Microbial biomass, nitrogen and phosphorus mineralization, and mesofauna in boreal conifer and deciduous forest floors following partial and clear-cut harvesting

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Abstract: The effects of partial and clear-cut harvesting on forest floor physical, chemical, and biological properties, forest floor mesofauna, and nutrient cycling were investigated in conifer- and deciduous-dominated stands of Alberta's mixedwood boreal forest. Forest floor samples were collected 2.5 years after harvest from clearcuts, strip-cut corridors in a partial cut, green tree retention patches in a partial cut, and uncut control sites. Partial cuts showed intermediate decreases in annual litter input and NH_4-N between uncut and clear-cut sites of both the deciduous and conifer stands, as did microbial biomass, PO_4-P, mesofauna abundance (total, Acari, and Collembola), and fine root biomass in the conifer stands. In the deciduous stands, microbial biomass and fine root biomass in partial- and clear-cut treatments were not significantly different, but were significantly reduced compared with the uncut controls. Mesofauna abundance was reduced in the corridors of the partial-cut treatment compared with partial-cut patch, clear-cut, and uncut treatments. In both deciduous and conifer stands, NO_3-N was elevated in the partial-cut corridors and clearcuts compared with partial-cut patch and uncut treatments. Findings from this study show that negative impact to forest floor properties associated with clear-cut harvesting may be reduced in partial-cut harvesting systems.

Résumé : Les effets de la coupe à blanc et de la coupe partielle sur les propriétés physiques, chimiques et biologiques de la couverture morte, sur la mésofaune de la couverture morte et sur le recyclage des nutriments ont été étudiés dans des peuplements dominés soit par des conifères, soit par des feuillus, dans la forêt mixte boréale de l'Alberta. Des échantillons de la couverture morte ont été prélevés dans des sites coupés à blanc, dans les corridors de coupes partielles par bandes, dans les îlots de réserves de coupes partielles et dans des sites témoins non coupés deux ans et demi après la récolte. La coupe partielle a entraîné une diminution de l'apport annuel de litière et de N (NH_4) intermédiaire entre les sites coupés à blanc et les sites non coupés dans les deux types de peuplements de même qu'une diminution de la biomasse microbienne, du P (PO_4), de l'abondance de la mésofaune (totale, d'acariens et de collemboles) et de la biomasse des racines fines dans les peuplements résineux. Dans les peuplements feuillus, la biomasse microbienne et la biomasse de racines fines ne différaient pas significativement entre la coupe partielle et la coupe à blanc mais étaient significativement plus faibles que dans les sites témoins non coupés. L'abondance de la mésofaune dans les corridors de la coupe partielle était inférieure à celle observée dans la coupe partielle avec réserves, dans la coupe à blanc et dans les sites non coupés. Tant dans les peuplements résineux que feuillus, N (NO_3) était plus élevé dans les corridors de la coupe partielle et dans la coupe à blanc que dans la coupe partielle avec réserves ou dans les sites non coupés. Les résultats de cette étude montrent que l'impact négatif de la coupe à blanc sur les propriétés de la couverture morte peut être minimisé avec des systèmes de coupe partielle.

[Traduit par la Rédaction]

Introduction

Previous research on the effects of forest removal on the soil system has focused primarily on the impacts of clear-cut harvesting, which has been shown to affect many soil properties, processes, and biological populations. Canopy removal associated with clear-cutting can increase the amounts of solar radiation and precipitation that reach the soil surface, thereby increasing soil temperature, diurnal temperature fluctuations, and soil moisture (Keenan and Kimmins 1993). Decreased levels of nutrients such as total N and C, NO_3-N, and available P in forest floors (Schmidt et al. 1996) and nutrient losses from the soil profile (Dahlgren and Driscoll 1994) following clear-cutting have been documented. In addition, several studies have reported decreased soil fungal biomass and soil mesofauna abundance following clear-cut harvesting (Bååth 1980; Seastedt and Crossley 1981). The relationship of soil microclimate, nutrient levels, and soil organisms with soil quality or "health" has not been clearly defined; however, forest practices that minimizes disturbance are being sought.

Partial-cut and selective harvesting systems are gaining interest as alternative practices to clear-cutting. Compared with clear-cut harvesting, green tree retention areas in

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partial-cut systems have smaller changes in soil microclimate and soil physical, chemical, and biological properties (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 (Siira-Pietikäinen et al. 2001; Barg and Edmonds 1999; Youngblood and Titus 1996). However, further examination of the effect of partial harvest on forest floor properties, forest floor mesofauna, and nutrient cycling is needed to gauge the sustainability of this practice.

The present research was initiated to compare the effects of clear-cut and partial-cut harvesting on forest floor physical, chemical, and biological properties in conifer- and deciduous-dominated stands of the boreal mixedwood forest. Specific objectives were (*i*) to evaluate the effects of clear-cutting and partial cutting relative to uncut sites on forest floor physical, chemical, and biological properties, (*ii*) to determine the effects of clear-cutting and partial cutting relative to uncut sites on decomposition potential and nutrient mineralization potential, (*iii*) to compare the abundance of soil mesofauna in clear-cut, partial-cut, and uncut sites and relate changes in abundance with changes in the physical and (or) chemical environment associated with forest harvesting. The overall objective was to determine whether partial-cut harvests retained forest floor properties more similar to those of uncut forests compared with clear-cut harvests. We hypothesized that changes in forest floors in partially cut sites would be intermediate between those of uncut and clear-cut sites.

This research forms one component the Ecosystem Management Emulating Natural Disturbance (EMEND) in the mixedwood boreal forest of northern Alberta (Sidders and Spence 2001). EMEND is a 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.

Materials and methods

Site description and experimental design

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

The EMEND study area has both coniferous- and deciduous-dominated 80- to 140-year-old stands. Two replicate conifer and deciduous stands were divided at random into 10-ha clear-cut, partial-cut, or uncut sites. In the present study, the partial-cut site was divided into two treatments, the strip-cut corridors and the retention patches, since impacts on forest floor physical, chemical, and biological properties may differ between these two areas. Thus the treatments considered in this study are clearcut, partial-cut patch (patch), partial-cut corridor (corridor), and uncut control.

Harvesting occurred in the winter of 1998–1999. Conventional full-tree harvesting using a feller–buncher and direct route skidding was used in the clear-cut sites. The harvesting method within the partial-cut site was a two-pass system, which consisted of strip-cutting machine corridors on the first pass and selectively logging retention patches on the second pass. The machine corridors were created using a feller–buncher–forwarder (skidder) full tree system and were 5 m wide and spaced at 20-m intervals. All corridors were 100% tree removal and were 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 were 15 m wide and had a 1:3 stem removal to total stem ratio (one of every three trees was 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 with an additional 25% tree removal from the selectively logged retention patches, for a total of 50% partial cut over the 10-ha site.

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.) BSP (black spruce), *Abies balsamea* (L.) Mill. (balsam fir), *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. (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), *Sherpherdia canadensis* (L.) Nutt. (Canada buffaloberry), *Alnus crispa* (Ait.) Pursh (green alder), and *Alnus tenuifolia* Nutt. (river alder) (Sidders and Spence 2001).

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

Sampling regime

Sampling was conducted in June 2001, 2.5 years post-harvest. A 50-m transect was established in each treatment, and samples were taken at 10-m intervals for a total of five samples per treatment per site. A total of 80 samples were taken (two stand types × two replicates per stand × four treatment sites (uncut, patch, corridor, clearcut) × five samples per treatment). Transects were oriented north–south to coincide with the direction of corridors and retention patches. At each sampling point, a 25 cm × 25 cm quadrat of forest floor was excavated to a depth of 15 cm for physical, chemical, and biological measurements, and a 5.5 cm diameter core was sampled for mesofauna assessments. A separate PVC soil corer was used for each core sample, and each core was stored in the corer until extraction to minimize disturbance to the fauna during transport from the field to the laboratory. Forest floor samples and cores were stored at 4 °C until ready for processing.

Litter input was determined by placing litter traps, consisting of 26 cm × 53 cm trays, approximately 1 m from each sample point along each transect. Litter was collected after 1 year, separated into litter types (leaf or needle litter and coarse woody litter), dried at 80 °C, and weighed.

In the laboratory, the dimensions of each forest floor quadrat were determined, and the depth of the litter and F–H horizons was measured. Litter, slash, green vegetation, and moss on the surface were removed, oven-dried, and weighed. The F–H layer was separated from any underlying mineral soil and passed through a 4-mm sieve. Sieved forest floors were stored in plastic bags at 4 °C until ready for analysis.

Physical and chemical measurements

Forest floor moisture content (expressed as percent dry mass (dm)) was measured gravimetrically using an 80 °C drying oven. Organic matter content (%) was estimated using the loss-on-ignition method, where ovendried samples (105 °C) were combusted in a muffle furnace at 400 °C for 24 h (Nelson and Sommers 1982).

Forest floor chemical measurements included pH, electrical conductance (EC), total and available N, and total and available P. The pH of the samples was measured with a glass electrode pH meter using a slurry of 1:10 forest floor (dm) to deionized water ratio. The filtrate of the slurry was used to determine the EC. The EC of the filtrate was measured in decisiemans per metre using a Markson digital conductivity meter.

Total N and P concentrations were determined by the micro-Kjeldahl procedure (no pretreatment or catalyst) (adapted from Bremner and Mulvaney 1982). Dried and ground samples were digested in H_2SO_4 and H_2O_2, and colourimetric determinations of NH_4^+ and PO_4^- concentrations were made using a Technicon Autoanalyser II (Technicon Industrial Systems 1970). Available N (nitrate and ammonium) and available P (phosphate) were extracted from samples with KCl (Keeney and Nelson 1982) and medium Bray's extract (Olsen and Sommers 1982), respectively, and analysed using the same autoanalyser.

Biological measurements

Basal respiration and microbial biomass measurements evaluated C mineralization potential. Basal respiration of 5 g dm equivalent of field-moist, sieved forest floor was measured as CO_2 evolution (μL CO_2·sample $dm^{-1}·h^{-1}$) using an infrared gas analyser (Anderson 1982). Microbial biomass C (mg C_{mic}/g dm) was estimated using the substrate-induced respiration method of Anderson and Domsch (1978) with glucose as the substrate. The amount of glucose required for maximum initial response in the forest floor from coniferous and deciduous stands was determined prior to biomass analyses and was found to be 60 mg glucose/g dm deciduous forest floor and 40 mg glucose/g dm conifer forest floor.

Nitrogen and P mineralization potentials were estimated using a laboratory-based, 6-week aerobic incubation method, where the production of NH_4-N, NO_3-N, and PO_4-P is measured under constant temperature and moisture conditions (Hart et al. 1994*b*). Five grams dm equivalent of field-moist forest floors was extracted with KCl or Bray's extract and analysed for NH_4-N, NO_3-N, and PO_4-P concentrations using the Technicon Autoanalyser II (Technicon Industrial Systems 1970), before and after a 6-week incubation period at 22 °C. Net mineralization rates were estimated by comparing final concentrations with the initial concentrations.

Litter decomposition potential was estimated as percent mass loss of aspen leaves after 3 months of incubation in the laboratory. For each forest floor sample (80 total), 1 g (air dm) of senesced aspen leaves was placed on the surface of 10 g dm equivalent of field-moist deciduous or conifer forest floor held in a plastic container. Samples were covered with a perforated lid and incubated under constant temperature (22–23 °C) and moisture conditions for 3 months. Moisture of containers was monitored weekly and adjusted to the original mass with deionized water. Litter decomposition was estimated as the difference in dry mass of leaves before and after incubation and corrected to ovendry mass to estimate percent mass loss.

Mesofauna measurements

Intact forest floor cores were extruded from the plastic corers, divided into 4-cm sections, and placed in a Macfadyen extractor, where a temperature and moisture gradient forces fauna to move down the core into a picric acid fixative over a period of 10 days. Fauna were filtered from the picric acid and preserved in 70% ethanol solution. Abundances of Acari, Collembola, and other mesofauna were determined using a dissecting microscope.

Soil bulk density (kg/m^3) was estimated using the core method (Blake and Hartge 1986). Cores from fauna samples were used to calculate bulk density after extraction to 50 °C and correcting for moisture at 105 °C. Fine root biomass (g dm roots/g dm forest floor) was measured by washing roots from dry cores, separating them into size classes based on diameter (0–2 and 2–6 mm), and drying them at 80 °C.

Statistical analysis

Initial analysis of differences between uncut deciduous and conifer stands was performed by a Student's *t* test using $p < 0.05$ as the significance level. A three-factor analysis of variance (ANOVA) was performed to test for differences among the means for each parameter and to assess variation caused by site, stand, and treatment. For this analysis the general linear model for randomized block designs in SYSTAT version 7.0 (SYSTAT Inc. 1997) was employed. Results were considered significant at $p < 0.05$. Further, one-way ANOVA with a Tukey's test was performed separately for each stand type to assess the effects of harvesting intensity. Data in violation of the ANOVA model assumptions were transformed; in particular, fauna densities were log transformed to normalize the data. Pearson's correlation coefficients were used to determine relationships between mesofauna (total, Acari, Collembola) abundance and forest floor moisture, bulk density, fine root biomass, microbial biomass, and total and available N and P.

Results

Uncut forest comparison

Forest floor physical, chemical, and biological properties differed between conifer and deciduous stands (Table 1). Bulk density, pH, and moisture content were lower in coni-

Table 1. Physical, chemical, and biological properties from forest floors in uncut deciduous and conifer stands.

	Deciduous	Conifer	p value
Forest floor depth (cm)	6.3 (0.8)	8.9 (0.7)	0.030
Soil bulk density (kg/m^3)	0.16 (0.02)	0.11 (0.01)	0.041
Moisture content (% dm)	249 (22.4)	168 (11.8)	0.005
Organic matter content (% LOI)*	81.5 (2.0)	82.4 (2.0)	ns
pH (H_2O)	6.2 (0.1)	5.2 (0.2)	0.000
Electrical conductivity (dS/m)	0.25 (0.05)	0.18 (0.02)	ns
Total N (mg/g dm)	20.1 (0.34)	16.0 (0.43)	0.000
Total P (mg/g dm)	1.6 (0.04)	1.2 (0.05)	0.000
Basal respiration (μL CO_2·g dm^{-1}·h^{-1})	110.4 (8.4)	85.3 (8.1)	0.045
Microbial biomass (mg C/g dm)	21.2 (1.8)	15.9 (1.4)	0.033
Root biomass, <2 mm diameter (g/g dm)	0.06 (0.01)	0.02 (0.01)	ns
Root biomass, 0–6 mm diameter (g/g dm)	0.08 (0.02)	0.05 (0.01)	0.016
Decomposition potential (% mass loss after 3 months)	46.6 (1.1)	43.1 (1.9)	ns
Litter input (g·m^{-2}·year^{-1})†	228 (21)	216 (13)	ns
Total mesofauna abundance (individuals/g dm)	21.8 (3.6)	40.1 (7.0)	0.031
Total Acari abundance (individuals/g dm)	16.5 (2.7)	31.9 (5.3)	0.017
Total Collembola abundance (individuals/g dm)	4.9 (1.1)	7.8 (1.9)	ns

Note: Values are means with SEs given in parentheses (n = 10); p values are based on Student's standardized t test; ns denotes not significant (p > 0.05).
*LOI, loss on ignition.
†Annual litter input includes leaf, needle, and twig litter.

Table 2. Nitrogen and P availability in forest floors from uncut coniferous and deciduous stands, and net N and P mineralization during 6 weeks of laboratory incubation.

	Deciduous	Conifer	p value
Initial NH_4-N (μg/g)	233 (31)	145 (39)	ns
NH_4-N after 6 weeks (μg/g)	54 (11)	44 (24)	ns
NH_4-N mineralized per 6 weeks (μg/g)	–179 (35)	–101 (28)	ns
Initial NO_3-N (μg/g)	78 (72)	1 (0.1)	0.003
NO_3-N after 6 weeks (μg/g)	537 (92)	48 (29)	0.000
NO_3-N mineralized per 6 weeks (μg/g)	459 (71)	47 (29)	0.000
Initial mineral N (NH_4-N+NO_3-N) (μg/g)	311 (94)	146 (39)	ns
Mineral N after 6 weeks (μg/g)	590 (88)	92 (34)	0.000
Net N mineralized per 6 weeks (μg/g)	279 (66)	–54 (43)	0.001
Initial PO_4-P (μg/g)	89 (7)	121 (12)	0.036
PO_4-P after 6 weeks (μg/g)	139 (20)	99 (7)	ns
PO_4-P mineralized per 6 weeks (μg/g)	50 (17)	–22 (6)	0.001

Note: Values are means with SEs given in parentheses (n = 10); p values are based on Student's standardized t test; ns denotes not significant (p > 0.05).

fer stands than in deciduous stands, while forest floor depth was greater in the conifer stands. Total N, total P, available nitrate, basal respiration, and microbial and root biomasses were significantly higher in the deciduous stands.

Conifer forest floors had higher amounts of available P and had significantly greater total mesofauna and Acari abundance compared with deciduous forest floors. Collembola abundance was also slightly greater in conifer forest floors, but this difference was not significant.

Initial NH_4-N concentrations in forest floors and amounts of NH_4-N mineralized after 6 weeks of incubation were not significantly different between conifer and deciduous stands (Table 2). In contrast, NO_3-N availability and the amount of NO_3-N mineralized were significantly greater in the deciduous than in the conifer stands. Total available N (NH_4-N + NO_3-N) did not differ significantly between stand type; however, the net amount of N mineralized after 6 weeks of incubation in the laboratory was significantly greater in the deciduous forest floor than in the conifer forest floor. Initially, levels of PO_4-P were significantly greater in the conifer forest floor than in the deciduous forest floor. After 6 weeks of incubation, the amount of PO_4-P mineralized in the conifer stand was negative (i.e., net immobilization), while the amount of PO_4-P in the deciduous stands increased during incubation.

Harvesting effects on soil physical and chemical properties

There were no significant effects of harvesting on organic matter or electrical conductivity, and effects seen in other

Table 3. Physical and chemical properties of the forest floors of uncut, partial-cut (patch and corridor), and clear-cut sites in coniferous and deciduous stands.

	Uncut	Patch	Corridor	Clearcut
Conifer stand (*n* = 40)				
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 (kg/m^3)	0.11 (0.01)b	0.12 (0.01)ab	0.14 (0.01)ab	0.17 (0.02)a
Moisture content (% dm)	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 (in water)	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 dm)	16.0 (0.43)a	15.9 (0.55)a	13.9 (0.85)a	14.7 (0.94)a
Total P (mg/g dm)	1.2 (0.05)a	1.2 (0.06)ab	1.2 (0.07)ab	1.0 (0.06)b
Deciduous stand (*n* = 39)				
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 (kg/m^3)	0.16 (0.02)a	0.16 (0.01)a	0.17 (0.01)a	0.17 (0.01)a
Moisture content (% dm)	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 (in water)	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 dm)	20.1 (.34)ab	21.9 (.77)a	20.1 (.67)ab	18.7 (.92)b
Total P (mg/g dm)	1.64 (0.04)a	1.42 (0.06)ab	1.36 (0.06)b	1.56 (0.07)ab

Note: Values are means with SEs given in parentheses. Within each row, values followed by the same letter are not significantly different, based on one-way analysis of variance and Tukey's test ($p > 0.05$).

*LOI, loss on ignition.

physical and (or) chemical properties were observed primarily in the conifer stands (Table 3). In the conifer stands, forest floor depth in the partial-cut corridors was significantly reduced relative to the uncut control and clear-cut treatments. Also, clear-cutting in the conifer stands resulted in higher bulk density. Moisture contents were greater in all harvest treatments compared with the uncut control in the conifer stands. Total P was significantly reduced in the partial-cut corridors of the deciduous stands and in the clear-cut treatments of the conifer stands relative to the uncut treatments.

Harvesting effects on soil biological parameters

Significant effects of harvesting treatment were seen in basal respiration, microbial biomass C, fine root biomass (Figs. 1*a*, 1*b*, 1*c*), and annual litter input (Figs. 2*a* and 2*b*). In the deciduous stands, all harvest treatments had lower basal respiration compared with the uncut control treatment. In the conifer stands only clear-cutting significantly reduced basal respiration in the forest floor; patch and corridor forest floors from the partial-cut sites were not significantly different from the uncut control. In the deciduous stands, the uncut control had significantly greater microbial biomass C than the harvested treatments. In the conifer stands, microbial biomass C decreased with increasing tree removal, but only the clear-cut treatment was significantly lower than the uncut control treatment.

Fine root biomass (g/g dm forest floor) in the 0–6 and <2 mm diameter size classes showed similar response patterns to treatment. In the deciduous stands, fine root biomass was significantly reduced in both the partial- and clear-cut sites (Fig. 1*c*). Mean fine root biomass in the 0–6 mm diameter size class in deciduous stands was in the following order among treatments: uncut > retention patch = corridor = clearcut (Table 4). In the conifer stands, fine root biomass did not differ significantly between the uncut control and partial-cut patch treatments, and both treatments had greater fine root biomass than the partial-cut corridor and clear-cut treatments. This trend was most pronounced for the 0–6 mm root diameter size class, with uncut > retention patch > corridor = clearcut (Table 4).

Total annual litter input from field estimations was significantly reduced in the partial- and clear-cut sites compared with the uncut sites in both the deciduous and conifer stands (Figs. 2*a* and 2*b*). Litter inputs in the retention patches and strip-cut corridors of the partial-cut treatments did not differ significantly and were greater than those in the clearcuts. Total annual litter inputs in the conifer clearcuts were zero (g dm/m^2) at many sample locations.

Decomposition potential, measured as percent mass loss from aspen leaves after 3 months of incubation in the laboratory, did not show any significant differences among treatments or between stands.

Harvesting effects on available nutrients and mineralization processes

Ammonium N levels in the forest floor were lowest in the clear-cut treatments in both stand types; NH_4-N in the partial-cut corridor was intermediate between the clear-cut and uncut treatments (Fig. 3*a*). Nitrate N data in the deciduous stands were highly variable, but tended to be higher in the partial-cut corridor and clear-cut treatments (Fig. 3*b*). The same pattern was observed in the conifer stands, where NO_3-N was significantly higher in the partial-cut corridors and clearcuts than in the uncut controls. No impact of harvesting on PO_4-P was measured in the forest floor of the deciduous stands. In contrast, PO_4-P in the partial-cut corridors and clear-cut treatments of the conifer stands was significantly reduced relative to the uncut control (Fig. 3*c*).

Fig. 1. Basal respiration (*a*), microbial biomass C (*b*), and fine root biomass (<2 mm diameter) (*c*) in forest floors of uncut, partial-cut (patch and corridor), and clear-cut sites in conifer and deciduous stands. Values are means ± SE. Values with the same letter within each stand type are not significantly different.

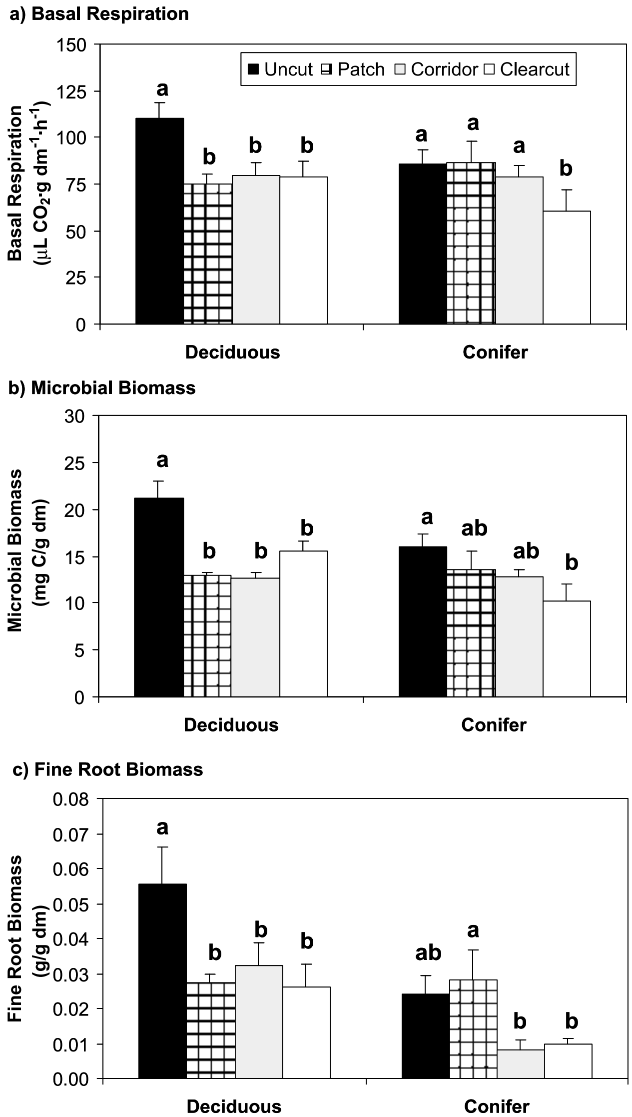


Fig. 2. Annual litter input in uncut, partial-cut (patch and corridor), and clear-cut sites in conifer (*a*) and deciduous (*b*) stands. Columns are divided into the mean amount recorded for each litter type. Other litter includes twigs, cones, and bark. Standard error bars are for total annual litter input. Values with the same letter within each stand type are not significantly different in total annual litter input.

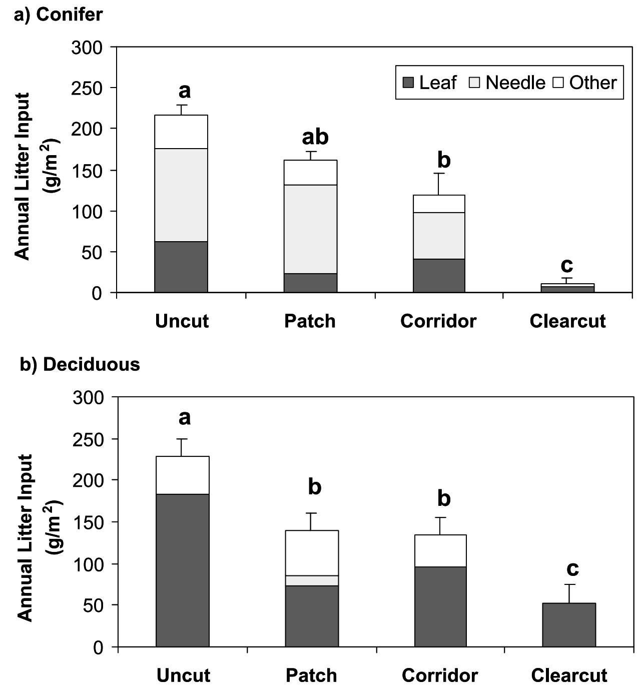


Table 4. Fine root biomass in the 0–6 mm diameter class in uncut, partial-cut (patch and corridor), and clear-cut sites in the deciduous and conifer stands.

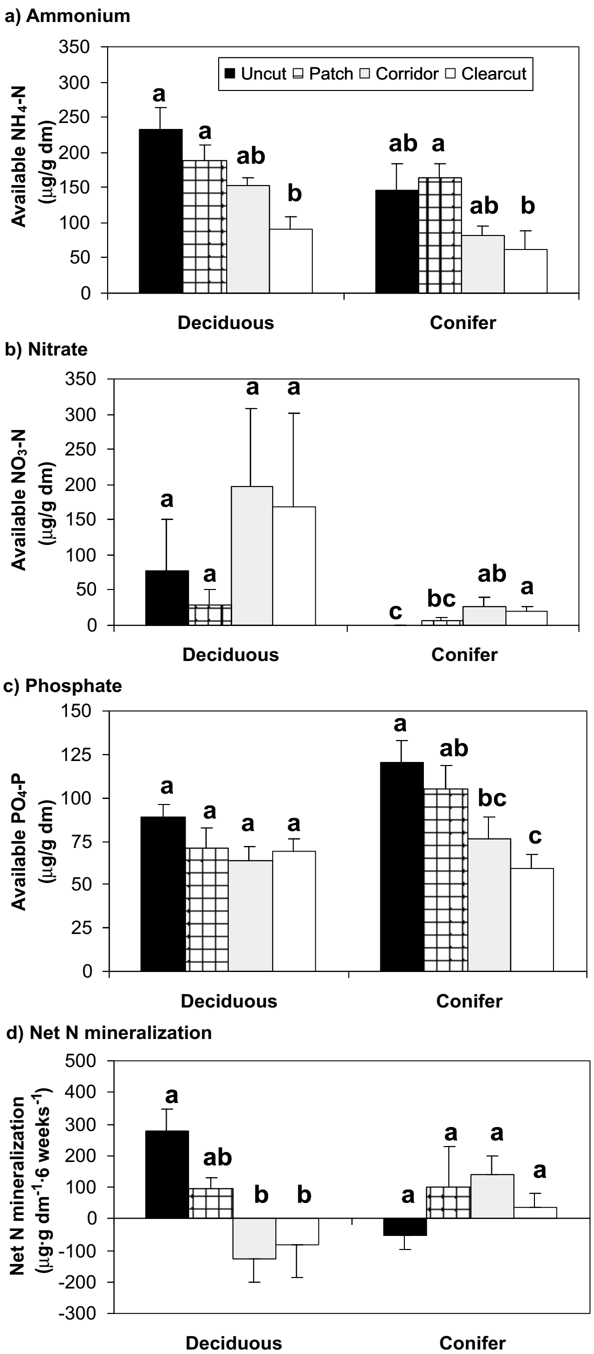
Treatment	Fine root biomass (g root/g dm)
Deciduous stand	
Uncut	0.08 (0.02)a
Patch	0.04 (0.01)ab
Corridor	0.04 (0.01)ab
Clearcut	0.04 (0.01)b
Conifer stand	
Uncut	0.05 (0.01)a
Patch	0.04 (0.01)ab
Corridor	0.02 (0.01)b
Clearcut	0.02 (0.01)b

Note: Values are means with SEs given in parentheses. Within a stand type, values followed by the same letter are not significantly different, based on one-way analysis of variance and Tukey's test ($p > 0.05$).

Net nitrogen mineralization in deciduous forest floors after 6 weeks of incubation in the laboratory was greatest in the uncut control and partial-cut retention patch treatments. In contrast, net N mineralization was negative in the partial-cut corridors and clear-cut treatments (Fig. 3*d*). In the conifer treatments there was net immobilization of N in the uncut sites and net mineralization of N in the harvested treatments, but the differences were not significant.

Rates of N and P mineralization were highly variable (Table 5). No clear treatment effects on net NH_4-N and NO_3-N production were measured in the conifer forest floors, although the amount of NH_4-N and NO_3-N mineralized tended to be higher in the partial-cut and clear-cut treatments than in the uncut control. In contrast, net NO_3-N in the deciduous forest floors was significantly lower in the cut treatments than in the uncut treatment after 6 weeks of incubation. Although initial available N was not significantly different among treatments in either stand type, net NH_4-N mineralization was more negative in the uncut treatment than in the cut treatment. The amounts of NH_4-N mineralized to NO_3-N in the deciduous forest floors were significantly lower in the clear-cut than uncut treatments, with rates in the partial-cut treatments being intermediate between uncut and clear-cut treatments. In the conifer stands, there was no significant treatment effect on net NO_3-N mineralization.

Fig. 3. Available ammonium (*a*), nitrate (*b*), phosphate (*c*), and net nitrogen mineralization potential (*d*) in forest floors of uncut, partial-cut (patch and corridor), and clear-cut sites in conifer and deciduous stands. Values are means ± SE. Values with the same letter within each forest stand type are not significantly different.



In both stand types, the amount of PO_4-P in the forest floors after 6 weeks of incubation was significantly lower in the partial-cut corridors and clear-cut treatments. Rates of PO_4-P mineralization were negative in all treatments with the exception of the uncut deciduous samples.

Analysis of soil mesofauna

Acari (mites) and Collembola (springtails) accounted for 98% (70 and 28%, respectively) of the total mesofauna extracted in this study. The remaining 2% of fauna collected from these forest floors included various other mesofaunal taxa, predominantly insect larvae. Therefore, patterns of total mesofauna abundance were influenced primarily by Acari abundance. Acari and Collembola were more abundant in conifer than deciduous forest floors (Figs. 4*b* and 4*c*). Acari abundance and mesofauna abundance totals were significantly reduced in the partial-cut corridor treatment in the deciduous stands and in the clear-cut treatment of the conifer stands. There was no clear pattern of treatment on Collembola abundance in either stand type. There was no significant treatment effect on Collembola in the conifer stands, possibly due to high sample variability (Fig. 4*c*). Deciduous stands showed significant reductions in Collembola abundance in the partial-cut corridors, but not in the clear-cut treatments.

Correlation analysis of Acari, Collembola, and total mesofauna abundance with selected forest floor variables suggests that mesofauna communities within conifer and deciduous stands are very different (Table 6). In the conifer stands, total mesofauna, total Acari, and total Collembola were positively correlated with microbial biomass, total P, NH_4-N, and PO_4-P. Acari abundance was also positively correlated with fine root biomass (<2 mm diameter). In contrast, Acari abundance and, consequently, total mesofauna were negatively correlated with bulk density. In the deciduous forest floors, Collembola and total mesofauna were negatively correlated with moisture content. Acari and Collembola abundance had a weak negative correlation with pH; however, this correlation was not seen when the total mesofauna abundance was considered. Total mesofauna were weakly correlated with fine root biomass (<2 mm diameter) in the deciduous stands.

Discussion

Forest stand type

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 and organic matter accumulation, and lower pH in the conifer stands than the deciduous stands can also be attributed to differences in litter quality and foliar chemistry between deciduous and conifer overstories (Paré and Bergeron 1996). Also, higher net N mineralization rates were observed in the deciduous stands than the conifer stands, as has been reported previously (Frazer et al. 1990; 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 immobilization of N by microbes and decrease net N mineralization rates, which, in turn, reduces available soil N (Côté et al. 2000). Low levels of NH_4-N and NO_3-N were measured in the conifer stands in this study, suggesting that this forest may indeed be N poor. In contrast, higher nutrient levels (total N and P, NH_4-N, NO_3-N) and higher N and P mineralization rates in the deciduous stands indicate that this stand type is more fertile and potentially more productive than the conifer stands.

Total mesofauna densities in the uncut deciduous and conifer forest floors compared favourably with densities found

Table 5. Nitrogen and P availability in forest floors from uncut, partial-cut (patch and corridor), and clear-cut sites in coniferous and deciduous stands, and net N and P mineralization during 6 weeks of laboratory incubation.

	Uncut	Patch	Corridor	Clearcut
Conifer stand (*n* = 40)				
Initial N (NH_4-N+NO_3-N) (µg/g)	146 (39)a	171 (20)a	108 (21)a	83 (23)a
Final N after 6 weeks (µg/g)	92 (34)a	270 (132)a	247 (75)a	121 (37)a
NH_4-N after 6 weeks (µg/g)	44 (24)a	22 (8)a	4 (1)a	9 (3)a
NO_3-N after 6 weeks (µg/g)	48 (29)a	249 (134)a	243 (74)a	112 (37)a
PO_4-P after 6 weeks (µg/g)	99 (7)a	94 (8)a	59 (6)b	44 (8)b
NH_4-N mineralized per 6 weeks (µg/g)	–101 (28)ab	–143 (23)b	–78 (13)ab	–53 (24)a
NO_3-N mineralized per 6 weeks (µg/g)	47 (29)a	242 (129)a	217 (71)a	91 (36)a
PO_4-P mineralized per 6 weeks (µg/g)	–22 (6)a	–12 (15)a	–17 (12)a	–15 (4)a
Deciduous stand (*n* = 39)				
Initial N (NH_4-N+NO_3-N) (µg/g)	311 (94)a	219 (32)a	350 (110)a	259 (130)a
Final N after 6 weeks (µg/g)	590 (88)a	314 (40)b	221 (51)b	176 (58)b
NH_4-N after 6 weeks (µg/g)	54 (11)a	35 (13)a	15 (2)a	36 (15)a
NO_3-N after 6 weeks (µg/g)	537 (92)a	279 (49)b	206 (52)b	140 (52)b
PO_4-P after 6 weeks (µg/g)	139 (20)a	63 (9)b	50 (6)b	59 (8)b
NH_4-N mineralized per 6 weeks (µg/g)	–179 (35)b	–154 (31)ab	–138 (13)ab	–55 (20)a
NO_3-N mineralized per 6 weeks (µg/g)	459 (71)a	250 (51)ab	8 (70)ab	–28 (102)b
PO_4-P mineralized per 6 weeks (µg/g)	50 (17)a	–8 (14)b	–14 (8)b	–10 (7)b

Note: Values are means with SEs given in parentheses. Within each row, values followed by the same letter are not significantly different, based on one-way analysis of variance and Tukey's test ($p > 0.05$).

in sub-boreal spruce forests in British Columbia (Battigelli 2000). Fauna abundance is usually higher in forested systems than in nonwooded systems and specifically in forest systems with extensive amounts of aerobic organic matter (e.g., forest floors of conifer stands) (Seastedt 1984).

Effects of harvest on the 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, which can lead to increased soil moisture (Keenan and Kimmins 1993); uncut retention areas have been shown to reduce these effects (Barg and Edmonds 1999). However, in this study moisture content in the partial-cut sites was not significantly different from that in clear-cut sites and was greater than that in uncut control sites of both deciduous and conifer stands.

Site disturbance was minimal owing to a lack of site preparation; however, compaction associated with the harvesting process was apparent in the strip-cut corridors of the partial-cut conifer stands, where a decrease in forest floor depth and an increase in soil bulk density were measured. This is consistent with Startsev et al. (1998), who found that trafficking by skidders significantly increased soil bulk density after only one pass, and that maximal compaction occurred after only three passes of a skidder. Soil compaction may have contributed to decreased microbial respiration and biomass in this study, since soil respiration has been found to correlate negatively with soil bulk density (Startsev et al. 1998).

Biological properties

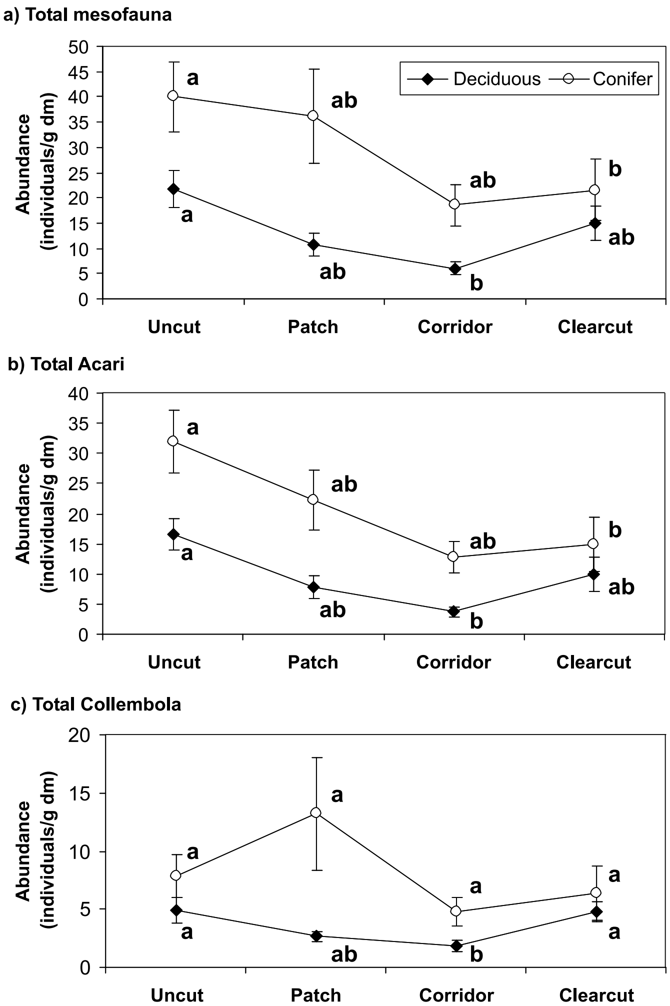
Reductions in microbial biomass in clearcuts compared with uncut forests have been reported by Bååth (1980), and Chang et al. (1995) found less microbial biomass in the forest floors of 3- and 10-year-old plantations than in the forest floor of old-growth forests. Increases in microbial biomass following harvesting have also been reported (Entry et al. 1986; Barg and Edmonds 1999), and a lack of significant long-term changes in basal respiration and microbial biomass following harvesting is not uncommon (Seastedt and Crossley 1981; Marra and Edmonds 1998). Litter and root exudates are a primary resource for microbes, and roots are especially important for organisms associated with root biomass, such as the mycorrhizal fungi (Bååth 1980). Decreased annual litter input and root biomass in all harvested sites in this study may have contributed to the reduction in microbial biomass.

Alterations in soil temperature and moisture due to tree removal may accelerate organic matter decomposition in the field (Covington 1981). However, many studies exhibit no consistent or overall pattern of decomposition rates in clear-cut forest floors (Prescott et al. 2000). No harvesting treatment effects on litter decomposition were evident in the present study, perhaps because moisture and temperature were standardized across all treatments during the 3-month laboratory incubation period.

Chemical properties

Total N, NO_3-N, NH_4-N, PO_4-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 difference in these nutrients (Maynard and MacIsaac 1998) between cut and uncut forests. A progressive reduction in NH_4-N from uncut to partial-cut to clear-cut sites in both stand types suggests a gradient effect associated with harvesting intensity. A reduction in NH_4-N in the partial-cut and clear-cut sites may be the result of increased nitrification observed in these sites after harvesting. More NO_3-N in the partial-cut corridors and clear-cut treatments

Fig. 4. Total mesofauna (*a*), Acari (mites) (*b*), and Collembola (springtails) (*c*) in forest floors of uncut, partial-cut (patch and corridor), and clear-cut sites in conifer and deciduous stands. Values are means ± SE. Values with the same letter within each forest stand type are not significantly different.



than in the partial-cut patch and uncut treatments confirms that there was an increase in NO_3-N with increased timber removal.

Increased available NO_3-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, there was no effect of harvest on decomposition rates, and microbial biomass was reduced in all harvesting treatments in this study. An alternative hypothesis for increased NO_3-N suggests that decreases in C inputs following clear-cutting decrease microbial biomass and microbial immobilization of N, thereby increasing NO_3-N levels (Hart et al. 1994*a*; Prescott 1997). Nitrate N is susceptible to leaching, and consequently, reduced levels of NO_3-N have been found also in forest floors of mixed northern hardwood forests following harvesting disturbance (Dahlgren and Driscoll 1994).

Laboratory nitrogen mineralization

Laboratory incubation studies, such as that in the present study, control for temperature, moisture, and plant uptake. Thus lower observed rates of net N mineralization and nitrification in the harvested deciduous sites during controlled laboratory incubation suggest that reduced microbial biomass and (or) changes in substrate quality induced the differences in mineralization rates. In both stand types, patterns of net N mineralized appeared to depend primarily on nitrification rates.

Conflicting field and laboratory mineralization rates are not uncommon, and often differences in mineralization rates in the field associated with harvesting treatment are not exhibited under controlled laboratory conditions. Studies involving laboratory mineralization experiments are thought to represent potential mineralization rates only and are not necessarily indicative of field mineralization rates (Frazer et al. 1990).

Mesofauna

A reduction in Acari and total mesofauna abundance with increased timber removal, especially in conifer stands, has been observed in other studies (Vlug and Borden 1973; Seastedt and Crossley 1981; Bird and Chatarpaul 1986; Blair and Crossley 1988; Marra and Edmonds 1998). Reductions in fauna densities between cut and uncut forests may be attributed to changes in soil moisture and temperature (Marra and Edmonds 1998), changes in amount and type of organic input (Huhta et al. 1967), and changes in soil aeration (i.e., soil compaction) after harvesting (Battigelli 2000). In this study, Pearson's correlation coefficients suggested that soil compaction contributed significantly to reducing fauna, particularily in the conifer sites.

The lack of significant differences in mesofauna abundance (total, Acari, and Collembola) between the deciduous clearcuts and uncut controls may be due to extensive tree, herb, and grass regeneration in the clear-cut treatment of this stand type. High variability may also have obscured treatment effects in both forest types. High variability in Collembola abundance in field studies is not uncommon (Vlug and Borden 1973; Seastedt and Crossley 1981) and is possibly due to population response to patchy distribution of organic matter input after tree removal (i.e., reductions in litter and additions of harvesting residues). Although increases in Collembola abundance following harvest have been observed (Huhta et al. 1967; Bird and Chatarpaul 1986; Marra and Edmonds 1998), this was not the case in the present study.

The variables that were best correlated with changes in fauna abundance in the conifer stands were bulk density, microbial biomass, total P, PO_4-P, and NH_4-N. Moisture content, pH, and fine root biomass in the deciduous stands best correlated with changes in faunal abundance in this stand type. Acari and Collembola abundance correlated positively with microbial and fine root biomass in both stand types. As many Acari and Collembola are fungivorous, faunal densities may be directly related to food abundance. This may explain some treatment differences in the mesofauna data, as both microbial biomass and fine root biomass were reduced following harvesting. Further study to explore the relationship between the Acari and Collembola and forest floor variables, before and after harvesting, may provide further insight into factors that determine the structure and composition of forest floor mesofauna communities.

Table 6. Pearson's correlation coefficients for soil mesofauna abundance and selected forest floor variables in conifer and deciduous stands.

	Total mesofauna	Total Acari	Total Collembola
Conifer stand (*n* = 40)			
Moisture content	0.016	–0.168	0.301
pH (H_2O)	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*
Initial NH_4-N	0.429*	0.367*	0.438*
Initial NO_3-N	0.000	–0.036	0.000
Initial PO_4-P	0.446*	0.433*	0.373*
Fine root biomass (<2 mm diameter)	0.272	0.338*	0.117
Deciduous stand (*n* = 39)			
Moisture content	–0.493**	–0.142	–0.426*
pH (H_2O)	–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
Initial NH_4-N	0.261	–0.019	0.207
Initial NO_3-N	0.135	0.058	0.142
Initial PO_4-P	0.129	–0.017	0.098
Fine root biomass (<2 mm diameter)	0.335*	0.122	0.296

Note: *, correlation is significant at the 0.05 level (two-tailed); **, correlation is significant at the 0.01 level (two-tailed).

Conclusion

Biological properties of the conifer and deciduous forest floors, in particular soil respiration, microbial biomass, annual litter input, and fine root biomass, declined in both the partial-cut and clear-cut harvesting sites. Clear-cutting and partial cutting changed physical forest floor properties (forest floor depth, soil bulk density, soil moisture) in the conifer stands, but not in the deciduous stands. There was no harvesting effect on percent organic matter or electrical conductivity in forest floors of either stand type. Available NH_4-N, NO_3-N, and PO_4-P concentrations in the partial-cut treatments were intermediate compared with clear-cut and uncut treatments. Ammonium N and PO_4-P concentrations decreased, while NO_3-N concentrations increased in harvested treatments. Decomposition potential, as measured in a laboratory incubation study, showed no effect of harvest treatment. Decreased abundance of total mesofauna, Acari, and Collembola in partial-cut corridors and clearcuts are thought to be related to decreases in food resources (root and microbial biomass) and to decreased soil pore space (habitat) through compaction associated with harvesting.

In many cases, within the partial-cut harvesting treatment, green tree retention patches and strip-cut corridors differed in the effects of tree removal on forest floor properties. Green tree retention areas were more likely to retain forest floor properties similar to those of uncut sites, whereas the strip-cut corridors tended to be more similar to clearcuts. Mesofauna was less abundant in corridors than in clearcuts. Overall, the effects of partial-cut harvesting were less pronounced than the effects of clear-cut harvesting for many forest floor properties in this mixedwood boreal forest.

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