Dissertationes Forestales 12

Logging residues and ground vegetation in nutrient dynamics of a clear-cut boreal forest

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Academic dissertation

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ABSTRACT

In this thesis are studied the role of decomposing logging residues and developing ground vegetation in nutrient dynamics of a clear-cut area. The main aims were to study how much nutrients are released from logging residues during the first three years after clear-cutting and what is the role of ground vegetation in the retention of nutrients on site after clear-cutting. The study was conducted in eastern Finland in a Norway spruce dominated mixed forest, part of which was clear-cut and part left uncut. The decomposition of Norway spruce (*Picea abies* (L.) H. Karst.), Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth) logging residues i.e. foliage, fine roots (diameter ≤2 mm) and branches (diameter ≤1 cm), were studied using the litterbag method. Above- and below-ground biomass of the ground vegetation was sampled on one uncut plot and two clear-cut plots one year before and five years after clear-cutting.

In total, 33 % of the dry mass and C, 49 % of P, 90 % of K and 8 % of Ca were released from logging residues in three years, but there was no net release of N because more N accumulated in the roots and branches than was released from the foliage. The loss of mass, C, P and K was greatest during the first year, whereas there was no net release of Ca until the third year. Most of the released nutrients originated from the foliage. Total ground vegetation biomass and nutrient pools decreased after clear-cutting to one half or even lower, but returned to pre-cutting levels within 4-5 years, and the pools of P and K became even larger. In the first year after clear-cutting more N and Ca accumulated in the logging residues than were stored in the ground vegetation.

The results indicate that logging residues are a potential source of the elevated dissolved C and P, K and Ca observed in surface waters soon after clear-cutting, but are not a net source of N during the first three years. The ground vegetation is capable of taking up only a small fraction of the nutrients that are released from logging residues during the first two years after clear-cutting and the decomposing dead ground vegetation is a potential source of leached nutrients. The results suggest that nutrients released from logging residues are initially retained on site primarily through soil processes and microbial immobilization. Solely microbial immobilization in logging residues can initially play a more important role in the retention of N and Ca than the ground vegetation. Ground vegetation, however, recovers rapidly from clear-cutting and it becomes thereafter a significant nutrient sink.

Keywords: biomass, branches, foliage, nutrient release, nutrient retention, roots

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Joensuu, October 2005

Marjo Palviainen

LIST OF ORIGINAL ARTICLES

The thesis is based on the following articles, which are referred to in the text by their Roman numerals.

I. Palviainen, M., Finér, L., Kurka, A.-M., Mannerkoski, H., Piirainen, S. & Starr, M. 2004. Decomposition and nutrient release from logging residues after clear-cutting of mixed boreal forest. Plant and Soil 263: 53-67.

II. Palviainen, M., Finér, L., Kurka, A.-M., Mannerkoski, H., Piirainen, S. & Starr, M. 2004. Release of potassium, calcium, iron and aluminium from Norway spruce, Scots pine and silver birch logging residues. Plant and Soil 259: 123-136.

III. Palviainen, M., Finér, L., Mannerkoski, H., Piirainen, S. & Starr, M. 2005. Changes in the above- and below-ground biomass and nutrient pools of ground vegetation after clear-cutting of a mixed boreal forest. Plant and Soil (in print).

IV. Palviainen, M., Finér, L., Mannerkoski, H., Piirainen, S. & Starr, M. 2005. Responses of boreal forest ground vegetation species to clear-cutting – Aboveground biomass and nutrient contents during the first 7 years. Ecological Research (in print)

In studies I, II, III and IV, M. Palviainen carried out statistical analyses and was responsible for planning and writing the articles. In addition, M. Palviainen participated in nutrient analyses (I, II), sampling the ground vegetation and sorting the samples in the laboratory (III, IV). Co-authors provided the idea for the study, designed experiments and commented manuscripts.

CONTENTS

1. INTRODUCTION

1.1 Background

Decomposition of organic matter, mineral weathering, wet and dry deposition, nitrogen (N) fixation and root exudates are sources of nutrients in forest ecosystem (Likens and Bormann 1995). The nutrients can be taken up by vegetation, immobilized by microbes or retained in the soil by various adsorption processes such as ion exchange, complexation, precipitation and the formation of secondary minerals (Likens and Bormann 1995, White 1997). Nutrients can be lost from the system through leaching, gaseous emissions (i.e. volatilisation and denitrification) and biomass removal.

The annual deposition of nutrients and the rates of weathering and decomposition are low in Finnish forests compared to the values in central Europe (Järvinen and Vänni 1990, Berg et al. 1993, White and Blum 1995, Fisher and Binkley 2000, Hjellbrekke 2000, Ruoho-Airola et al. 2003). The input of N from biological fixation is reported to range from 0.3 kg ha^{-1} a^{-1} to 3.8 kg ha^{-1} a^{-1} in Fennoscandian coniferous forests (Granhall and Lindberg 1980, Rosén and Lindberg 1980). In undisturbed boreal forests, nutrients are effectively retained in the ecosystem, and leaching (Helmisaari and Mälkönen 1989, Piirainen et al. 1998, 2002a, Mattson et al. 2003, Finér et al. 2004) and gaseous losses (Paavolainen and Smolander 1998) are small. Forestry operations, especially clear-cutting, can cause considerable changes in nutrient pools and fluxes, however.

In Finland, 86 % of the land area is covered by forests and most of the forests are under timber production (Peltola 2004). The main tree species are Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst.) and birch (*Betula pendula* Roth, *Betula pubescens* Ehrh.). Annually thinnings are carried out on 300 000 - 400 000 ha and clear-cuttings on 100 000 – 150 000 ha, which correspond to 2-3 % of the total forest area. The nutrient losses caused by biomass removal vary depending on the harvesting method, tree species and the specific nutrients involved (Mälkönen 1975, 1976). Clear-cuttings are mostly done by removing only the stems with bark and leaving the stumps, roots, branches and foliage, which are referred to as logging residues, on the site. Efforts to increase the use of renewable forms of energy may result in an increase in whole-tree harvesting in the future. The removal of logging residues may acidify the soil (Staaf and Olsson 1991) and decrease tree growth (Egnell and Valinger 2003), soil nutrient pools (Bengtsson and Wikström 1993, Olsson et al. 1996), and the amount of soil organic matter, which may subsequently affect the temperature conditions, water-holding capacity and nutrient retention in the soil (Jurgensen et al. 1997).

Leaving logging residues on the site greatly increases the amount of decomposable material in the soil. The amount of logging residues produced depends on the tree species and developmental stage of the tree stand. The dry mass of Norway spruce tree tops is two times greater than that of Scots pine of similar height and diameter (Hakkila 1991), and the amount of above-ground residues remaining on site is generally from two to three times greater after clear-cutting a mature stand than after thinning a young stand (Hynynen 2001). The nutrient input derived from logging residues is several times greater than that from the annual litterfall, which contains only a few percent of the total amount of nutrients in the trees (Mälkönen 1974, Helmisaari 1995). In general, about 75, 80, 70 and 60 % of the standing tree biomass pools of N, phosphorus (P), potassium (K) and calcium (Ca), respectively, remain on site as logging residues after clear-cutting a mature Norway spruce forest (Nykvist 1971, Mälkönen 1975, Kubin 1977).

Clear-cutting results in marked changes in nutrient fluxes. Decomposition can be accelerated after clear-cutting because the soil temperature and moisture are increased as the shading effect of trees, the interception of water by the canopy and water uptake by the trees are reduced (Lundin 1979, Kubin and Kemppainen 1991). Increased decomposition of organic layer has been observed after clear-cutting in several forest ecosystems (Covington 1981, Jurgensen et al. 1997, Martin et al. 2002). Clear-cutting has also been found to enhance mineralization in the organic layer in Finnish forest soils (Smolander et al. 2001), but it is not clear whether the conditions caused by clear-cutting accelerate the decomposition of fresh logging residues. The deposition of inorganic N to the forest floor may be greater after clear-cutting because N is no longer retained in the canopy, whereas the deposition flux of carbon (C), K and Ca may decrease because leaching from the canopy ceases (Helmisaari and Mälkönen 1989, Piirainen et al. 2002b, 2004). The amounts of N fixed also probably change. Nitrogen fixation of feather mosses is lower in early than in late successional boreal forests (Zackrisson et al. 2004), but N fixation by bacteria living in decomposing wood (Granhall and Lindberg 1980, Jurgensen et al. 1984) may increase after clear-cutting because large amounts of woody debris are added to the soil. Nutrient uptake decreases because the trees are removed and the ground vegetation often at least partly dies as a result of clear-cutting (Atlegrim and Sjöberg 1996, Nykvist 1997).

Nutrient losses generally increase after clear-cutting. Clear-cutting may stimulate nitrification or denitrification, thus potentially increasing N losses to the atmosphere and the leaching of nitrate (NO_3^-) and base cations (Likens et al. 1969, Paavolainen and Smolander 1998). Furthermore, increased mineralization, reduced nutrient uptake and hydrological changes such as an elevated ground water table and increased water yield, runoff and peak flows increase the risk of nutrient leaching (Lundin 1979, Rosén 1984, Swank et al. 2001). Elevated C, N, P, K and Ca concentrations have been observed in soil solution (Nohrstedt et al. 1994, Smolander et al. 2001, Piirainen et al. 2002b, 2004) and in outlet streams (Grip 1982, Rosén et al. 1996, Ahtiainen and Huttunen 1999) after clear-cutting of boreal forests. Also NO_3^- concentrations in groundwater have increased after clear-cutting (Kubin 1998, Rusanen et al. 2004). Leaching deteriorates water quality, causes eutrophication of surface waters, and may decrease site productivity (Ahtiainen and Huttunen 1999, Grigal 2000). The initiation, magnitude and duration of increased leaching vary somewhat according to the catchment properties (e.g. Wiklander 1981, Lepistö et al. 1995). Leaching is usually greatest during the first years after clear-cutting and it can take nearly ten years or even longer until the nutrient concentrations in ground and surface waters return to pre-cutting levels (Wiklander 1981, Rosén et al. 1996, Kubin 1998, Ahtiainen and Huttunen 1999). Leached nutrients may originate from logging residues, the organic layer and/or dead ground vegetation. Also increased N deposition due to reduced canopy uptake may increase N leaching. Logging residues are considered to be the main source of leached nutrients, but the release of nutrients may sometimes occur with a time delay and N especially has been observed even to accumulate in decomposing logging residues (Barber and Van Lear 1984, Fahey et al. 1988, Hyvönen et al. 2000, Ouro et al. 2001).

The developing ground vegetation may play an important role in nutrient retention before stand re-establishment (Emmett et al. 1991a, Fahey et al. 1991a, Kimmins et al. 2002). The vegetation reduces nutrient losses directly by taking up nutrients and, indirectly, by decreasing the volume of water percolating down through the soil and the availability of N for nitrification or denitrification (Gholz et al. 1985). Tree seedlings can also act as a nutrient sink, but the biomass of the ground vegetation is often higher than that of the tree seedlings during the early successional stages (Bergquist et al. 1999, Staples et al. 1999). More nutrients are also needed to produce the amount of ground vegetation dry matter equivalent to that of tree seedlings

(Mälkönen 1974). In general, pioneer species also have a better ability to absorb available nutrients from the soil than tree seedlings (Hangs et al. 2003, Nilsson and Örlander 2003).

Little is known about the decomposition and nutrient dynamics of logging residues, the responses of ground vegetation to clear-cutting and the capacity of the ground vegetation to retain nutrients in boreal areas although these processes largely determine the amount and duration of leaching. Furthermore, no studies have been carried out in boreal forests, in which the amounts of nutrients that are released from logging residues, stored in the ground vegetation and leached, would have been quantified simultaneously in the same site.

1.2 Factors affecting the decomposition rate

Decomposition means the degradation of organic matter, as a result of which water, heat and mineral nutrients are released and the majority of the C is returned back to the atmosphere as CO_2 (Swift et al. 1979). Part of the carbon and other nutrients can be released as dissolved organic forms (Vestgarden 2001, Hafner et al. 2005). In boreal forests, the decomposition process is mainly carried out by fungi and bacteria (Persson et al. 1980), which produce degrading enzymes (Killham 1994). Soil animals mix decomposable material into the soil, regulate the structure and functioning of microbial communities, and fragment organic matter into small particles thereby increasing the surface area for microbes to attack (Setälä et al. 1988, Killham 1994). Physical processes also play an important role in decomposition (Berg and McClaugherty 2003). Part of the nutrients and soluble constituents are released by mechanical leaching, and wet-dry, freeze-thaw and hot-cold cycles fragment the decomposable material.

Water-soluble substances (e.g. sugars, fatty acids and amino acids) are decomposed first, followed by hemicelluloses, cellulose and finally lignin and lignified compounds (Berg and McClaugherty 2003). Nutrients can be released at a rate that is proportional to the mass loss, or even more rapidly if nutrient availability does not limit microbial activity and if the decomposable material is subjected to intense fragmentation and mechanical leaching (Laskowski et al. 1995, Berg and McClaugherty 2003). On the other hand, the nutrients limiting microbial activity are effectively immobilized and the absolute amount of certain nutrients can even increase during decomposition (Berg and Staaf 1981, Edmonds 1987, Fahey et al. 1991b).

The decomposition rate is determined by environmental conditions, the chemical composition of the material and decomposer community (Swift et al. 1979, Berg and McClaugherty 2003). Temperature and moisture have been shown to be the most important environmental factors controlling the decomposition rate in Fennoscandian boreal forests (e.g. Jansson and Berg 1985).

High concentrations of nutrients and soluble substances, low carbon/nutrient ratios (e.g. C/N, C/P) and low lignin concentrations enhance decomposition (Melillo et al. 1982, Johansson 1994, Silver and Miya 2001, Berg and McClaugherty 2003). The chemical composition differs between tree species and between foliage, root and wood material (Voipio and Laakso 1992, Johansson 1995, Berg and McClaugherty 2003). The decomposition of Scots pine, Norway spruce and silver birch foliage litter has been studied relatively extensively in Fennoscandian forests but less is known about the decomposition of the roots and branches of these species (Berg and McClaugherty 2003). Logging residues can decompose faster than litter (Lundmark-Thelin and Johansson 1997) because logging residues probably contain higher concentrations of nutrients than naturally formed litter due to that nutrients are translocated from dying parts to growing tissues before litter shedding (Helmisaari 1992). The decomposition and nutrient dynamics of the logging residues of the main tree species have so far been investigated only in a few studies in Fennoscandia (Staaf and Berg 1980, Lundmark-Thelin and Johansson 1997, Hyvönen et al. 2000).

Fine logging residues including foliage, fine roots and small branches are the probable source of leached nutrients soon after cutting because they are the most nutrient-rich parts of the trees (Mälkönen 1974, Kubin 1977) and decompose faster than coarse residues, i.e. stumps, coarse roots and thick branches (Fahey et al. 1988, Hyvönen et al. 2000). The decomposition of coarse residues takes several years or decades because their low concentrations of nutrients and soluble sugars, high C/N and C/P ratios, high lignin concentration and the small surface area to volume ratio associated with large diameter make them resistant to decomposition (Barber and Van Lear 1984, Mattson et al. 1987, Fahey et al. 1991b, Hyvönen et al. 2000, Berg and McClaugherty 2003).

The altered microclimate may have an effect on the decomposition rate after clear-cutting. The average air and soil temperatures are generally higher in the clear-cut area than in the forest because the amount of incoming solar radiation increases because there is no longer a canopy to absorb, emit and reflect radiant energy (Kubin and Kemppainen 1991, Keenan and Kimmins 1993). Removal of the tree canopy does not only increase the flux of net radiative heat transfer from the atmosphere to the soil during the day, but also increases the upward emission of long-wave thermal radiation from the vegetation and soil to the atmosphere at night (Hornbeck 1970). Therefore, the diurnal variation in temperatures is greater in the open area than in the forest (Kubin and Kemppainen 1991). The decreased interception increases the depth of the snow cover in clear-cut areas (Poikolainen and Kubin 1985) which, in turn, may increase soil temperatures and the wintertime decomposition rate. Soil moisture also can be higher in clear-cut areas than in forest because of the decreased interception and transpiration (Lundin 1979). On the other hand, the fluctuations of soil moisture are increased after clear-cutting and the organic layer and upper mineral soil can be temporarily drier in clear-cut areas than in undisturbed forest due to the increased evaporation caused by higher soil temperatures and wind speeds (Bååth 1980, Schwendenmann 2000, Redding et al. 2003). The environmental conditions in clear-cut areas may thus periodically be unfavourable to decomposers. Clear-cutting has been observed to change the decomposer community structure and decrease microbial biomass and enzyme activity, which may affect the decomposition rate (Huhta 1976, Niemelä and Sundman 1977, Bååth 1980, Siira-Pietikäinen et al. 2001, Hassett and Zak 2005).

It has generally been believed that increased temperature and moisture following clear-cutting accelerate decomposition (e.g. Witkamp 1971). However, decomposition rates have been reported to be faster (Klemmedson et al. 1985, Prescott et al. 1993), slower (Abbott and Crossley 1982, Blair and Crossley 1988, Yin et al. 1989, Cortina and Vallejo 1994, Prescott 1997) or the same (Will et al. 1983, Johansson and Grälls 1989, Hope et al. 2003) in clear-cut areas compared to undisturbed forest. Apparently the effects of clear-cutting on decomposition vary depending on the regional climatic variables, site properties and decomposable material (Kim et al. 1996, Moorhead et al. 1999, Prescott 2000). Furthermore, clear-cutting may have a different impact on the decomposition of foliage and branches than of roots because decomposition has been found to be slower at the soil surface but faster below the organic horizon in clear-cut areas than in the forest (Binkley 1984). The lack of knowledge about the effects of clear-cutting on the decomposition rate in boreal forests has restricted the development of accurate simulation models concerning the effects of harvesting on soil C storage (Liski et al. 1998).

1.3 Development of ground vegetation after clear-cutting

The ground vegetation plays an important role in the nutrient cycle of boreal forests because it consumes more nutrients per unit dry matter produced than the trees and accounts for a significant proportion of the annual stand litterfall (Mälkönen 1974, Helmisaari 1995). The importance of ground vegetation is emphasized after clear-cutting because it becomes the major living vegetation component when the trees are removed. Nutrient leaching has been shown to be considerably higher from clear-cut areas, that are treated with herbicides than from similar sites with intact vegetation (Likens et al. 1970), and the nutrient concentrations in the soil solution following harvesting have decreased concurrently with vegetation development (Stevens and Hornung 1990, Emmett et al. 1991b, Staaf and Olsson 1994, Örlander et al. 1996). The significance of the ground vegetation in nutrient retention after clear-cutting has mostly been studied in temperate forests (Likens et al. 1970, Stevens and Hornung 1990, Emmett et al. 1991a, Fahey et al. 1991a, Mou et al. 1993, Kimmins et al. 2002). In boreal forests, the biomass and nutrient pools of the ground vegetation following clear-cutting have been seldom reported because the effects have generally been studied from the species diversity viewpoint and the responses are described by changes in coverage, frequency and species number (Bråkenhielm and Liu 1998, Bergstedt and Milberg 2001, Jalonen and Vanha-Majamaa 2001). The few Fennoscandian studies that have followed changes in biomass (Olsson and Staaf 1995, Nykvist 1997) and nutrient pools (Nykvist 1977, Nilsson and Örlander 1999) of the ground vegetation after clear-cutting have not considered the below-ground parts, despite the fact that the majority of the ground vegetation biomass is in the roots (Havas and Kubin 1983).

The success and growth of the vegetation depends on many environmental factors and the optimum and tolerance ranges vary between species (Tamm 1953, Busby et al. 1978, Kellomäki and Hari 1976, Kellomäki et al. 1977). The availability of water and nutrients directly affects growth, whereas the effects of temperature and light takes place through their effects on the physiological processes. Temperature also affects indirectly by regulating the availability of water and nutrients. The tree stand, soil type, soil nutrient status, topography, elevation and latitude regulate the availability of these resources and largely determine the composition of the vegetation (Nieppola and Carleton 1991, Pitkänen 1997, Reinikainen et al. 2000).

Removal of the tree stand changes light conditions, microclimate and the availability of nutrients, which affect the biomass and species composition of the ground vegetation and ultimately nutrient uptake and retention. The responses of the ground vegetation depend on the site fertility and the intensity and timing of harvesting, vegetation changes being greatest and fastest in the most fertile sites (Salemaa and Jukola-Sulonen 1998). Furthermore, clear-cutting has a greater effect than other felling methods (Atlegrim and Sjöberg 1996, Bergstedt and Milberg 2001, Jalonen and Vanha-Majamaa 2001), and summer harvesting more of an impact than winter harvesting (Berger et al. 2004). Damage to the vegetation caused by the logging machinery and falling trees during logging operation, death of propagule sources, i.e. seeds, spores, seedlings, rootstocks and rhizomes (Jonsson 1993, Qi and Scarratt 1998), the disruption and compaction of the soil, altered microclimate (Keenan and Kimmins 1993) and covering by logging residues (Stevens and Hornung 1990, Fahey et al. 1991a, Olsson and Staaf 1995) can all have detrimental effects on the ground vegetation.

The coverage of feather mosses (*Pleurozium schreberi* Brid. and *Hylocomium splendens* (Hedw.) B. S. & G.) and ericaceous dwarf shrubs (*Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L.), that are the dominant ground vegetation species in Finnish forests (Reinikainen et al. 2000), has been shown to decrease considerably after clear-cutting (Atlegrim and Sjöberg 1996, Hannerz and Hånell 1997, Jalonen and Vanha-Majamaa 2001, Bergsted and Milberg

2001, Bock and Van Rees 2002, Fenton et al. 2003). These species are adapted to grow in shade and relatively constant moisture conditions, and they may suffer from the increased intensity of light, high near-ground temperatures, episodic drought and decreased air humidity in clear-cut areas (Tamm 1953, Kellomäki and Hari 1976, Kellomäki et al. 1977, Busby et al. 1978). In contrast, the coverage of grasses and herbs generally increases after clear-cutting (Reinikainen et al. 2000) and especially *Deschampsia flexuosa* (L.) Trin. and *Epilobium angustifolium* L. become abundant (Bergquist et al. 1999, Bergstedt and Milberg 2001) because they benefit from increased light and nutrient availability (Foggo 1989, Broderick 1990). Pioneer species in general can store nutrients effectively due to their rapid growth rate and high demand for nutrients (Marks and Bormann 1972, Boring et al. 1981, Kimmins et al. 2002). Little is known about how much nutrients are stored in the ground vegetation after clear-cutting in boreal forests, how rapidly suffering species will recover, or how different species contribute to nutrient retention.

1.4 Aims and hypotheses of the study

The main aim of this thesis was to study the role of decomposing logging residues and developing ground vegetation in nutrient dynamics after clear-cutting. The main hypotheses were that logging residues are a source of leached C, P, K and Ca during the first three years after clear-cutting and that the ground vegetation, especially pioneer species, play an important role in nutrient retention after clear-cutting. Because logging residues were known to have relatively high C/N ratios (Finér et al. 2003), N was expected at least initially to be immobilized in logging residues.

More specifically, the aims were:

1. to determine how much C, N, P, K and Ca are released from Norway spruce, Scots pine and silver birch logging residues (fine roots, foliage and small branches) during the first three years after clear-cutting of a Norway spruce dominated, mixed boreal forest in eastern Finland (I, II),
2. to study whether the decomposition is faster in a clear-cut area than in a mature forest (I, II),
3. to investigate the above- and below-ground biomass and nutrient pools of the ground vegetation during the first five years after clear-cutting (III),
4. to study the responses of the main ground vegetation species to clear-cutting during the first seven years (IV)
5. to assess the significance of ground vegetation in the retention of nutrients after clear-cutting (III, IV), and
6. to compare the amounts of nutrients that are released from logging residues to the amounts of nutrients that are simultaneously stored in the ground vegetation, leached and derived from deposition. The effect of logging residues removal on site nutrient status is also discussed.

This study is a part of the VALU-research project studying the effects of clear-cutting on water and nutrient fluxes in a boreal forest (Finér et al. 1997).

2. MATERIALS AND METHODS

2.1 Study site

Three permanent plots (50 m x 50 m) were established in a mixed coniferous forest located in the Kangasvaara catchment in eastern Finland (63° 51' N, 28° 58' E, 220 m a.s.l.). The site type was *Vaccinium-myrtillus*-type according to the Finnish site type classification (Cajander 1949). The average age of the stand in the three study plots was 140 years, and the stem volume was 260 m^3 ha^{-1}, of which 53 % was Norway spruce (*Picea abies* (L.) H. Karst.), 33 % Scots pine (*Pinus sylvestris* L.) and 14 % deciduous trees (mainly white and silver birch, *Betula pubescens* Ehrh., *B. pendula* Roth and some European aspen, *Populus tremula* L.). The number of stems per hectare (height > 1.3 m) was 1433, of which 75 % was spruce, 8 % pine and 17 % deciduous trees. The field layer vegetation was dominated by dwarf shrubs (*Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L.) and the bottom layer by feather mosses (*Pleurozium schreberi* Brid. and *Hylocomium splendens* (Hedw.) B. S. & G.) (III). The soil type was a Haplic podzol (FAO 1988) and the texture type sandy till. The average depths of the organic (O), eluvial (E) and illuvial (B) horizons were 3, 12 and 35 cm, respectively. The stone content (> 20 mm) of the upper 0.3 m layer of the soil, determined by the steel rod penetration method of Viro (see Tamminen and Starr 1994), was 0.28 m^3 m^{-3}. The underlying bedrock is granodiorite.

Clear-cutting (8.3 ha) was carried out in August-October 1996 with a mechanical harvester. Merchantable-sized (diameter > 8 cm) stems with bark were removed and the logging residues (stumps, roots, branches and foliage) were left on the site. Two of the plots were situated in the clear-cut area, whereas the third plot was left uncut to serve as a control. The clear-cut plots were located some 100 m from the forest edge and the uncut plot some 70 m from the clear-cut edge.

Automatic weather stations (CR 10, Campbell Scientific Ltd., UK) were set up in the uncut forest and clear-cut area close to the plots for continuous recording of air temperatures. Precipitation in the clear-cut area and stand throughfall in the uncut forest were collected using permanently open collectors (Piirainen et al. 2002a). The mean annual air temperature recorded in the uncut plot averaged 1.7 ºC and throughfall 484 mm during 1996-2003. In the clear-cut area the mean annual air temperature averaged 2.0 ºC during 1996-2003 and the bulk precipitation 546 mm. The average length of the growing season was 143 days and the effective temperature sum 1037 ºC (the sum of (T_d - 5), where T_d is daily mean temperature exceeding + 5 ºC during the growing season). The long-term (1960-1990) mean annual temperature for the area is 1.4 ºC, temperature sum 1055 ºC and precipitation 540 mm (Climatological Statistics…1991).

The nutrient pools of the tree stand and soil before clear-cutting (Piirainen 2002, Finér et al. 2003) and nutrient fluxes including deposition, litterfall and leaching below the O-, E-, and B- horizons both before and after clear-cutting (Piirainen et al. 1998, Piirainen 2002, Piirainen et al. 2002a, 2002b, 2004) have been determined in this same study site. A detailed description of the study area is presented by Finér et al. (1997).

2.2 Decomposition experiment

Decomposition of Norway spruce, Scots pine and silver birch fine roots (diameter ≤ 2 mm), branches (diameter ≤ 10 mm) and foliage (I, II) was determined by measuring the mass loss with the litterbag method. The samples were air-dried (20 ºC) and 2 g of spruce and pine needles, 0.5 g of birch leaves, 1 g of roots and 5 g of branches, was placed in separate nylon bags (mesh size 0.5 x 0.5 mm for spruce needles and 1 x 1 mm for other fractions).

One objective was to test whether clear-cutting increases the decomposition rate. Due to the important effect of substrate chemical composition on the decomposition rate, logging residues were used as a standard material and they were also placed in the uncut forest. Ten experimental blocks (2 m x 2 m) were established in the forest plot and in one clear-cut plot. Six bags of each logging residue fraction were randomly placed about 20 cm apart within each block. The bags containing foliage and branches were placed to the surface of the forest floor, whereas those containing roots were buried under the organic layer. The experiment started on 4-5 June 1997 and the retrieval of the bags took place annually on 4-5 June for three successive years. On each sampling occasion two randomly chosen bags of each logging residue fraction from each of the 10 blocks per plot were retrieved. The exterior of the litterbags was carefully cleaned with a brush, any roots growing into the bags were removed, the bags were air-dried (20 ºC), weighed and subsamples were taken for dry mass determination (105 ºC for 24 h).

2.3 Sampling the ground vegetation

Ground vegetation biomass sampling was carried out in mid-July during 1996-2003 on all three plots. Mosses, field layer and roots (III) were sampled in the uncut plot during 1996-2001 and in the clear-cut plots one year before (1996) and five years after clear-cutting (1997-2001). The field layer included dwarf shrubs, grasses, herbs and tree seedlings up to a height of 0.5 m. The different moss and field layer species (IV) were sampled in the uncut plot during 1996-2003 and in the clear-cut plots one year before (1996) and seven years after clear-cutting (1997-2003).

The above-ground parts of the ground vegetation were harvested each year from 20 quadrats (0.5 m x 0.5 m) located systematically along the sides of each of the plots. The biomass of roots and rhizomes (later included in the term roots) was determined by coring (III). Cylindrical cores from the organic horizon (core diameter 137 mm) and from the upper mineral soil layer (core diameter 35 mm) from depths of 0-5 cm and 5-20 cm were systematically taken from each quadrat after sampling the above-ground parts of the vegetation. The sampling depth did not exceed 20 cm because the majority of the roots of the ground vegetation and trees occur in the organic layer and the upper mineral soil (e.g. Makkonen and Helmisaari 1998, Helmisaari and Hallbäcken 1999). The samples were put into plastic bags and stored in a freezer (-18 °C) until further preparation.

In the laboratory, the ground vegetation was divided into three compartments: mosses, field layer and roots. Only living parts were included in the study.

Mosses were further separated into four species groups: 1) *Pleurozium schreberi* Brid., 2) *Hylocomium splendens* (Hedw.) B. S. & G., 3) *Dicranum* sp., and 4) other species. The group of other species consisted mainly of *Polytrichum commune* Hedw., *Ptilium crista-castrensis* Hedw. and *Aulacomnium palustre* (Hedw.) Schwaegr.

The field layer was separated into five species groups: 1) *Vaccinium myrtillus* L., 2) *Vaccinium vitis-idaea* L., 3) *Deschampsia flexuosa* (L.) Trin., 4) *Epilobium angustifolium* L., and 5) other species. Other species were mainly *Melampyrum pratense* L., *Linnaea borealis* L., *Rubus saxatilis* L., *Convallaria majalis* L., *Solidago virgaurea* L., and tree seedlings (*Juniperus communis* L., *Picea abies* (L.) H. Karst. and *Sorbus aucuparia* L.).

The ground vegetation roots were separated from the soil cores by hand, mineral particles attached to the roots were removed with a brush, and the roots were divided into three diameter classes: < 1 mm, 1-2 mm and 2-5 mm. The roots of the ground vegetation were separated from the trees roots on the basis of their morphology and colour.

The samples were dried in ventilated ovens (60 °C, 24 h) and weighed. Subsamples were taken for dry mass determination (at 105 °C, 24 h) and the biomass was calculated as kg ha^{-1}. Stoniness was taken into account in the root biomass calculations.

2.4 Nutrient analyses

The contents of the litterbags and ground vegetation samples were milled before nutrient analyses. Nitrogen concentrations were determined from a micro-Kjeldahl digestion (ISO 7150/1 1984) with a spectrophotometer (Perkin-Elmer Lambda 11), and the concentrations of P, K and Ca were determined from a HNO_3-H_2O_2 digestion (Halonen et al. 1983) by inductively coupled plasma atomic emission spectrophotometer (ARL 3580 OES). Carbon concentrations were determined from the logging residues using a CHN-analyzer (Carlo-Erba NA 1500). The C concentration of the ground vegetation was assumed to be 50 % of dry mass.

2.5 Calculations and statistical analyses

The biomass of different tree compartments (kg ha^{-1}) was estimated by using allometric functions. The breast height diameter, height and crown length of all living trees (height > 1.3 m) on the three study plots were measured in September 1992 and again in July-August 1996 (Finér et al. 2003). Based on the distribution of breast height diameter values, sample trees were felled in connection with clear-cutting on the two clear-cut plots. The biomass of stem wood, stem bark, foliage and branches (kg ha^{-1}) was estimated by applying allometric functions developed by Finér et al. (2003). The stump and coarse root biomass of pine and spruce were calculated using the allometric functions presented by Marklund (1988) and those of birch with functions presented by Finér (1989). The biomass of fine roots (< 2 mm) was determined by the core method (Finér et al. 2003). Derivation of the allometric biomass functions and calculation of biomass components at the stand-level are described in detail by Finér (1989) and Finér et al. (2003).

Nutrient amounts in the different tree compartments and ground vegetation were calculated by multiplying the dry masses by the corresponding nutrient concentrations. The results from the litterbag study (i.e. remaining dry mass and the amount of nutrients as % of initial) were used to calculate the mass loss and release of nutrients from logging residues at the stand level (kg ha^{-1}).

Since there were no replicates at the treatment level (clear-cut and uncut forest), statistically any differences between the clear-cut and forested plot cannot be attributed to the effects of clear-cutting alone because inherent differences between the locations on which the plots were established can confound treatment effects (Hurlbert 1984). Taking into consideration that before clear-cutting site type, tree stand (Finér et al. 2003), ground vegetation (III) soil properties (Piirainen et al. 2002a, 2002b, 2004) and climate conditions (III) were similar at the plots before clear-cutting it is very probable that the observed differences are treatment caused effects rather than pre-existing differences among study plots. The differences between the plots were thus considered to be mainly due to clear-cutting.

Differences in the decomposition of logging residues and the biomass of ground vegetation between the plots were tested by a linear mixed model procedure, which takes into account the dependence (i.e. temporal and spatial correlation) between different observations (Littell et al. 1996). The model in the logging residue studies was (I, II):

$$y_{ijkl} = m + A_i + B_k + (AB)_{ik} + C_l + (BC)_{kl} + (ABC)_{ikl} + D_{jk} + (AD)_{ijk} + e_{ijkl} \qquad (1)$$

where y_{ijkl} is the remaining mass or nutrient content as % of initial amount, m the overall mean, A_i is the fixed effect of logging residue fraction (i.e. foliage, roots and branches of different species) $i = 1,\ldots 9$, B_k = the fixed effect of plot $k = 1, 2$ (i.e. treatment), $(AB)_{ik}$ = the fixed effect of interaction between logging residue fraction and plot, C_l = the fixed effect of year $l = 1,\ldots 4$, $(BC)_{kl}$ = the fixed effect of interaction between plot and year, $(ABC)_{ikl}$ = the fixed effect of interactions between logging residue fraction, plot and year, D_{jk} = the random effect of block j on the plot k, $(AD)_{ijk}$ = the random effect of interaction between logging residue fraction and block on the plot and e_{ijkl} = the random error.

Following model was used in the ground vegetation studies (III, IV):

$$y_{ij} = m + A_i + B_j + (AB)_{ij} + e_{ij} \qquad (2)$$

Where y_{ij} = is biomass, m the overall mean, A_i the fixed effect of plot $i = 1, 2, 3$, B_j = the fixed effect of year $j = 1,\ldots 6$ (III) and $j = 1,\ldots 8$ (IV), $(AB)_{ij}$ = the fixed effect of interaction between plot and year and e_{ij} = the random error.

The Bonferroni test was used to determine statistical significance for multiple comparisons in all the analyses. Statistical analyses of decomposition experiment (I, II) were performed with SAS (SAS® for Windows 6.12, 1997), and of the ground vegetation data (III, IV) with SPSS (SPSS for Windows, Version 12.0, SPSS 2002).

3. RESULTS

3.1 Decomposition of logging residues

Among the fine logging residue fractions studied, foliage decomposed the fastest, followed by fine roots and branches (Table 1). The mass loss of foliage differed significantly ($p < 0.001$) between all tree species. Pine and birch roots decomposed faster ($p < 0.001$) than spruce roots, but the difference between pine and birch roots was not significant. Pine branches decomposed faster ($p < 0.001$) than spruce and birch branches.

The release of C followed the mass loss. Nitrogen accumulated in the pine and birch roots and conifer branches during decomposition but released from other fractions. Phosphorus was relatively rapidly released from all logging residue fractions, except from pine branches. The majority of K was released, and most of it already during the first year (II). Calcium was released from roots and foliage but accumulated in branches.

In total, 33 % of the dry mass and C, 49 % of P, 90 % of K and 8 % of Ca was released in three years (I, II). There was no net release of N because more N accumulated in the roots and branches than was released from the foliage. Foliage contained the greatest amounts of N, P, and K, whereas branches contained most of the C and Ca. The majority of the released nutrients originated from the foliage.

Table 1. Remaining mass and the amount of carbon, nitrogen, phosphorus, potassium and calcium in different logging residue fractions as % of the initial amount after three years of decomposition at the clear-cut plot (mean ± SE, n = 10).

Fraction	Mass	C	N	P	K	Ca
Foliage						
Pine	35.4 (2.6)	34.9 (2.5)	91.6 (7.6)	48.2 (3.5)	6.1 (0.7)	40.8 (3.6)
Spruce	60.2 (2.3)	54.3 (2.0)	99.8 (3.5)	35.5 (2.6)	7.5 (0.6)	84.5 (3.6)
Birch	11.2 (2.8)	11.0 (2.8)	17.1 (6.6)	7.6 (2.5)	1.3 (0.4)	4.8 (1.5)
Roots						
Pine	48.4 (3.4)	54.4 (3.9)	127.0 (11.8)	77.6 (5.7)	9.1 (1.5)	57.7 (7.1)
Spruce	69.8 (2.3)	73.9 (2.7)	81.1 (14.7)	74.2 (5.3)	15.6 (1.8)	58.2 (8.0)
Birch	54.7 (2.9)	60.8 (3.5)	117.0 (9.2)	55.1 (3.9)	14.6 (1.7)	49.3 (6.9)
Branches						
Pine	70.2 (1.1)	74.4 (1.3)	162.9 (15.1)	106.9 (6.4)	11.4 (1.7)	111.5 (4.9)
Spruce	79.6 (1.1)	80.9 (1.4)	119.1 (8.6)	60.8 (4.2)	14.3 (1.7)	117.9 (7.6)
Birch	82.8 (1.2)	86.6 (1.2)	92.1 (8.9)	42.8 (2.2)	14.8 (0.8)	105.4 (4.3)

In general, mass loss was relatively similar in the clear-cut plot than in the uncut plot or even significantly slower, in the case of spruce needles and birch roots (I). Birch leaves were the only fraction that decomposed faster in the clear-cut plot than in the forest plot. However, the release of some nutrients were accelerated in the clear-cut plot: C was released significantly faster from birch leaves (I), Ca from pine and spruce roots and K from foliage and branches of all tree species (II) in the clear-cut plot than in the forest plot.

3.2 Changes in the biomass and nutrient pools of the ground vegetation after clear-cutting

The biomass of the ground vegetation was 5307 kg ha^{-1} before clear-cutting and contained 46.9 kg N ha^{-1}, 4.1 kg P ha^{-1}, 16.2 kg K ha^{-1} and 13.9 kg Ca ha^{-1} (III). The biomass and nutrient pools first clearly decreased after clear-cutting, being lowest in the second year, the biomass decreasing by 46-65 % in the cut plots. The nutrient pools decreased as follows: N 54-72 %, P 36-68 %, K 51-71 % and Ca 57-74 %. Mosses were at first virtually eliminated after clear-cutting (> 90 % decrease in biomass) and their biomass remained significantly lower ($p < 0.01$) in the clear-cut plots than in the uncut plot throughout the whole seven-year period (III, IV). Especially feather mosses, that were dominant species in the mature forest, suffered from clear-cutting. *P. schreberi* recovered within five years, but the biomass of *H. splendens* was still significantly lower ($p < 0.01$) in the clear-cut plots than in the uncut plot seven years after clear-cutting.

Also the field layer biomass decreased initially after clear-cutting because the biomass of *V. myrtillus* and *V. vitis-idaea*, that were dominant species in the uncut forest, declined. The biomass of *V. vitis-idaea* returned to the pre-cutting level in three years and that of *V. myrtillus* in four years. The biomass of *D. flexuosa* increased considerably after clear-cutting and *E. angustifolium* dispersed to the clear-cut plots 3-5 years after clear-cutting. Consequently, the field layer biomass returned to the initial level in three years and increased more than two-fold thereafter (III, IV).

A considerable proportion (> 70 %) of the field layer biomass was in the roots. After clear-cutting the root biomass decreased somewhat, the roots became more concentrated in the organic layer and more biomass was accumulated in the above- than below-ground parts.

Total biomass and nutrient pools of the ground vegetation returned to the pre-cutting level in five years and the pools of P and K became even larger. *D. flexuosa* and *E. angustifolium* contributed to nutrient retention due not only to their biomasses but also because of their high nutrient concentrations. *E. angustifolium* had higher concentrations of all the studied elements compared to the dwarf shrubs; the concentrations of N, P and K were 2-3 times higher (IV). *D. flexuosa* also had higher P and K concentrations than dwarf shrubs, but N concentrations were similar and Ca concentrations considerably lower. The importance of mosses as a nutrient sink decreased after clear-cutting but *V. myrtillus*, although reduced after cutting, maintained a relatively high proportion of the ground vegetation biomass and nutrient contents.

4. DISCUSSION

4.1 Logging residues and ground vegetation in nutrient dynamics of a clear-cut area

4.1.1 Nutrient pools and fluxes before clear-cutting

The biomass and nutrient pools of the ground vegetation before clear-cutting (Figure 1) were within the range reported for Norway spruce and Scots pine dominated forests in Fennoscandia (Mälkönen 1974, Nykvist 1977, Havas and Kubin 1983, Mäkipää 1994, Helmisaari 1995, Makkonen and Helmisaari 2001). The C, N, P, K and Ca pools of the ground vegetation were relatively small (≤ 2 %) compared to total ecosystem pools (soil + tree stand + ground vegetation). The annual deposition of nutrients in the study site was typical for this region and, as usual, low in comparison to levels in central Europe and southern Finland (Järvinen and Vänni 1990, Hjellbrekke 2000, Ruoho-Airola et al. 2003). Nutrient pools in the soil, the amount of nutrients in litterfall and nutrient leaching corresponded to values reported for coniferous forests in Fennoscandia (Helmisaari and Mälkönen 1989, Helmisaari 1995, Liski and Westman 1995, Olsson et al. 1996, Ilvesniemi et al. 2002).

4.1.2 Nutrient content and decomposition of logging residues

More biomass and C were removed from the site with stems and bark than was left on the site in the form of logging residues (Figure 2). A relatively large proportion of C (40 %) and most of the N (76 %), P (82 %), K (96 %) and Ca (60 %) that was bound in the tree biomass remained on the site in the logging residues. The nutrient input caused by logging residues was enormous compared to the annual litterfall in the uncut forest (Figure 1). The amount of C in the logging residues was 45-fold and that of other nutrients about 20- to 30-fold compared to the annual litterfall in the forest before clear-cutting. The amounts of C, N, P, K and Ca in logging residues (coarse and fine) corresponded to 94 %, 18 %, 6 %, 26 % and 17 %, respectively, of the corresponding amounts in the soil (Figures 1 and 2). The removal of logging residues would thus substantially reduce the N, K and Ca stocks at the site. Compared to the soil available pools, logging residues contained only slightly more P but about two times that much K and Ca than the soil.

Deposition alone can compensate for the losses of N, P and K caused by stem harvesting during a 100-year rotation but is insufficient to compensate for the Ca losses in this study site

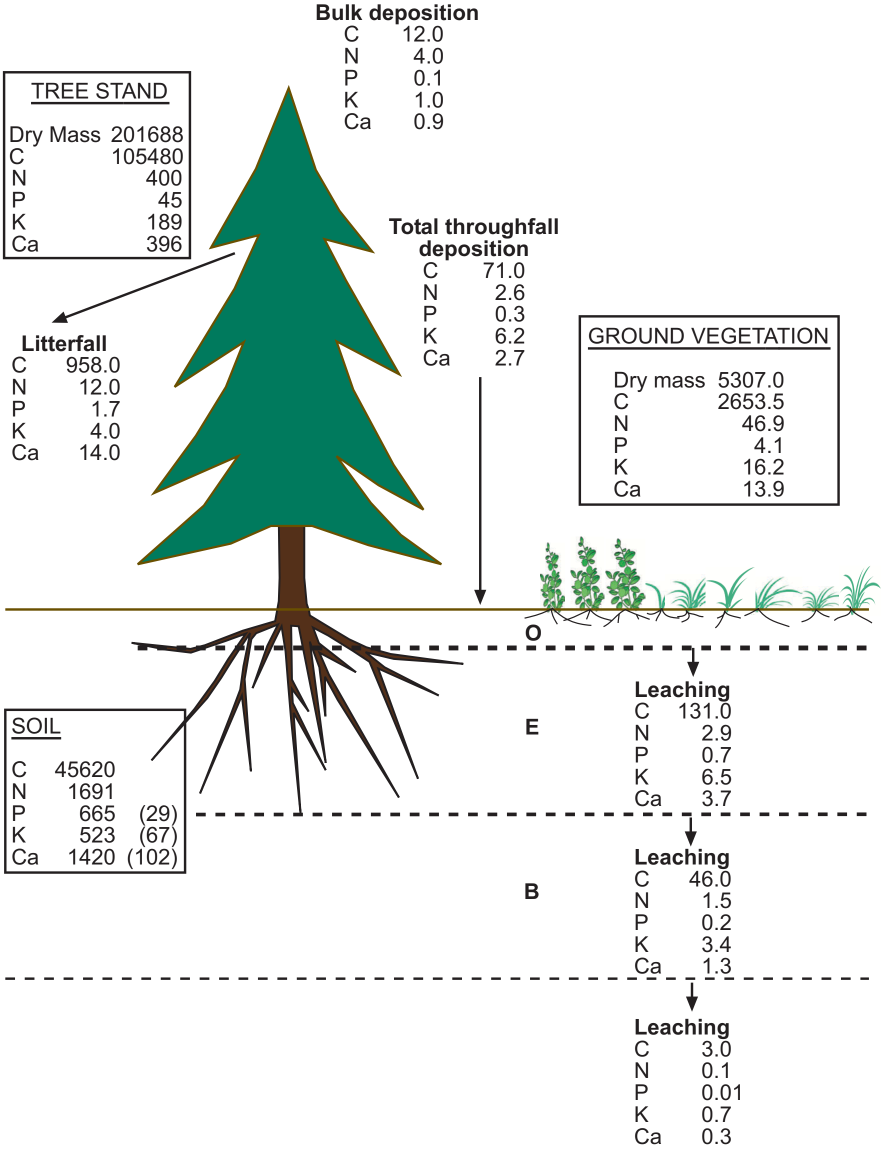

Figure 1. The amount of C, N, P, K and Ca (kg ha^{-1}) in the above- and below-ground parts of the trees and ground vegetation (Paper III) and in the soil to a depth of 35 cm (Piirainen 2002), and inputs (kg ha^{-1} a^{-1}) from litterfall and from bulk and total throughfall deposition (throughfall and stemflow) and output (kg ha^{-1} a^{-1}) through leaching before clear-cutting (Piirainen et al. 1998, Piirainen 2002, Piirainen et al. 2002a). The term leaching is used to mean the output of solutes in the percolate from below a soil horizon which exceeds the input to that horizon (O-, E- and B-horizons). Nutrient fluxes are average values for the years 1993-1996. Soil C and N concentrations were determined using a LECO CNH-600 analyser, soil P, K and Ca from the O-horizon from a HNO_3-H_2O_2 digest, and from the E- and B-horizons from an *Aqua regia* (HNO_3+HCl) digest by ICP emission spectrometry (TJA Iris Advantage), and soil available P, K and Ca pools (kg ha^{-1}, presented in parenthesis) from a NH_4Ac (pH 4.65) extraction by flame atomic absorption spectrometry (Perkin Elmer 5000).

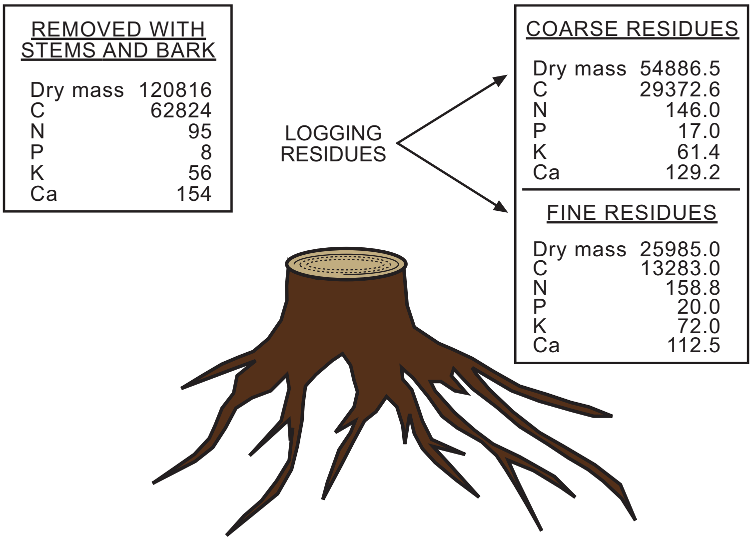

Figure 2. Dry mass and the amount of C, N, P, K, and Ca (kg ha^{-1}) in the removed stems and bark and in the fine and coarse logging residues. The fine residues include foliage, roots (diameter ≤ 2 mm) and branches (diameter ≤ 1 cm) and the coarse residues stumps, coarse roots (diameter > 2 mm) and branches (diameter > 1 cm).

(Figures 2 and 3). Whole-tree harvesting (the removal of above-ground parts) would have lead to 1.3, 2.8, 3.5, 2.3 and 1.9 times greater C, N, P, K and Ca losses, respectively, compared to stem only harvesting. This is in agreement with the findings of Mälkönen (1975, 1976) that, among the macronutrients, the loss of P is proportionally greatest in pine and spruce forests when whole-tree harvesting is compared to stem only harvesting. Complete-tree harvesting (the removal of above-ground parts, stumps and coarse roots) would have removed 1.6, 3.9, 5.0, 3.1 and 2.5 times more C, N, P, K, and Ca, respectively, than stem only clear-cutting. The loss of N caused by complete-tree harvesting (371.0 kg ha^{-1}) and whole-tree harvesting (267.3 kg ha^{-1}) exceeds the replacement from the atmosphere during a 100-year rotation (250 kg ha^{-1}) at this site (calculation based on the average N deposition for the years 1997-1999). If the foliage is left on the site and only stems and branches are removed, deposition could replace the N losses (186.6 kg ha^{-1}). Leaving the foliage at the site and the N input from deposition are, however, not sufficient to replace the nutrient losses caused by removal of the stems, branches, stumps and coarse roots (290.3 kg ha^{-1}). Removal of logging residues may thus results in an appreciable loss of N from the ecosystem. In reality, the nutrient losses would not probably be so great because, in practice, about 60-80 % of the crown mass is usually removed in whole-tree harvesting (Hakkila 2002). In order to obtain better estimates of the N replacement after harvesting, the input from N fixation should be known.

The observed mass losses (I) were comparable to those reported for Scots pine and Norway spruce needles and branches after 3-4 years following clear-cutting in Sweden (Lundmark-Thelin and Johansson 1997, Hyvönen et al. 2000). The mass losses of roots were also close to the values reported earlier for root litters of the studied species (Berg 1984, Johansson 1984, Lõhmus and Ivask 1995). The differences in mass loss between fractions (foliage, roots, branches) and between species (pine, spruce and birch) can be attributed to differences in their

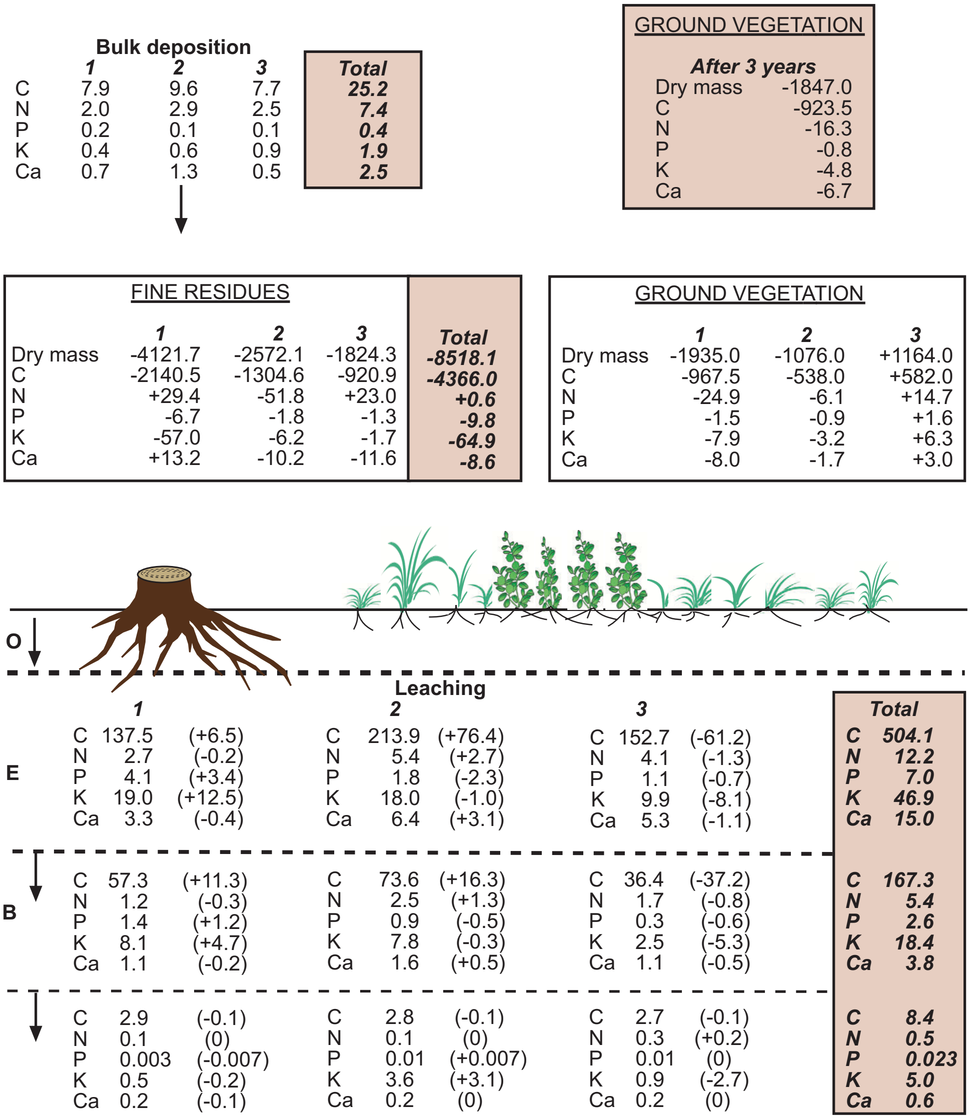

Figure 3. Bulk deposition and leaching of nutrients (kg ha^{-1} a^{-1}) below O-, E-, and B-horizons in the first, second and third year after clear-cutting, and total leaching and deposition during three years (Piirainen 2002, Piirainen et al. 2002b, 2004). Changes in the dry mass and nutrient contents of logging residues and ground vegetation (kg ha^{-1}), and the amount of leaching (kg ha^{-1}) in the first, second and third year after clear-cutting compared to the previous-year values (minus signs indicate a decrease and plus signs an increase). Total amount of released (-) or accumulated (+) nutrients in logging residues during three years compared to the initial amount and the biomass and nutrient pools of ground vegetation compared to the pre-cutting values three years after clear-cutting.

chemical composition and physical structure (I, II, Mikola 1954, Johansson 1984, Voipio and Laakso 1992, Berg and McClaugherty 2003).

There was no net release of N from logging residues during the first year after clear-cutting (Figure 3). A small release occurred during the second year, but N again accumulated in the third year. The mass loss and the release of C, P and K from logging residues were the greatest during the first year. The net release of Ca did not occur until the third year. Although the release of Ca occurred in the second year, the amount of Ca in the logging residues was still higher than the initial amount because external Ca accumulated in the first year.

The accumulation of N and Ca in logging residues, especially in branches, has been observed in several studies (Barber and Van Lear 1984, Fahey et al. 1991b, Carlyle et al. 1998, Hyvönen et al. 2000, Ouro et al. 2001). Accumulation indicates that nutrient concentrations in the decomposing material were below the requirements of decomposers (Berg and Staaf 1981). Isotope experiments have indicated that, at the same time as nutrients are released, external nutrients are incorporated into the decomposing litter (Berg 1988, Lindahl et al. 2001). Basically the increase in nutrient content may be due to the presence of fungal hyphae, but experiments have shown that the fungal biomass alone is not great enough to explain the observed increase in nutrient contents (Berg and Söderström 1979, Fahey 1983). The translocation of nutrients into decomposing material from the forest floor by fungal hyphae (Chadwick et al. 1998, Lindahl et al. 2001), N fixation (Granhall and Lindberg 1980, Jurgensen et al. 1984) and the nutrient supply from wet and dry deposition (Rosén and Lundmark-Thelin 1987, Emmett et al. 1991b) may have increased the nutrient content in logging residues.

Carbon is a structural component of plants and its release is closely related to mass loss (Berg and McClaugherty 2003), whereas P and especially K are generally rapidly released from finest logging residue fractions (Staaf and Berg 1980, Lundmark-Thelin and Johansson 1997, Hyvönen et al. 2000). In general, 80-90 % of the K has been found to be released from conifer logging residues already during the first year after clear-cutting (Barber and Van Lear 1984, Fahey et al. 1988, Fahey et al. 1991b, Titus and Malcolm 1999). The rapid release of K is largely due to that it presents in plants as water-soluble salts (Salisbury and Ross 1985) and thus easily released by leaching without microbial activity (Tukey 1970, Laskowski et al. 1995).

In Finnish forest soils, weathering is estimated to release about 0.02, 1.0 and 3.0 kg ha^{-1} a^{-1} of P, K and Ca, respectively (Starr et al. 1998, Fisher and Binkley 2000). It can therefore be assumed that a considerably larger amount of P and K, but probably a slightly smaller amount of Ca, was released from logging residues in the three years (Figure 3) compared to the inputs received from deposition and weathering during this period.

4.1.3 Development of ground vegetation and its role in the retention of nutrients after clear-cutting

In addition to logging residues, dead ground vegetation increased the amount of decomposable material in the soil. The amount of nutrients stored in the ground vegetation decreased during the first two years after cutting as follows: 1505.5 kg ha^{-1} for C, 31.0 kg ha^{-1} for N, 2.4 kg ha^{-1} for P, 11.1 kg ha^{-1} for K and 9.7 kg ha^{-1} for Ca. This nutrient input was small ($\leq$ 10 %) compared to the amounts of nutrients that were added to the soil in coarse and fine logging residues, but corresponded to 20 % of the amount of N and 10-15 % of the amounts of other nutrients that were added to the soil in fine residues. It should be noted however, that ground vegetation can have a relatively large impact on short-term nutrient fluxes after clear-cutting because dead ground vegetation decomposes faster than tree compartments (Mikola 1954, Johansson 1993).

Part of the ground vegetation probably died during the logging operation after which the high light intensity, temporary drought stress, soil compaction and logging residues may have had a negative effect on growth and survival (Tamm 1953, Kellomäki and Saastamoinen 1975, Busby et al. 1978, Keenan and Kimmins 1993, Olsson and Staaf 1995, Atlegrim and Sjöberg 1996). The field layer vegetation recovered fairly soon compared to mosses (III, IV). Conceivably, the disruption of mosses after clear-cutting has improved the germination of vascular plants. The biomass of dwarf shrubs returned to the pre-cutting levels relatively fast. Dwarf shrubs can effectively regenerate from rhizomes and are probably rapidly capable of replacing the biomass that was destroyed during harvesting because they have been shown to recover rapidly also from frost or herbivory caused damages (Tolvanen 1997, Tolvanen and Laine 1997). *D. flexuosa* in turn grows rapidly when the light and nutrient availability improves (Foggo 1989) and its flowering and seedling production are abundant in open areas (Scurfield 1954). After 3-5 years also *E. angustifolium* dispersed to the clear-cut plots but did not reach a very high biomass (IV). *E. angustifolium* is considered as a nitrogen indicator species (Bråkenhielm and Liu 1998), and perhaps it did not appear on the study plots until 3-5 years after clear-cutting because there was no net release of N from the logging residues during the first three years after cutting (I).

The shift in biomass allocation from roots to above-ground parts and concentration of the roots in more superficial soil layers after clear-cutting (III) were probably due to changes in species composition (IV). It is known that grasses and herbs at least have more superficial roots than dwarf shrubs (Taskinen et al. 2003).

The biomass and nutrient pools returned to pre-cutting levels in five years and the pools of P and K became even greater (III). The increase in the P and K pools was proportionally greater than that of the biomass. This was due to increase in the biomass of *E. angustifolium* and *D. flexuosa* which had high concentrations of P and K in their tissues (IV). The amounts of nutrients accumulated in the above-ground parts of the ground vegetation after clear-cutting correspond well with those reported for a Norway spruce stand in northern Sweden (Nykvist 1977). In more southerly Norway spruce forests, the development of ground vegetation after clear-cutting has been found to be faster and the amounts of accumulated nutrients greater (Nykvist 1977, Örlander et al. 1996, Nilsson and Örlander 1999, Ring et al. 2003) than in this study site. Part of the nutrients are only temporarily stored in the ground vegetation because a relatively large proportion of the annual ground vegetation production returns to the soil as litterfall in the autumn (Mälkönen 1974). After clear-cutting the ground vegetation recycles nutrients at a faster rate compared to the ground vegetation of old-growth forest because a higher proportion of the annual production is lost as litterfall each year because the proportion of mosses and dwarf shrubs out of the biomass is decreased and that of grasses and herbs increased (Mälkönen 1974).

A decrease in ground vegetation biomass during the first two years after clear-cutting reduces nutrient uptake and potential retention in the system, which may increase nutrient leaching. Furthermore, the observed reduction in rooting depth may promote leaching from deeper soil layers, and decomposing dead ground vegetation can act as a source of leached nutrients.

Nutrient uptake by ground vegetation after clear-cutting was estimated (Table 2) by using the annual biomass production values reported by Tamm (1953) and Mälkönen (1974). It can be seen that the majority of nutrients taken up is initially used for the biomass production of roots, mosses and *V. myrtillus*, but the importance of grasses and herbs in nutrient uptake increases with time. The calculations indicate that the ground vegetation is capable of taking up only a small fraction of the nutrients that are released from logging residues during the first two years after clear-cutting (Figure 3). In the third year the ground vegetation can take up all P and K that are released from logging residues and received from deposition but is not able to utilise all the released Ca. The results suggest that nutrients released from logging residues are initially retained primarily through soil processes and microbial immobilization. In the first year after clear-cutting more N (29.4 kg ha^{-1}) and Ca (13.2 kg ha^{-1}) accumulated in the logging residues than were stored in the ground vegetation (22 kg N ha^{-1} and 5.9 kg Ca ha^{-1}), indicating that microbial immobilization in logging residues at first played a more important role in the retention of N and Ca than the ground vegetation. From the third year onwards, the ground vegetation becomes a significant nutrient sink. In the fifth year after clear-cutting, nutrient uptake by ground vegetation (22.1 kg N ha^{-1}, 2.6 kg P ha^{-1}, 14.2 kg K ha^{-1} and 6.2 kg Ca ha^{-1}) is the same order of magnitude as the nutrient uptake by trees in this study site before clear-cutting (Piirainen 2002).

4.1.4 Relationship of decomposing logging residues and developing ground vegetation to nutrient leaching

Considerably more C was released from logging residues than was leached down through the soil horizons (Figure 3). Furthermore, the mineral soil C pool increased only by 112 kg ha^{-1} after clear-cutting over the three-year study period in this same study plot (Piirainen 2002b) indicating that the majority of the released C was lost to the atmosphere as CO_2. Nitrogen and Ca were not released from logging residues in the first year and the leaching of N and Ca did not increase either. Although there was no net release of N from logging residues during the third year, increased N leaching was observed below the organic horizon. Similarly, in the second year there was increased Ca leaching although no net release of Ca from logging residues occurred, indicating that N and Ca must also have been released from dead ground vegetation, the organic layer and/or coarse logging residues. Several studies have indicated that, during the first few years after clear-cutting, N is not released from logging residues but is leached from the organic layer (Covington 1981, Rosén and Lundmark-Thelin 1987, Emmett et al. 1991b, Stevens et al. 1995). Presumably, dead ground vegetation was also a source of leached nutrients (Mikola 1954, Johansson 1993), but it is unlikely that coarse residues would have been N and Ca sources because they decompose slowly and N and Ca are generally accumulated rather than released from coarse roots and branches during the initial stages of decomposition (Edmonds 1987, Fahey et al. 1988, Scheu and Schauermann 1994, Hyvönen et al. 2000). Increased leaching of N has also been observed in ground water (Mannerkoski et al. 2005) and stream water (Ahtiainen et al. 2003) after clear-cutting in this study site.

The pulse of P and K released from logging residues was clearly observed in the soil water (Figure 3). The leaching of P and K below the O-horizon followed the release of P and K from logging residues, with the leaching being the greatest during the first year after clear-cutting and then starting to diminish. However, in the first year more P and K was released from logging residues than was leached below the O-horizon, indicating that part of the released P and K was retained in the organic layer and ground vegetation. Phosphorus could also have accumulated in coarse residues because this element often limits the decomposition of coarse woody debris (Barber and Van Lear 1984, Laiho and Prescott 1999). Although the released amount of K decreased after the first year, the leaching of K below the O-horizon remained high. Potassium was also probably rapidly mineralised from decomposing dead ground vegetation (Johansson 1993) and coarse residues (Fahey et al. 1988, Fahey et al. 1991b, Krankina et al. 1999). Logging residues have been shown to be the source of leached P and K also in other studies, because leaving the logging residues on site have resulted in higher P and K

Table 2. The biomass and estimated nutrient uptake of ground vegetation (kg ha^{-1}) during the first three years after clear-cutting. Annual biomass production of mosses, *V. myrtillus*, *V. vitis-idaea* and roots were estimated to be 33, 45, 35 and 40 %, respectively. These estimates are based on the values reported by Tamm (1953) and Mälkönen (1974). The above-ground parts of grasses and herbs are annual and are thus renewed each year.

	Dry mass	N	P	K	Ca
1. Year					
Mosses	421.9	1.43	0.21	0.72	0.47
V. myrtillus	216.3	1.06	0.11	0.55	0.38
V. vitis-idaea	15.1	0.06	0.01	0.03	0.02
Grasses and herbs	3.8	0.04	0.01	0.02	0.01
Roots	2714.5	6.05	0.69	1.94	1.42
Total	**3371.6**	**8.64**	**1.03**	**3.26**	**2.30**
2. Year					
Mosses	63.3	0.27	0.03	0.08	0.09
V. myrtillus	162.5	1.04	0.12	0.59	0.34
V. vitis-idaea	45.1	0.22	0.03	0.12	0.07
Grasses and herbs	60.0	0.87	0.10	0.52	0.28
Roots	1965.4	4.51	0.47	1.08	1.05
Total	**2296.3**	**6.91**	**0.75**	**2.39**	**1.83**
3. Year					
Mosses	522.5	2.11	0.25	0.51	0.75
V. myrtillus	268.9	1.50	0.19	1.25	0.35
V. vitis-idaea	56.7	0.25	0.03	0.21	0.06
Grasses and herbs	351.6	3.97	0.56	3.61	1.02
Roots	2260.0	6.31	0.60	1.16	1.17
Total	**3459.7**	**14.14**	**1.63**	**6.74**	**3.35**

levels in soil water compared with whole-tree harvesting (Staaf and Olsson 1994, Stevens et al. 1995).

During the first three years after clear-cutting, less C, P and K, but more N and Ca were leached below the O-horizon than were released from logging residues. The amount of N derived from deposition remained unchanged after clear-cutting, whereas C, P, K and Ca deposition decreased (Figures1 and 3) that may have partly decreased the leaching losses of these nutrients.

Although large amounts of nutrients were released from logging residues and the ground vegetation suffered from clear-cutting, the nutrient fluxes below the B-horizon were small indicating that mineral soil efficiently retains nutrients (Figure 3, Piirainen 2002). Only a small proportion of the P (9.8 kg ha^{-1}) and K (64.9 kg ha^{-1}) released from the logging residues was lost into the stream. The leaching of P and K into the stream was only 0.02 kg ha^{-1} and 2.3 kg ha^{-1} higher during the first three years after clear-cutting compared to the pre-cutting levels (Ahtiainen et al. 2003) indicating that the released nutrients were effectively retained within the catchment. Nutrient losses caused by leaching were small compared to the losses caused by the removal of stems (Figures 2 and 3).

This study supports the findings that logging residues can act as a N sink and thus counteract the leaching of N after clear-cutting (Barber and Van Lear 1984, Fahey et al. 1991b, Carlyle et al. 1998). The results suggest that the nutrient losses caused by whole-tree harvesting can not merely be estimated on the basis of the amount of nutrients that is removed with logging residues, because the removal of branches may increase the leaching of nutrients that are released from needles, older litter, organic layer and dead ground vegetation.

4.1.5 Other processes

Weathering, N fixation and the decomposition of coarse residues and dead ground vegetation were not measured in this study. It is not clear whether weathering rates are affected by clear-cutting and thus contribute to the increased concentrations of P, K and Ca in the soil solution. The decrease in the biomass of mosses (III) probably decreased the N input to the system, because the N fixation of feather mosses in mature forests in Scandinavia can be about the same magnitude (1.5 - 2 kg ha^{-1} a^{-1}) as the input from deposition (DeLuca et al. 2002). On the other hand, the logging residues may have increased the N input into the system through N fixation by providing a habitat for free-living, N-fixing microbes (Granhall and Lindberg 1980). Ground vegetation may significantly affect the nutrient fluxes in clear-cut areas because ground vegetation that dies as a result of clear-cutting and the litterfall of ground vegetation are probably relatively easily decomposable (Mikola 1954, Johansson 1993), and considerable amount of nutrients are cycled through ground vegetation annually (Mälkönen 1974, Helmisaari 1995). Coarse residues can play an even more important role as a N sink than fine residues because they decompose slowly and probably more N is accumulated in this material due to the lower N concentration and C/N ratio (Hyvönen et al. 2000, Berg and McClaugherty 2003) and greater N fixation (Granhall and Lindberg 1980).

4.2 Decomposition in the clear-cut area compared to the uncut forest

Although the average air and soil temperatures were higher and more rainfall reached the ground in the clear-cut area than in the forest, this did not lead to higher mass losses (I). The decomposition of spruce needles and birch roots was actually significantly slower at the clear-cut plot than at the forest plot. Episodic drought, high near-ground temperatures and fluctuations in soil moisture and temperature (Bååth 1980, Kubin and Kemppainen 1991, Schwendenmann 2000, Redding et al. 2003) may have decreased microbial biomass and activity and altered the decomposer community structure in the clear-cut area (Huhta 1976, Bååth 1980, Siira-Pietikäinen et al. 2001, Hassett and Zak 2005) that may have had retarding effect on decomposition. Destruction of the moss cover after clear-cutting (III) may have further increased the moisture and temperature fluctuations in the soil surface and the organic layer because the moss layer has an insulating effect. Moreover, the loss of root exudation may have decreased microbial activity in the clear-cut area (Zhu and Ehrenfeld 1996). The decomposition of roots, branches and foliage has not earlier been compared between clear-cut and forest areas in Finland. Johansson and Grälls (1989) studied the decomposition of Norway spruce needle litter in a clear-cut area and forest in Sweden and did not observe any increased decomposition in the clear-cut area, either.

Removal of the forest canopy subjects decomposing material to greater wetting-drying and freezing-thawing cycles which may increase fragmentation and the leaching of nutrients and soluble substances (Taylor and Parkinson 1988). This may be the reason for the observed increased decomposition of birch leaves in the clear-cut area (I), because birch leaves contain high amounts of soluble compounds (Johansson 1995). Physical processes have probably had a lesser effect on the decomposition of needles, roots and branches because they contain only small amounts of soluble compounds (Johansson 1995, Berg and McClaugherty 2003), and the cuticle and waxes in the needles and root and branch bark protects against mechanical damage and forms an obstacle to leaching. This finding is consistent with the results of Kim et al. (1996) and Prescott (1997), who found that clear-cutting increased the mass loss of broadleaf litter but retarded the decomposition of conifer needles. More intense fragmentation and mechanical leaching may be the reason for the observed faster nutrient release in the clear-cut plot (I, II).

4.3 Generalization of the results

This study consisted of only one experimental site that hampers the generalization of the results. The lack of replicate reference and treated plots is a common limitation in this kind of comparative studies (e.g. Fahey et al. 1991a, 1991b, Lundmark-Thelin and Johansson 1997, Bock and Van Rees 2002) because in general there are no sufficiently resources to conduct these types of studies in several sites. The results received here are likely valid only in the coniferous dominated forests, which grow on sites with medium fertility, situate relatively north and receive low deposition loads. The development of ground vegetation after clear-cutting differs between site types (Salemaa and Jukola-Sulonen 1998). It is also known that the abundance of species differs between high and low deposition areas (Rosén et al. 1992, Mäkipää 1998). In more fertile sites, logging residues can be expected to contain higher concentrations of nutrients than in this study site, and accordingly, nutrients are likely released faster and the accumulation of N in logging residues does not necessarily occur. The results suggest that in birch-dominated forests, nutrients are released faster from logging residues than in coniferous forests (I, II), and there is net release of N from birch logging residues during the first three years after clear-cutting (I, Table 4).

5. CONCLUSIONS

Carbon, P and especially K are rapidly released from logging residues, whereas the release of Ca is slow and there is no net release of N during the first three years following clear-cutting. The results suggest that logging residues are a potential source of the C, P, K and Ca leached during the first three years after clear-cutting, but that leached N probably originates from the organic layer and decomposing dead ground vegetation. The accumulation of N in logging residues can initially play an important role in the retention of N on the site, especially as the ground vegetation suffers from clear-cutting. The results suggest that the effect of whole-tree harvesting on the nutrient status of the site cannot be merely estimated by taking into account the amount of nutrients that is removed from site with logging residues because microbial immobilization in logging residues can promote N retention and attenuate leaching. The role of logging residues as a nutrient sink requires further study, and it would be also important to determine how long N will retain in logging residues. Calcium is also released from logging residues with delay. The results imply that microbial immobilization in logging residues initially plays a more important role in the retention of N and Ca than the ground vegetation. The results provide no evidence that clear-cutting consistently results in more rapid decomposition and nutrient release from logging residues, but suggests that the decomposition of birch leaves and in some cases also the release of K and Ca can be faster in clear-cut areas possibly due to more intense fragmentation and mechanical leaching.

The ground vegetation is capable of taking up only a small fraction of the nutrients released from logging residues during the first two years after clear-cutting and the decomposing dead ground vegetation is a potential source of leached nutrients. The results suggest that nutrients released from logging residues are initially retained primarily through soil processes and microbial immobilization but ground vegetation becomes a significant nutrient sink soon after clear-cutting.

As this study was conducted in only one experimental site, broad generalizations cannot be made. However, this study provides detailed information about the nutrient pools and fluxes after clear-cutting a Norway spruce dominated forest. In the future the release of nutrients from coarse logging residues, organic layer and dead ground vegetation after clear-cutting should be studied. Performing more accurate nutrient budget estimations also necessitates investigations on changes in the soil nutrient pools.

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