>99% conifer and >96% deciduous), but altered the chemical and biological properties of the conifer and deciduous F/H materials (Table 4.1). The

Table 4.1 Initial conditions (Day 0) in extracted (defaunated) and unextracted (control) mesocosms to show the effect of the defaunation process on the chemical and biological properties of conifer and deciduous F/H material. Values are means with SE given in parentheses.

Soil Property	Unit	Conifer (n=10)		Deciduous (n=10)	
		Unextracted	Extracted	Unextracted	Extracted
Microarthropod abundance	number/g dwt	6.08 (1.4) a	0.06 (0.0) b	9.42 (0.7) a*	0.16 (0.1) b
Microbial biomass	mg C/g dwt	13.5 (0.1) a	6.9 (1.7) b	13.0 (0.3) a*	9.1 (0.5) b
Basal respiration	µg ĊO₂/hr/g dwt	24.1 (0.3) a	21.7 (0.3) b*	12.0 (0.2) a	11.5 (0.1) a
Available NH₄-N	µg/g dwt	11.7 (0.0) b	167.9 (46) a*	30.5 (11) b	572.8 (34) a*
Available NO ₃ -N	µg∕g dwt	0.14 (0.3) b	0.68 (0.0) a	0.24 (0.1) b	1.31 (0.3) a*
Available PO ₄ -P	μg/g dwt	140 (3.9) b	238 (3.7) a*	75 (0.9) b	207 (10) a*

Note: Within each row, within each forest stand type, values followed by the same letter are not significantly different, based on a two-sample t-test (p>0.05) (* designates significance at p<0.001).

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defaunation process significantly reduced microbial biomass and basal respiration, and significantly increased NH₄-N, NO₃-N, and PO₄-P in the conifer and deciduous F/H soil.

4.3.2 Microarthropod Abundance

Microarthropod densities in the conifer mesocosms at the outset of the experiment were significantly higher in the refaunated high-density treatment than all other treatments (Fig. 4.1 a). This trend changed at Day 30, when the unextracted conifer treatment had the greatest microarthropod abundance followed by the high-density, lowdensity and no-fauna treatments. At Day 60, the unextracted control and the low-density treatments had higher average microarthropod abundance than the high-density treatment and significantly higher abundance than the no-fauna treatment. All treatments in the conifer mesocosms, including the no-fauna treatment, increased in average microarthropod abundance over the duration of the experiment.

In the deciduous mesocosms, initial microarthropod densities were not significantly different between refaunated low-density, refaunated high-density and unextracted control mesocosms, but were all significantly greater than the no-fauna mesocosms (Fig. 4.1 b). Decreases in microarthropod abundance from initial refaunated densities were seen at Day 30 in the low and high-density treatments, whereas in the unextracted F/H soil, microarthropod numbers increased and were significantly greater than all other treatments at Day 30 and 60. Microarthropod numbers increased in the low and high-density mesocosms between Day 30 and Day 60, but were still significantly lower than the unextracted control treatment at Day 60. The no-fauna mesocosms at Day Figure 4.1 Average microarthropod densities in a) conifer and b) deciduous mesocosms (extracted no-fauna, refaunated low-density, refaunated high-density, unextracted control treatments) after 0, 30, and 60 days. Within each stand type, bars (means \pm SE) with the same letters are not significantly different based on a 1-way ANOVA and Tukey's HSD test (p>0.05).






60 were significantly lower than the high-density and control mesocosms. Numbers of microarthropods in the no-fauna treatments of both conifer and deciduous mesocosms remained negligible throughout the experiment (absolute numbers of microarthropods at Day 60 ranged from 4-31/conifer mesocosm, and 0-3/deciduous mesocosm).

4.3.3 Microarthropod Community Structure

At the initiation of the experiment, community structure within the mesocosms, expressed as % relative abundance of microarthropod suborders, differed between the unextracted control mesocosms and the extracted no-fauna and refaunated mesocosms. However, over time the relative composition of the microarthropod suborders varied amongst the treatments (Table 4.2). In both conifer and deciduous unextracted controls, the relative abundance of arthropleonid and symphypleonid collembola increased during the 60-day experiment, while oribatid mites decreased in relative abundance. The opposite trend was seen in the three treatments that had been extracted and either refaunated (low and high-density) or not (no-fauna). In both conifer and deciduous nofauna, low-density and high-density fauna treatments, oribatid mites increased in relative abundance during the 60-day experiment, while arthropleonid and symphypleonid collembola decreased in relative abundance.

Over the course of the experiment, the community structure of microarthropods in the refaunated low and high-density treatments was similar. All conifer and deciduous treatments tended to be dominated by oribatid mites and/or arthropleonid collembola;

a) Conifer -	Unextracted control			Extracted no-fauna		
	<u>Day 0</u>	<u>Day 30</u>	<u>Day 60</u>	<u>Day 0</u>	<u>Day 30</u>	<u>Day 60</u>
Oribatida	65	59	40	33	20	70
Prostigmata	9	4	5	33	0	22
Astigmata	11	5	3	33	0	2
Mesostigmata	2	4	1	0	0.	2
Symphypleonid	1	5	28	0	0	0
Arthropleonid	13	23	23	0	80	2

 Table 4.2 Relative abundance (% of total) of microarthropod suborders in unextracted control, extracted no-fauna, refaunated low-density, and refaunated high-density treatments of a) conifer and b) deciduous mesocosms.

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	Refaunated low-density			Refaunated high-density			
	Day 0	<u>Day 30</u>	<u>Day 60</u>	<u>Day 0</u>	<u>Day 30</u>	<u>Day 60</u>	
Oribatida	43	62	73	49	42	51	
Prostigmata	19	1	9	17	3	3	
Astigmata	1	2	0	0	0	0	
Mesostigmata	2	4	6	1	1	0	
Symphypleonid	2	7	0	1	0	18	
Arthropleonid	33	24	13	27	55	28	

b) Deciduous	Unextracted control			Extracted no-fauna			
	Day 0	Day 30	<u>Day 60</u>	<u>Day 0</u>	Day 30	Day 60	
Oribatida	45	55	36	0	89	100	
Prostigmata	6	4	6	13	0	0	
Astigmata	2	1	1	0	0	0	
Mesostigmata	4	3	2	0	0	0	
Symphypleonid	3	8	10	13	0	0	
Arthropleonid	41	29	45	75	11 ·	. 0	
	Refaunated low-density			Refaunated high-density			
	Day 0	Day 30	<u>Day 60</u>	<u>Day 0</u>	<u>Day 30</u>	<u>Day 60</u>	
Oribatida	33	57	75	28	39	67	
Prostigmata	20	10	5	16	14	9	
Astigmata	1	0	1	1	1	0	
Mesostigmata	2	1	0	2	3	0	
Symphypleonid	2	1	0	5	10	· 16	
Arthropleonid	41	31	18	48	33	8	

Table 4.2 cont.

Note: All values are the mean relative abundance of each suborder (% of total) for all treatments and reflect only general trends.

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relative abundances of astigmatid and mesostigmatid mites were consistently low in all treatments.

4.3.4 Microbial Biomass, Basal Respiration and Decomposition Potential

Microbial biomass at Day 30 had a significant positive relationship with total microarthropod density in conifer and deciduous mesocosms (Fig. 4.2 a, b); however this trend was not significant at Day 60 (Fig. 4.2 c, d). Regression analysis at Day 30 using the various microarthropod suborders revealed a significant positive relationship between oribatid mites and microbial biomass in the deciduous mesocosms (y=0.0213x+6.0049, $R^2=0.2653$, p=0.049). In the conifer mesocosms, there was a significant positive relationship between microbial biomass C and prostigmatid mites and arthropleonid collembola (y=0.1687x+12.126, $R^2=0.309$, p=0.031 and y=0.0083x+12.12, $R^2=0.2703$, p=0.047, respectively). Microbial biomass decreased in all treatments over the duration of this experiment.

Basal respiration of conifer and deciduous soil decreased significantly (RM-ANOVA, p=0.000) over the course of the study in all mesocosms (Fig. 4.3 a, b). The unextracted control mesocosms consistently had higher basal respiration than the other treatments (RM-ANOVA, p=0.009 in conifer, p=0.000 in deciduous). Regression analysis at Day 30 and Day 60 were not consistent, but suggested an overall negative relationship between respiration and microarthropod density (Fig. 4.4). This negative relationship was supported when basal respiration was regressed against oribatid mite densities (conifer Day 30, y= -0.0054x + 18.259, R²=0.2535, p=0.056; deciduous Day 60, y= -0.0003x + 4.9245, R²=0.3192, p=0.028), regressed against prostigmatid mite densities

Figure 4.2 Regression analysis for microbial biomass (mg C/g dwt) in no-fauna, low-fauna, and high-fauna treatments as a function of microarthropod abundance (#/g dwt) for a) conifer Day 30, b) deciduous Day 30, c) conifer Day 60, and d) deciduous Day 60. Unextracted control data were not included in the analyses. Data points are absolute values and represent individual mesocosms.

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Figure 4.3 Basal respiration ($\mu g CO_2/g dwt/h$) in a) conifer and b) deciduous nofauna, low-density, high-density, and unextracted control treatments over the 60day duration of the experiment. Data points are means \pm SE.

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Figure 4.4 Regression analysis of basal respiration (μ g CO₂/g dwt/h) in no-fauna, low-fauna, and high-fauna treatments as a function of microarthropod abundance (#/g dwt) for a) conifer Day 30, b) deciduous Day 30, c) conifer Day 60, and d) deciduous Day 60. Unextracted control data were not included in the analyses. Data points are absolute values and represent individual mesocosms.

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(conifer Day 30, y= -0.0815x +18.14, R^2 =0.2535, p=0.056) and regressed against symphypleonid collembola densities (deciduous Day 60, y= -0.0009x +4.8658, R^2 =0.387, p=0.014).

The decomposition potential, expressed as % mass loss of aspen leaves over 30 and 60 days, was not significantly different between treatments in either the conifer or deciduous mesocosms (data not presented). In general, decomposition potential was greater in the deciduous mesocosms than the conifer mesocosms, but total microarthropod abundance showed no relationship with % mass loss of aspen in either conifer or deciduous mesocosms at 30 or 60 days (Fig. 4.5). Although the decomposition potential in the deciduous mesocosms at Day 60 showed no relationship with total microarthropod abundance, there was a significant positive relationship with the number of symphypleonid collembola present (y=0.018x + 29.692, $R^2=0.3933$, p=0.012).

4.3.5 N and P Availability

There was no significant relationship between total microarthropod density and extractable NH₄-N or NO₃-N in the soil after 30 or 60 days incubation (Fig. 4.6, Fig. 4.7). However, symphypleonid collembola were negatively related to NO₃-N availability on Day 30 in the conifer mesocosms (y=-0.0497x +3.4451, R²=0.3591, p=0.018). Ammonium-N levels increased in the conifer mesocosms over the duration of the experiment, and decreased in the deciduous mesocosms. Levels of NO₃-N during the 60day experiment increased in both conifer and deciduous mesocosms. Figure 4.5 Regression analysis of decomposition potential (% mass loss from aspen) in no-fauna, low-fauna, and high-fauna treatments as a function of microarthropod abundance (#/g dwt) for a) conifer Day 30, b) deciduous Day 30, c) conifer Day 60, and d) deciduous Day 60. Unextracted control data were not included in the analyses. Data points are absolute values and represent individual mesocosms.







Figure 4.6 Regression analysis for NH_4 -N (μ g/g dwt) in no-fauna, low-fauna, and high-fauna treatments as a function of microarthropod abundance (#/g dwt) for a) conifer Day 30, b) deciduous Day 30, c) conifer Day 60, and d) deciduous Day 60. Unextracted control data were not included in the analyses. Data points are absolute values and represent individual mesocosms.



Microarthropod abundance (#/g dwt)

Figure 4.7 Regression analysis for NO_3 -N (µg/g dwt) in no-fauna, low-fauna, and high-fauna treatments as a function of microarthropod abundance (#/g dwt) for a) conifer Day 30, b) deciduous Day 30, c) conifer Day 60, and d) deciduous Day 60. Unextracted control data were not included in the analyses. Data points are absolute values and represent individual mesocosms.

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Available PO_4 -P increased in all mesocosms over the 60-day experiment, and had an overall positive relationship with total microarthropod abundance at both sample times 30 and 60 days (Fig. 4.8). However, these relationships were not significant. No significant relationship between PO₄-P and any of the microarthropod suborders was observed.

4.4 Discussion

4.4.1 Defaunation Process

The defaunation process successfully removed most adult microarthropods from the sieved F/H soil; however, the appearance of microarthropods at Day 30, and particularly at Day 60, in the no-fauna mesocosms suggests that the defaunation process did not kill viable microarthropod eggs. The defaunation process involved heating the F/H material to a maximum temperature of 50°C for 48 hours, a temperature that far exceeds the maximum thermal death point (TDP) of 41.5°C reported for oribatid mites (Madge 1965). The TDP of a species is dependent on the exposure time at an elevated temperature, the relative humidity, and the physiological condition of the animals (e.g. starvation, acclimation). Species specific TDPs are also related to the degree of integumental sclerotisation (Madge 1965). However, no information is available on the TDP of microarthropod eggs. Figure 4.8 Regression analysis for PO_4 -P (μ g/g dwt) in no-fauna, low-fauna, and high-fauna treatments as a function of microarthropod abundance (#/g dwt) for a) conifer Day 30, b) deciduous Day 30, c) conifer Day 60, and d) deciduous Day 60. Unextracted control data were not included in the analyses. Data points are absolute values and represent individual mesocosms.

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High temperatures and dessication associated with the defaunation process resulted in reduced basal respiration and microbial biomass C, presumably due to the mortality of sensitive components of the microbial community. Release of nutrients from the killed microbial biomass explains the increase in NH₄-N, NO₃-N, and PO₄-P in heatextracted soils. This phenomenon is well documented and forms the basis of the fumigation-extraction method for measuring soil microbial biomass N (Brookes *et al.* 1985).

4.4.2 Microarthropod Abundance

Refaunation was more successful in the conifer treatments than in the deciduous treatments. The initial reduction in microarthropod abundance in the low and high-density deciduous treatments may have been due to the death of microarthropods that were sensitive to handling during the refaunation process. Nevertheless, over the course of the experiment, the microarthropods survived and reproduced. Indeed, after 60 days microarthropod densities in conifer and deciduous unextracted controls, low-fauna and high-fauna treatments were greater than those measured in corresponding conifer and deciduous uncut and clear-cut field sites. Constant moisture and reduced predator populations in the mesocosms may have promoted reproduction by the microarthropods (Setälä *et al.* 1991). Also, reproduction by parthenogenic species of mites and springtails may have contributed to the increase in microarthropods observed in the mesocosms.

Disturbance effects on microarthropod populations in the field (e.g. following forest harvest) are well documented, and these effects may persist for years (Blair and Crossley 1988, Hoekstra et al. 1995). The rapid increase in microarthropod abundance under controlled laboratory conditions raises questions as to the mechanisms that cause a persistent reduction in microarthropods in the field after disturbance. In the case of forest harvesting, compaction due to heavy machinery reduces soil pore space (habitat) and this may limit recolonisation of these sites by microarthropods (Battigelli 2000). Removal of overstory vegetation also increases the range of temperature and moisture conditions to which surface dwelling organisms are exposed (Keenan and Kimmins 1993). For example, maximum surface soil temperatures may approach, or exceed 40°C in clear-cut sites in the summer (Vlug and Borden 1973, Abbott et al. 1980, Seastedt and Crossley 1981, Bird and Chatarpaul 1986) and these temperature extremes may inhibit microarthropod survival and reproduction. Conditions in the laboratory during incubation, such as constant temperature and moisture, and the use of sieved F/H soils in mesocosms do not depict forest floor conditions in the field following clear-cut harvesting, and created a suitable environment for microarthropods to reproduce.

4.4.3 Microbial Biomass, Basal Respiration and Decomposition Potential

The majority of microarthropods (>50% Acari: Oribatida) in boreal forest soils are fungivores, and thus would be expected to have a direct effect on the amount of microbial biomass. Grazing on microbial biomass can stimulate microbial growth and lead to increased microbial biomass (Seastedt 1984). In the present study, the significant positive relationship between microarthropod abundance and microbial biomass at Day 30 may have been a result of microarthropod grazing on microbial biomass.

Microarthropod abundance did not have a significant relationship with basal respiration. The contribution of soil microarthropods to basal respiration is presumed to be low: 1-5% of the total heterotrophic CO₂ evolution in conifer soil systems and 3-13% in deciduous soil systems (Persson 1989). Similar mesocosm studies have found no effect of microarthropod density or community structure on CO₂ efflux (Persson 1989, Mikola and Setälä 1998). While others have shown that cumulative CO₂-C loss from mesocosms with fauna was higher than from mesocosms with microbes alone (Setälä *et al.* 1991). Within the acarine suborders, oribatid mites have been observed to significantly increase basal respiration (Maraun *et al.* 1998). This was not observed in the present study, and suggests that basal respiration is relatively insensitive to the activities of soil microarthropods.

Although microarthropod grazing may have a stimulatory effect on microbial biomass and respiration at low microarthropod densities, higher densities may lead to overgrazing and reduce microbial respiration (Hanlon and Anderson 1979). This is not believed to be the case in this study, since reductions in microbial biomass and basal respiration were observed not only in the low and high-density fauna treatments, but also in the no-fauna treatment. Relative to the densities of the large springtail species used by Hanlon and Anderson (1979) in their fungal grazing experiments (100-200 *Folsomia*

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candida/g dwt soil), the densities tested in the present experiment were low (0-125 individuals/g dwt soil). This may explain why Hanlon and Anderson observed a decrease in microbial biomass in the presence of high densities of springtails, while no effect of density was observed in this study.

In a review by Seastedt (1984), the average estimated increase in litter decay due to microarthropod activity was 23%. Douce and Crossley (1982) also found litter mass losses were higher in field plots with microarthropods compared with plots that had been defaunated. However, they also found that environmental variables, specifically moisture, had a stronger effect on decomposition rates than the presence of microarthropods. In the present study, the decomposition potential of aspen leaves was not affected by an increasing abundance of microarthropods. This suggests that the role of microarthropods during the early stages of litter decay is negligible.

4.4.4 N and P Availability

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Persson (1989) estimated that mites and collembola contributed between 10 and 26% of the net N mineralisation in F/H soils, and many mesocosm studies have shown that the presence of soil animals increases levels of available NH₄-N, NO₃-N, or both to varying degrees (Persson 1989, Bardgett and Chan 1999). However, Setälä *et al.* (1991) suggested that microarthropod fungal grazers could immobilise nutrients held within fungal standing crops, and that a sufficient level of predation by upper trophic levels is required to release these nutrients from the grazer trophic level. Over the course of the

present study, numbers of microarthropods increased significantly. This increase in microarthropod biomass may have immobilised microbial nitrogen, and this explains the lack of a microarthropod effect on N availability in the various treatments. Since predation levels were reduced in the mesocosms, compared to field systems, release of nutrients from the fungivorous microarthropods would be expected to be negligible. Other mesocosm experiments also have found no significant effects of microarthropods on N availability (Heneghan and Bolger 1998).

Phosphate availability was positively related to the density of total microarthropods, although the relationships were not significant. Bardgett and Chan (1999) and Setälä *et al.* (1991) have also observed greater P availability with increased microarthropod abundance in mesocosms. That microarthropods are instrumental in P cycling is supported also by field measurements at the EMEND site. Here, a significant positive correlation was observed between microarthropod abundance and PO₄-P in the forest floor (chapter 3).

The long-term implications of reduced microarthropod densities in the field following forest harvest are unclear. Microarthropods have both direct and indirect effects on microbial communities, microbial biomass, decomposition and nutrient cycling and these effects are difficult to separate. Results from this study suggest that microarthropods are important in P cycling. Thus, a reduction in microarthropod numbers after clear-cutting, in combination with changes in microbial biomass and nutrient availability may play a role in determining forest regeneration patterns. Until we understand the role of microarthropods in belowground food webs more completely, attempts should be made to reduce the impact of forest harvesting on biological communities as much as possible. Partial-cut harvesting is an option.

4.5 Conclusions

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- Microarthropods reintroduced to fauna-free soil survived and reproduced over the 60day duration of the experiment. Under laboratory conditions, a rapid increase in microarthropod numbers was observed. In contrast, microarthropod populations in clear-cuts in the field did not recover rapidly and were still significantly depressed 2.5 years after harvest. Environmental factors not tested in the lab, such as soil bulk density and fine root biomass may explain the discrepancy between lab and field responses.
- 2. Increased microarthropod abundance had a significant positive relationship with microbial biomass, as would be expected from fauna communities composed mainly of fungivores.
- 3. This laboratory study corroborates observations made in the field where a significant correlation was observed between microarthropod abundance and PO₄-P.
- 4. A relationship between microarthropod abundance and basal respiration, decomposition potential and nitrogen availability was not evident.

Chapter Five: GENERAL CONCLUSIONS

Advantages of partial-cutting practices include less physical disturbance to the forest floor, fewer changes in the soil microclimate, and a reduction in nutrient leaching (Dahlgren and Driscoll 1994). Partial-cut systems can also provide refuge for belowground organisms like mycorrhizal fungi (Barg and Edmonds 1999), and help maintain soil invertebrate communities (Siira-Pietikäinen *et al.* 2001), compared to clear-cut areas. The present study, conducted in coniferous and deciduous dominated stands of the mixed-wood boreal forest of Alberta, Canada, examined the effects of partial-cut and clear-cut harvesting on forest floor physical, chemical and biological properties, decomposition and nutrient cycling processes, and forest floor microarthropod populations.

The specific objectives of the research were:

- to compare the effects of clear-cutting and partial-cutting on forest floor physical (bulk density, moisture, forest floor depth), chemical (pH, NH₄-N, NO₃-N, PO₄-P) and biological (microbial biomass, basal respiration) properties to properties in uncut conifer and deciduous stands;
- to determine the effects of clear-cut and partial-cut forest harvest on litter decomposition and nutrient cycling processes by conducting litter decay and N and P mineralisation studies under controlled conditions in the laboratory;
- to compare the abundance and composition of the forest floor microarthropod community in clear-cut, partial-cut and uncut sites and to examine the

usefulness of oribatid mites as biological indicators of harvesting disturbance; and

 4) to determine the relative contribution of forest floor microarthropods to decomposition and nutrient cycling processes, in relation to clear-cut harvesting, and to provide insight into the possible relationship between fauna populations and forest floor properties.

The treatments that were examined in coniferous and deciduous stands were: 1) uncut, 2) retention patches of a 50% partial-cut, 3) strip-cut corridors of a 50% partialcut, and 4) clearcut.

Objective 1: Effects of Partial-cut Harvesting on Physical, Chemical, and Biological Properties.

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Partial-cutting reduced the amount of physical disturbance to the forest floor within the retention patches, but compaction associated with the harvesting process was apparent in the corridors of the conifer stands, where a decrease in forest floor depth and an increase in soil bulk density were measured. Clear-cutting of conifer stands also reduced forest floor depth and increased bulk density compared to uncut sites. Soil compaction in the partial-cut corridors and clearcuts resulted from trafficking of skidders during the harvesting process. Clearcuts received one pass of a skidder and the corridors received two passes during the tree removal process. Just one pass of a skidder can significantly increase soil bulk density (Startsev *et al.* 1998). Moisture contents were increased in the patch, corridor and clear-cut treatments, compared to the uncut control treatment, in both deciduous and conifer stands. More precipitation reaches the forest floor and evapotranspiration is reduced following canopy removal and this leads to an increase in soil moisture (Keenan and Kimmins 1993). Partial removal of trees can mitigate the effects of harvest on soil moisture (Barg and Edmonds 1999), although this was not the case here.

Available NH₄-N, NO₃-N and PO₄-P in soil of the partial-cut treatments were intermediate between those measured in clear-cut and uncut treatments, and a gradienttype trend associated with harvest intensity was observed. Indeed, NH₄-N and PO₄-P formed a gradient with treatment, with concentrations in uncut > patches > corridors > clearcuts. In contrast, NO₃-N followed a decreasing gradient with treatment, i.e. uncut < patches < corridors < clearcuts. Total N, NO₃-N, NH₄-N, PO₄-P, and total C have been shown to decrease in forest floors after clear-cutting (Schmidt *et al.* 1996); yet other studies have found an increase (Vitousek and Matson 1985; Frazer *et al.* 1990), or no significant effect of harvest on these nutrients (Maynard and MacIsaac 1998). Intermediate nutrient concentrations in the partial-cut treatments between the uncut and clear-cut treatments suggests that nutrient cycling processes were not as altered in partialcuts as in clearcuts.

An increase in NO₃-N in forest floors following clear-cut harvesting is commonly reported, and has previously been attributed to increased decomposition and nitrification rates due to increased microbial activity as a result of improved soil moisture and temperature conditions (Frazer *et al.* 1990). However, in the present study, no effects of harvest on decomposition rates were observed, and microbial biomass was reduced in the patch, corridor, and clear-cut treatments. Therefore, the alternative hypothesis, that a decrease in C inputs following harvest reduces microbial biomass and microbial immobilisation of N, thereby increasing NO₃-N levels (Hart *et al.* 1994a; Prescott 1997) may be more applicable.

Biological properties (basal respiration, microbial biomass, annual litter input and fine root biomass) of the deciduous forest floors were reduced in the patch, corridor, and clear-cut treatments compared with uncut control. These parameters are interrelated as litter and root exudates are the primary resource for microbes, and roots are especially important for organisms associated with roots, such as the mycorrhizal fungi (Bååth 1980). Decreased annual litter input and root biomass in patch, corridor, and clear-cut treatments in this study may have contributed to the reduction in microbial biomass and basal respiration rates observed in these treatments. Other researchers have reported a reduction in microbial biomass as a result of harvesting. Bååth (1980) reported reduced microbial biomass in clearcuts compared to uncut forests, and Chang *et al.* (1995) found less microbial biomass in the forest floors of 3 and 10-year-old plantations than in the forest floor of old-growth forests. Soil compaction may have also reduced microbial respiration and biomass in the forest floors surveyed in this study (Startsev *et al.* 1998).

Objective 2: Effects of Partial-cut Harvesting on Decomposition and Nutrient Cycling Processes

A rise in soil temperature and moisture due to tree removal may accelerate organic matter decomposition in the field (Covington 1981). The current research measured decomposition rates and nutrient mineralisation potentials under controlled conditions in the laboratory, and no effect of harvesting on decomposition was observed. Similar studies have also reported no consistent pattern of harvesting on decomposition rates (Prescott et al. 2000); also, conflicting results for N and P mineralisation in the lab and field are not uncommon. Often differences in mineralisation rates in uncut and clearcut treatments in the field are not observed under controlled laboratory conditions. Laboratory mineralisation studies are thought to represent potential mineralisation rates only, and, therefore are not necessarily indicative of field mineralisation rates (Frazer et al. 1990). In the laboratory, soil temperature and moisture conditions are controlled and plant uptake is not considered. Consequently, lower rates of net N mineralisation and nitrification measured in the soil from deciduous clearcuts in this study are most likely due to reduced microbial biomass and/or changes in substrate quality following harvesting. In both conifer and deciduous stands, patterns of net N mineralised appeared to depend primarily on nitrification rates.

Differences in foliar litter chemistry, specifically C:N ratios and lignin concentrations, in conifer and deciduous tree species influences forest floor nutrient availability (Paré and Bergeron 1996; Côté *et al.* 2000). Therefore, differences in forest floor properties observed in the deciduous and coniferous stands would be expected. Deciduous litter has lower C:N ratios and lignin concentrations than does conifer litter, which allows for more rapid release of N and higher N mineralisation rates in deciduous

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stands (Frazer *et al.* 1990; Côté *et al.* 2000). Greater forest floor depth, organic matter accumulation and lower pH in the conifer stands than the deciduous stands also have been attributed to differences in litter quality and foliar chemistry between deciduous and conifer overstory (Paré and Bergeron 1996).

Objective 3a: Effect of Partial-cut Harvesting on Microarthropod Populations

Partial-cut harvesting had less of an impact on forest floor microarthropod populations than clear-cut harvesting did in this mixed-wood boreal forest. Total microarthropod densities and densities of Acari were reduced following partial and clearcut harvesting, with oribatid and prostigmatid mite populations the most adversely affected by forest harvest. The decreased abundance of the most dominant oribatid mite, *Oppiella nova* (Oudemanns), created a carry-through effect to higher taxonomic levels, and thus significant reductions were seen in total oribatid, total Acari and total microarthropod numbers following forest harvesting.

Overall trends in microarthropod abundance were reflected in the cluster analyses, which showed that the corridor treatments in the conifer stands had the same pattern of reduction in microarthropod suborder density as the clear-cut treatment did. Microarthropod abundances in the conifer retention patches were only slightly reduced and not significantly different from the conifer uncut treatment. In the deciduous stands, the largest reduction in all microarthropod groups occurred in the corridors.

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A decline in microarthropods in the corridor and clear-cut treatments may be related to direct physical disturbance (compaction) of the forest floor. Compaction can significantly increase soil bulk density and decrease soil pore space inhabited by microarthropods (Startsev *et al.* 1998). Pearson's correlation coefficients showed a significant negative relationship between microarthropod abundance and soil bulk density, particularily in the conifer sites.

Deciduous clearcuts in this study showed extensive regeneration of aspen suckers, which could have mitigated changes in microarthropod numbers that potentially occurred immediately following harvesting. The establishment of overstory vegetation in the deciduous clearcuts may have stabilised the forest floor microclimate, regulated litter inputs, and reduced compaction. Rapid tree regeneration after clear-cutting may provide a more suitable environment for microarthropod growth and reproduction, and this would allow microarthropods to return to pre-harvest densities more quickly in deciduous than conifer clearcuts.

Reductions in forest floor microarthropods following harvest have been related to decreases in organic matter, litter input, microbial biomass, (Huhta *et al.* 1967, Bird and Chatarpaul 1986, Marra and Edmonds1998) and soil pore space (Vlug and Borden 1973, Battigelli 2000), and to changes in microclimate (Abbott *et al.* 1980, Seastedt and Crossley 1981, Marra and Edmonds 1998). In the present study, the reduction in forest floor microarthropods, and the alteration of microarthropod and oribatid mite community

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structure is probably a result of some, or all, of these factors. That Acari and Collembola abundances correlated positively with microbial and fine root biomass in both stand types supports the idea that abundances of these microarthropods are related to food availability. Compaction caused by harvesting would also have a negative effect on microarthropod densities. Minimising or mitigating the effects of harvesting on soil physical properties may be helpful in the maintenance or recovery of forest floor microarthropods altered by tree removal.

Objective 3b: Oribatid Mites as Indicators of Harvesting Disturbance

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Oribatid mites have long been identified as the microarthropod group most adversely affected by forest harvest (Seastedt and Crossley 1981, Bird and Chatarpaul 1986). This is supported by the present study, which found oribatid mites, along with the prostigmatid mites, as groups at greatest risk from harvesting disturbance. Partial and clear-cut harvesting reduced microbial biomass, fine root biomass and annual litter input in both stand types, thereby decreasing resource availability and causing a decline in forest floor oribatids.

Oribatid mites may take longer than other microarthropod groups to recover from decreased abundance following forest harvest due to low fecundity, slow developmental times, low metabolic rates and long generation times (Norton 1990). However, increased abundance of thelytokous (parthenogenic) oribatids in the families Brachychthoniidae, Trhypochthoniidae, Tectocepheidae, and Oppiidae following disturbance have been observed (Behan-Pelletier 1999). Thelytokous oribatid mites have a greater ability to recolonise disturbed habitats compared to non-parthenogenic oribatids. In this study, *Tryhypochthonius tectorum* (Berlese) and *Suctobelbella* sp. 2, both suspected parthenogenic species, increased in abundance, while other species known to be parthenogenic, such as *O. nova*, did not.

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Indices of oribatid mite species diversity in clear-cut treatments of both stand types were higher than indices in the uncut controls. This contradicts observations made by Marra and Edmonds (1998), who found that oribatid mite communities in undisturbed sites had higher species richness and diversity than in clear-cut sites. An increase in the diversity indices in the clear-cut treatments of this study is attributed to changes in the relative abundance of the most dominant species, *O. nova*. The reduction of *O. nova* in clear-cut sites was proportionally greater than any other oribatid mite species, thus leading to greater evenness of species within the oribatid community, and a reduction in the dominance of any particular oribatid species in the clearcuts.

Changes in the oribatid mite community following partial and clear-cut forest harvest were more quantitative (absolute abundance) than qualitative (relative abundance, community composition). Oribatid mites may be useful as biological indicators of harvesting disturbance as they are sensitive to changes in their environment and show measurable decreases in abundance when their habitat is disturbed. Due to the time and expertise required to identify oribatid mites to species level and the lack of described species, this study revealed that the use of oribatid mite species data as a measure of harvesting disturbance may not be cost and time effective. Oribatid mite abundance at
the suborder level was as sensitive as abundance at the species level to detect effects of harvesting disturbance.

Objective 4: The Contribution of Forest Floor Microarthropods to Decomposition and Nutrient Cycling

Lower microbial biomass and lower PO₄-P availability were related to lower densities of microarthropods in the laboratory mesocosm study. Other relationships between microarthropod abundance and basal respiration, decomposition potential and N availability were not evident. The majority of microarthropods in these systems are fungivores and thus are expected to have a direct effect on the amount of microbial biomass. The effect of microarthropod grazing on microbes may have a stimulatory effect on respiration rates and microbial biomass (Seastedt 1984). The significant positive relationship between microarthropod abundance and microbial biomass on Day 30 of this experiment may have been the result of microarthropod stimulation of the microbial biomass. This positive relationship between microarthropod abundance and microbial biomass was not as strong at Day 60 of the experiment. At high microarthropod densities overgrazing of microbial biomass can occur, although this was not believed to be the cause of the microbial decline over the duration of this experiment, as mesocosms were below overgrazing densities (Hanlon and Anderson 1979).

Microarthropod abundance did not have a significant relationship with basal respiration rate. Similar mesocosm studies have found no effect of microarthropods on

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 CO_2 evolution rates (Persson 1989), although the contribution of soil microarthropods to basal soil respiration is estimated to be 1-5% of the total heterotrophic CO_2 evolution in conifer soil systems and 3-13% in deciduous soil systems (Persson 1989).

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The average estimated increase of litter decay due to microarthropods is 23% (Seastedt 1984), however, in this experiment decomposition rates were not measurably affected by the abundance of microarthropods. Other factors, such as moisture, may have greater influence over decomposition rates than microarthropods do (Douce and Crossley 1982).

Many studies show that the presence of soil fauna increases levels of available NH₄-N, and/or NO₃-N, and that the estimated contribution of mites and collembola to net N mineralisation is between 10 and 49% in F/H soils (Persson 1989, Bardgett and Chan 1999). But, like this study, other mesocosm experiments have found no significant effects of microarthropods on N availability (Heneghan and Bolger 1998). The lack of a measurable effect of microarthropod abundance on the availability of N (NH₄-N, NO₃-N) may be due to N immobilisation at the microbial grazer trophic level without sufficient predation pressure to release these nutrients (Setälä *et al.* 1991). The increasing number of fungivorous microarthropods during the experimental period of this study may have immobilised N released from microbial biomass ingested by the soil fauna.

There was a trend for PO₄-P to be positively related to the density of total microarthropods. Bardgett and Chan (1999) and Setälä *et al.* (1991) also observed greater available P with increased microarthropod abundance. Also, the lab results

obtained in this study support the field observations that total microarthropod abundance was significantly, positively correlated with forest floor PO_4 -P.

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Microarthropod numbers increased rapidly under laboratory conditions. However, studies of reduced microarthropod abundance following forest harvest in the field have shown that these low microarthropod densities can persist for years (Blair and Crossley 1988, Hoekstra *et al.* 1995). Increases in microarthropod densities in the laboratory are attributed to reproduction by parthenogenic species of both mites and springtails, as well as to optimal moisture and temperature conditions, and reduced predator populations (Setälä *et al.* 1991). Factors that may contribute to persistent reduced microarthropod densities in the field following clear-cutting are loss of habitat (soil pore space) caused by compaction due to heavy machinery (Battigelli 2000); and increased surface soil temperatures beyond a tolerable range for microarthropods (Vlug and Borden 1973, Abbott *et al.* 1980, Seastedt and Crossley 1981, Bird and Chatarpaul 1986). The field portion of this study suggests that the establishment of overstory vegetation in deciduous clear-cuts may stabilise the forest floor microclimate and/or decrease the effects of compaction, allowing microarthropod numbers to increase.

The long-term implications of reduced microarthropod densities following forest clear-cutting are unclear. However, a reduction in microarthropod numbers, in combination with changes in microbial biomass and nutrient availability, may affect the productivity of harvested sites. Until we understand the role of microarthropods in belowground food webs more completely, we should attempt to reduce the impact of forest harvesting on soil biological communities.

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The overall objectives of this study were:

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- 1. to determine if forest floor properties, processes, and microarthropod populations would be less impacted by partial-cutting than clear-cutting; and
- 2. to determine whether changes in nutrient cycling resulting from forest harvesting were related to alterations in microarthropod communities.

The data show that the integrity of forest floor properties and microarthropod communities is better maintained in partial-cut than clear-cut systems in both conifer and deciduous forest types. A significant decrease in densities of mite and springtails in both conifer and deciduous stands following harvesting may reduce PO₄-P availability; however, effects on N cycling would be negligible based on the results of the laboratory mesocosm study. Nevertheless, protection of microarthropod communities through partial-cutting practices is recommended to ensure long-term sustainability of decomposition and nutrient cycling processes.

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