EFFECT OF VARIABLE RETENTION HARVESTING AND STAND TYPE ON SOIL NITROGEN AVAILABILITY IN BOREAL MIXEDWOOD FORESTS

by

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Abstract

Clear-cut harvesting has been shown to increase the nitrification rate and lead to elevated levels of soil nitrate in some forests. This change in nitrogen (N) cycling and availability could negatively affect regeneration, future site productivity as well as surrounding ecosystems. Variable-retention (VR) harvesting has been proposed as a more environmentally acceptable alternative to clearcutting. VR harvesting retains a portion of live trees in the cutblocks and it is assumed that this will create conditions more similar to uncut forests and mitigate the negative effects of clearcutting on the N cycle. In boreal mixedwood forests, maintenance of a deciduous component and management of mixed stands is currently encouraged, partly based on the assumption that deciduous trees facilitate faster N cycling and higher N availability. The evidence of this phenomenon is, however, equivocal. In boreal mixedwood forests in northern Alberta, I assessed whether the uncut deciduous-dominated forests had higher N availability and faster N cycling than coniferous-dominated forests, and whether N availability was related to the proportion of deciduous trees. I also assessed the effects of clearcutting and VR harvesting on soil N availability in boreal mixedwood forests and characterized pathways and rates of nitrification. Uncut stands of deciduous forests had higher availability of ammonium but did not have faster N cycling and higher nitrate levels as hypothesized. Clearcutting had little effect on soil N availability in all forest types. Net and gross rates of N mineralization and nitrification were not altered and N availability was not elevated by clearcutting. VR-harvested sites did not differ either from clearcuts or uncut stands. Despite very low soil nitrate concentrations, nitrification was an active process at all sites, even in uncut coniferous stands. Nitrification was carried out mainly by heterotrophs and both nitrate production and consumption increased with labile C addition. Clearcutting in these boreal forests did not create a soil environment dominated by nitrate at any site. VR harvesting of western boreal mixedwood forests may not be justified based on nutritional concerns as the effects of clearcutting on N availability were minimal.
# Table of Contents

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>ii</td>
</tr>
<tr>
<td>Table of Contents</td>
<td>iii</td>
</tr>
<tr>
<td>Lists of Tables</td>
<td>v</td>
</tr>
<tr>
<td>List of Figures</td>
<td>vii</td>
</tr>
<tr>
<td>List of Abbreviations</td>
<td>ix</td>
</tr>
<tr>
<td>Acknowledgements</td>
<td>x</td>
</tr>
<tr>
<td>Co-authorship Statement</td>
<td>xi</td>
</tr>
</tbody>
</table>

## 1 Introduction

1.1 Background

1.1.1 Nitrogen in forest soil
1.1.2 Nitrate cycling
1.1.3 Effect of forest type on N availability
1.1.4 Effect of harvesting on N availability

1.1.4.1 Clearcutting
1.1.4.2 Variable-retention harvesting
1.1.5 Variable-retention harvesting compared to natural disturbance in boreal mixedwoods

1.2 Rationale

1.3 Objectives

1.4 Site description

1.5 Thesis structure

1.6 References

## 2 Nitrogen dynamics in coniferous, deciduous and mixed boreal mixedwood forests

2.1 Introduction

2.2 Methods

2.3 Results

2.4 Discussion

2.5 Tables and figures

2.6 References

## 3 Effect of variable-retention harvesting on soil nitrogen availability in boreal mixedwood forests

3.1 Introduction

3.2 Methods

3.3 Results

3.4 Discussion

3.5 Tables and figures

3.6 References
### 4 Post-harvest soil nitrate dynamics in boreal mixedwood forests

- **4.1 Introduction** ................................................................. 98
- **4.2 Methods** ....................................................................... 99
- **4.3 Results** ....................................................................... 104
- **4.4 Discussion** ................................................................. 105
- **4.5 Tables and figures** ..................................................... 108
- **4.6 References** ............................................................... 113

### 5 Effect of clear-cut harvesting on phosphorus availability and phosphatase activity in boreal mixedwood forests

- **5.1 Introduction** ................................................................. 118
- **5.2 Methods** ....................................................................... 118
- **5.3 Results** ....................................................................... 120
- **5.4 Discussion** ................................................................. 121
- **5.5 Tables and figures** ..................................................... 123
- **5.6 References** ............................................................... 129

### 6 Concluding chapter

- **6.1 Synthesis of results** .................................................... 131
- **6.2 Strength and weaknesses of the project and potential sources of uncertainty** ........................................... 137
- **6.2.1 Measurements of N availability** ............................... 140
- **6.3 Management implications** ........................................ 142
- **6.4 Conclusions and recommendations** ........................... 144
- **6.4.1 Further research** ................................................... 144
- **6.5 References** ............................................................... 147
List of Tables

Table 1-1  Tree species composition in the vicinity of the sampling spots in the uncut stands of deciduous-dominated, mixed and coniferous-dominated forests

Table 1-2  Components of variance for completely randomized factorial split-plot model

Table 1-3  Degrees of freedom and F-test formulas for different factors in completely randomized factorial split-plot model

Table 2-1  Concentration [\(\mu g\ g^{-1}\)] and content [mg m\(^{-2}\)] of total C, and several forms of N in the forest floors in the three forest types, SON is soluble organic N

Table 2-2  Concentration [\(\mu g\ g^{-1}\)] and content [mg m\(^{-2}\)] of total C, and several forms of N in the upper 7 cm of mineral soil in the three forest types, SON is soluble organic N

Table 2-3  pH, gravimetric moisture, extractable P and microbial C concentrations in the forest floor and upper 7 cm of mineral soil in the three forest types

Table 2-4  Rates of net N mineralization and nitrification in the forest floor and upper 7 cm of mineral soil in the three forest types

Table 2-5  Correlations between soil-N variables and characteristics of vegetation in the immediate vicinity of sampling plots in all forest types. FF is forest floor, min is upper mineral soil, accum NO\(_3\) is NO\(_3\)-N accumulated after 6-wk incubation, accum SIN is soluble inorganic N accumulated after 6-wk incubation.

Table 3-1  NO\(_3\)-N concentration [\(\mu g\ g^{-1}\)] in the forest floor and upper 7 cm mineral soil under four retention levels in the three forest types

Table 3-2  NH\(_4\)-N concentration [\(\mu g\ g^{-1}\)] in the forest floor and upper 7 cm mineral soil under four retention levels in the three forest types

Table 3-3  Soluble organic N (SON) concentration [\(\mu g\ g^{-1}\)] in the forest floor and upper 7 cm mineral soil under four retention levels in the three forest types

Table 3-4  pH and gravimetric moisture in the forest floor and upper 7 cm of mineral soil under four retention levels in the three forest types

Table 4-1  Supply rate of nitrate and ammonium in the forest floor and upper 7 cm of mineral soil in un-cut and clear-cut sites in deciduous- and coniferous-dominated boreal mixedwood forests.

Table 4-2  Soluble organic C concentration and soluble C/N ratio in the forest floor and upper 7 cm of mineral soil in uncut and clearcut sites in deciduous- and coniferous-dominated forests.

Table 5-1  Iron and aluminum supply rate in the forest floor and upper 7 cm of mineral soil in uncut and clearcut sites in deciduous- and coniferous-dominated forests.

Table 5-2  Activity of acid and alkaline phosphatase in the forest floor and upper 7 cm of mineral soil in uncut and clearcut sites in deciduous- and coniferous-dominated forests, expressed per mass of soil and microbial biomass C.
Table 5-3  Soil water holding capacity and microbial biomass C in the forest floor and upper 7 cm of mineral soil in uncut and clearcut sites in deciduous- and coniferous-dominated forests.
List of Figures

<table>
<thead>
<tr>
<th>Figure 1-1</th>
<th>Studied components of soil-plant internal N cycle</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Figure 1-2</td>
<td>Map of EMEND project area</td>
<td>20</td>
</tr>
<tr>
<td>Figure 1-3</td>
<td>Sampling sites within the stands</td>
<td>21</td>
</tr>
<tr>
<td>Figure 2-1</td>
<td>Distribution of N (%) within the labile pool in forest floor and upper 7 cm of mineral soil in deciduous, mixed and coniferous stands. SON is soluble organic N, micrN is microbial N.</td>
<td>59</td>
</tr>
<tr>
<td>Figure 2-2</td>
<td>Tree density and species composition in the vicinity of sampling spots; a) number of trees per ha; b) basal area per ha.</td>
<td>60</td>
</tr>
<tr>
<td>Figure 2-3</td>
<td>Annual mass (a) and N content (b) of canopy litter in the three forest types (g m⁻²)</td>
<td>60</td>
</tr>
<tr>
<td>Figure 2-4</td>
<td>Relationship between concentration of soluble inorganic N in the forest floor and a) N input in foliar litter; b) decomposition rate in the three forest types.</td>
<td>61</td>
</tr>
<tr>
<td>Figure 3-1</td>
<td>Net nitrification rates (a) and net ammonification rates (b) during 6-week in-situ incubation of the forest floor and upper 7 cm of mineral soil in deciduous-dominated, mixed, and coniferous-dominated forests at four retention levels (0-100%).</td>
<td>86</td>
</tr>
<tr>
<td>Figure 3-2</td>
<td>Proportion of soluble N as soluble inorganic N (SIN) in the forest floor and upper 7 cm of mineral soil of deciduous-dominated, mixed, and coniferous-dominated forests at four retention levels (0-100%) in a) June and b) August.</td>
<td>87</td>
</tr>
<tr>
<td>Figure 3-3</td>
<td>Microbial N (a) and microbial C/N (b) in the forest floor and upper 7 cm of mineral soil of deciduous-dominated, mixed, and coniferous-dominated forests at four retention levels (0-100%).</td>
<td>88</td>
</tr>
<tr>
<td>Figure 3-4</td>
<td>Decomposition of foliar litter of aspen and spruce during the first year (a), and annual mass of canopy litter (b) in deciduous-dominated, mixed, and coniferous-dominated forests at four retention levels (0-100%).</td>
<td>89</td>
</tr>
<tr>
<td>Figure 3-5</td>
<td>Inorganic N (NO₃-N and NH₄-N) concentrations in the forest floor clearcuts and uncut stands of deciduous- and coniferous-dominated forests, one, three and four years after the harvest. The first and third year data are from Kishchuk (2002) and Lindo and Visser (2003).</td>
<td>90</td>
</tr>
<tr>
<td>Figure 4-1</td>
<td>NO₃-N gross production (a) and consumption (b) in the forest floor and upper 7 cm of mineral soil of clearcut and uncut deciduous- and coniferous-dominated forests.</td>
<td>110</td>
</tr>
<tr>
<td>Figure 4-2</td>
<td>NH₄-N gross production (a) and consumption (b) in the forest floor and upper 7 cm of mineral soil of clearcut and uncut deciduous- and coniferous-dominated forests.</td>
<td>111</td>
</tr>
<tr>
<td>Figure 4-3</td>
<td>Gross nitrification rates (a) and gross nitrate consumption rates (b) with and without addition of labile C (sucrose) during a 24-hour laboratory incubation of the forest floor of clearcut and uncut deciduous- and coniferous-dominated forests.</td>
<td>112</td>
</tr>
<tr>
<td>Figure 5-1</td>
<td>Concentration of extractable phosphorus (a) and phosphorus supply rate (b) in the forest floor and upper 7 cm of mineral soil in clearcut and uncut</td>
<td>126</td>
</tr>
</tbody>
</table>
deciduous- and coniferous-dominated forests

**Figure 5-2** Activity of acid phosphatase (a) and alkaline phosphatase (b) in the forest floor and upper 7 cm of mineral soil in clearcut and uncut deciduous- and coniferous-dominated forests.

**Figure 5-3** Relation of alkaline phosphatase activity to the concentration of inorganic N in the forest floor in clearcut and uncut deciduous- and coniferous-dominated forests.

**Figure 5-4** Ratio of inorganic N/P supply rates in the forest floor and upper 7 cm of mineral soil in clearcuts and uncut deciduous- and coniferous dominated forests (capital letters indicate harvesting effect; lower-case letters indicate forest type effect; bars represent standard errors).
<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>SIN</td>
<td>Soluble inorganic nitrogen</td>
</tr>
<tr>
<td>SOC</td>
<td>Soluble organic carbon</td>
</tr>
<tr>
<td>SON</td>
<td>Soluble organic nitrogen</td>
</tr>
<tr>
<td>VR</td>
<td>Variable retention</td>
</tr>
<tr>
<td>EMEND</td>
<td>Ecosystem management emulating natural disturbance</td>
</tr>
</tbody>
</table>
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Co-authorship Statement

The four main chapters have been co-written with following co-authors: Kirsten D. Hannam, Barbara Kishchuk and Cindy E. Prescott.

Lucie Jerabkova, thesis author, designed individual experiments, performed the research and data analysis and in cooperation with the co-authors prepared the manuscripts.

Kirsten Hannam was involved in the design of laboratory experiment measuring phosphatase activity and collaborated on preparation of the manuscript in chapter 5.

Barbara Kischhuk's role was identification and general research design. She also commented on and edited two manuscripts (chapter 2 and 3). Cindy Prescott, research supervisor, identified the research program, provided guidance throughout the project, and comments and edits of the four manuscripts.
Chapter 1: Introduction

1.1 Background
Clearcutting is the prevailing method of harvesting in Canada, particularly in the boreal forest region. In the province of Alberta almost 100% of harvesting is currently done by clearcutting (CCFM 2005). As the productivity in northern forests is largely limited by nitrogen (N), the effect of harvesting on N availability is of concern. Early evidence of increased nitrate levels and leaching mainly in temperate forests (Bormann et al. 1974; Frazer et al. 1990) led to concerns that clearcutting may reduce the productivity of future stands. This and other environmental concerns (e.g. biodiversity reduction) associated with clearcut-harvesting led to development of alternative harvesting systems, such as variable retention, in which a portion of the trees are left standing. It is of interest to know if variable-retention harvesting differs from clear-cut harvesting in its effect on soil N dynamics and whether it fulfills the mandate of more environmentally acceptable silvicultural practice in terms of soil N.

The aim of this study is to assess effects of variable-retention harvesting on N availability in three common types of boreal mixedwood forests in north-western Alberta, and to elucidate the mechanisms behind the observed changes in N cycling.

1.1.1 Nitrogen in forest soils
Nitrogen occurs in soils either in organic compounds or in inorganic forms, mainly nitrate and ammonium. The total concentration in forest soils ranges from less than 0.1% to about 1.6% (dry mass basis) (Dalias et al. 2002). Organic N is a predominant form of nitrogen in soil (Van Lear et al. 1990; Devito et al. 1999), while inorganic N (NH₄-N and
NO$_3$-N) usually forms less than 2% of the total soil nitrogen pool in undisturbed forest ecosystems (Melillo 1981). The soluble fraction of organic N (SON) is further differentiated as organic extractable N that can pass a 0.45 μm filter (Qualls et al. 2000). Ratios of nitrate to ammonium vary widely within various soil types but seldom exceed 1 (Davidson et al. 1992). Nitrate is the least abundant form of plant available nitrogen in forest soils. In the internal plant-soil cycle, nitrate and ammonium are produced through decomposition of organic material, depolymerization of large organic molecules and N mineralization. Nitrogen mineralization refers to the biological conversion of organic to inorganic forms of nitrogen (Hart et al. 1994b), and consists of the processes of ammonification and nitrification. Ammonification describes the conversion of organic N forms to ammonium, while nitrification refers to biological formation of nitrate (Tate 1995). Gross mineralization refers to the total production of mineral N compounds, whereas the term net mineralization refers to the net balance of mineral nitrogen production and immobilization. Similarly, net nitrification describes the result of gross production and immobilization of nitrate. Immobilization refers mainly to microbial N uptake but also to other processes that consume ammonium and nitrate within the soil such as NH$_4$-N fixation on clay.

Why is nitrogen limiting?
Most soil nitrogen is strongly bonded to carbon in organic compounds where it is both physically and chemically stable. Solubilization and mineralization of N requires a lot of energy and simultaneous activity of several enzymes. It is thought that under certain conditions returns from investing into construction of N-compound-lyzing enzymes may not be profitable for an organism because N itself is a necessary element of those
enzymes (Vitousek et al. 2002). The lower C/N ratio of cytoplasm of most micro-biota compared to their food source results in immobilization of N in microbial biomass, and the release of available N is delayed until the biomass turns over. Movement of nitrogen through the food chain is limited by the presence of protein-precipitating phenolic compounds, which are wide-spread in plant tissues (Vitousek et al. 2002). Furthermore, available N forms are relatively mobile and can be lost from ecosystems in dissolved or gaseous form, such as nitrate or nitrous oxide.

**Nitrogen availability**

As only a very small proportion of soil N is accessible to plants, it is usually N availability and not total N content that provides information about site fertility and productivity. Nitrogen is considered “available” when it is present in a form and concentration that can be utilized by plants (Bundy and Meisinger 1994). Although some organic forms of N have also been recognized as potential N sources for plant uptake (Näsholm 1998; Weigelt et al. 2005), inorganic N is the crucial resource for plant growth. It is not possible to measure N availability directly, but several indices have been developed. The simplest measure of N availability is the size of the extractable NH$_4$-N and NO$_3$-N pool. However, this pool varies greatly both temporally and spatially (Binkley and Hart 1989) and the small pool size at any one time does not necessarily reflect actual availabilities of NH$_4$-N and NO$_3$-N to plants. For this reason, rates at which N is mineralized, or amounts of potentially mineralizable N measured either under field or laboratory conditions, are considered better indicators of available N. Changes in soluble organic and microbial biomass N pools are important in longer-term perspectives as both serve as potential sources of available N (Myrold and Tiedje 1986; Van Veen et al. 1987). Ion-exchange resins have been used to estimate fluxes of plant available
nutrients (Subler et al. 1995; Hangs et al. 2004). Nitrogen supply rates measured by ion-exchange resins are said to be more biologically meaningful as the measurements integrate several factors affecting N availability, such as soil moisture, temperature and microbial immobilization and they have been shown to correlate with plant N uptake (Huang and Schoenau 1996).

1.1.2 Nitrate cycling
The effects of timber harvesting on soil nitrate concentration are of particular concern because of its high mobility and associated potential for N depletion and ground- and surface-water contamination (Vitousek et al. 1979). It has also been suggested that the higher nitrate levels in soil may hinder conifer regeneration on harvested sites because of their preference for ammonium (Kronzucker et al. 1997). The process of nitrification is considered “one of the least understood fluxes of the nitrogen cycle of forest ecosystems” (Killham 1990).

Nitrate can be produced by two physiologically distinct groups of soil microorganisms – autotrophs (chemo-lithotrophs) and heterotrophs (chemo-organotrophs). Autotrophic oxidation is comprised of two steps, each of which involves different groups of microorganisms. The first step, oxidation of ammonia to nitrite, is carried out by ammonia-oxidizing bacteria belonging to the genera Nitrospira and Nitrosomonas (β-subclass Proteobacteria) (Paul and Clark 1996). In soil, only Nitrobacter has been identified to be responsible for the second step - oxidation of nitrite to nitrate (De Boer and Kowalchuk 2001; Maron et al. 2003). The process of heterotrophic oxidation is more diverse, as it can be performed by several groups of microorganisms – bacteria, actinomycetes, as well as fungi - and includes oxidation of
both inorganic and organic sources of N (Schimel et al. 1984). Heterotrophic nitrifiers are less efficient (less production per unit of biomass) than autotrophs, but they may have higher biomass in the soil (Killham 1990) and may thus contribute more to total nitrification.

Autotrophic nitrification has been considered the dominant process in most soils (Killham 1987; Pedersen et al. 1999). However in forest soils, particularly in coniferous forests, where nitrifying activity was previously believed to be inhibited by low pH, heterotrophic nitrifying communities have been found to play an important role (Adams 1986) and many nitrifying heterotrophic bacteria and fungi have been identified.

Figure 1: Studied components of soil-plant internal nitrogen cycle
Acquisition of the majority of N for nitrate production from a source other than ammonium (Schimel et al. 1984; Killham 1990; Pedersen et al. 1999) has been reported as evidence of heterotrophic nitrifying activity. Heterotrophic nitrification is most pronounced in (but not restricted to) acidic soils (Alexander 1977).

Autotrophic nitrification has been detected acid forest soils and autotrophic nitrifiers isolated from soils at pH values well below the levels at which they ceased their activity in liquid cultures (De Boer et al. 1992; Carnol et al. 2002; Mintie et al. 2003). Several mechanisms, such as existence of microsites with higher pH, intracellular hydrolysis of urea, and existence of acid-tolerant bacteria strains have been proposed to explain how autotrophic nitrification in acid soils is possible (De Boer and Kowalchuk 2001). Several clusters of ammonia oxidizing bacterias were distinguished by variation in gene sequences of 16S rRNA and amoA (ammonia mono-oxygenase) (Purkhold et al. 2000; Laverman et al. 2005) and individual clusters were associated with specific environmental conditions (Stephen et al. 1996; Nugroho et al. 2005). Autotrophic nitrifiers were not only present but were the dominant nitrate producers in some acid forest soils (Mintie et al. 2003). The physiology of autotrophic nitrifying organisms has been extensively studied (Bollmann et al. 2002), but less information is available about heterotrophic nitrifiers due to their taxonomic and physiological diversity.

Many of the studies that suggest that nitrification is not an active process in forest soils (Rice and Pancholy 1972; Vitousek et al. 1979; Cole 1981) were examining changes in nitrification with stand age or along a secondary succession gradient. There is a trend towards lower NO$_3$-N concentrations and slower rates of net nitrification in mature forests or stands of later successional stages (Rice and Pancholy 1972; Reiners
1981; Vitousek et al. 1989; Davidson et al. 1992; Paré and Van Cleve 1993; Brais et al. 1995), though with exceptions (Robertson and Vitousek 1981). Several hypotheses have been suggested to account for low nitrate levels in mature forests. Most assumed that nitrate production was low, which was attributed to: 1) unfavorable conditions for nitrifiers, mainly low pH (Killham 1990); 2) allelochemical inhibition by late successional vegetation (Rice and Pancholy 1972); and 3) reduced NH$_4$ supply to nitrifiers.

Inhibition is thought to be caused mainly by phenolic compounds released from litter and root exudates (Gallet et al. 1999), monoterpenes (Paavolainen et al. 1998) and terpenoids (White 1986). However, Robertson (1982) has pointed out that oxidizable C is usually added together with the suspected inhibitor in some experiments, and that the C could be the cause of decreased nitrate levels. Phenolic compounds are thought to be an important source of C for heterotrophic organisms (DeLuca et al. 2002) and could increased nitrate immobilization.

Reduced NH$_4$ supply to nitrifiers due to wider C/N ratio in litter and thus higher NH$_4$ immobilization in mature forests (Vitousek et al. 1979; Robertson and Vitousek 1981) could also limit nitrification. However, experiments in which glycine has been added to soil increased net ammonification but not nitrification (Ste-Marie and Paré 1999; DeLuca et al. 2002), indicating that NH$_4$ supply did not limit nitrification.

In contrast to these hypotheses, that assume that lower nitrate level results from lower nitrification rates, Davidson et al. (1992) hypothesized that lower nitrate concentrations in mature coniferous forests are the result of high microbial nitrate immobilization. High rates of nitrate immobilization would be induced by excessive C
supply (relative to N). Conversely, higher rates of net nitrification with consequent higher nitrate concentrations in regenerating stands would be then a result of low C supply (relative to N) and thus microbial C limitation. The sensitivity of the nitrate production / consumption ratio to C availability was also apparent from a review of 100 studies measuring gross N mineralization and nitrification (Booth et al. 2005). However, rates of nitrate production were more strongly related to N mineralization than to C concentration or C / N ratio (Booth et al. 2005).

Effect of C on nitrate availability
Microbial activity, in general, has been shown to be largely C-limited (Grayston et al. 1996; Ekblad and Nordgren 2002). Soil microorganisms usually respond to C additions by increasing activity, rather than increasing microbial biomass (Gallardo and Schlesinger 1994; Groffman 1999). Increased activity, however, does not imply higher net mineralization rates and higher N availability; indeed, in most cases, C addition results in lower N availability (Prescott and McDonald 1994; Vance and Chapin 2001). However, C addition in some studies has resulted in increased nitrogen availability (Groffman 1999), which has been to faunal grazing on increased microbial biomass.

Vogt and Edmonds (1982) reported higher values of nitrate associated with lower C/N ratio of forest floor and upper mineral soil in Douglas-fir (Pseudotsuga menziesii) stands. Soil C/N has also been shown to be a fairly good predictor of net nitrification and nitrate leaching in eastern hardwoods (Lovett et al. 2002) and European forests (Gundersen et al. 1998), where no nitrate leached from sites with C/N higher than 30 and high leaching was observed from sites with C/N under 25. However, the negative correlation of N availability with substrate C/N ratio is not universal. Vitousek et al.
(1982) suggested that net N mineralization is better related to available C/N ratio, which cannot be measured directly or predicted from total C/N ratio. Booth et al. (2005) found that N mineralization rates were related to soil C/N ratio only after adjustments for soil C levels among different sites, and that nitrate production was not at all related to soil C/N ratio.

Although it had been assumed that microbial immobilization of inorganic N strongly favours the NH$_4$-N form (Vitousek and Matson 1984), microbial immobilization of NO$_3$-N may be an important mechanism of nitrate retention in forest soils. Microbial nitrate consumption, though lower than ammonium consumption (Davidson et al. 1992) can account for as much as 90% of gross nitrate production, and soil microorganisms might be capable of immobilizing all nitrate produced, if sufficient C is available (Stark and Hart 1997). Nitrate might also be immobilized by abiotic fixation into organic matter, which is also affected by C availability (Dail et al. 2001; Davidson et al. 2003), but this process has not been well studied. Gross nitrate production may exceed net nitrification by an order of magnitude (Stottlemyer and Toczydlowski 1999) and they may not be correlated (Hart et al. 1994a; Verchot et al. 2001). Thus studies that examine only net mineralization and nitrification may underestimate total nitrate production and the role of nitrate in forest ecosystems (Stark and Hart 1997).

1.1.3 Effect of forest type on soil N availability

Trees affect nutrient cycling by modifying forest floor and mineral soil. Distinctive morphological and physiological characteristics of tree species result in different microclimatic conditions, levels of light transmission, nutrient acquisition patterns (Hangs et al. 2003), nutrient accumulation (Alban 1982), and litter characteristics...
(Prescott 2002). As deciduous and coniferous trees represent two distinct plant forms they are expected to differ substantially in their effects on soil properties and nutrient availability. Deciduous trees are expected to promote higher N availability and faster N cycling as a result of higher quality litter that usually decomposes faster (Pastor 1987; Scott and Binkley 1997).

The most prominent differences between forest types are evident in the forest floor, which reflects the litter characteristics of different tree species. Forest floors of boreal aspen (*Populus tremuloides* Michx.) and birch (*Betula papyrifera* Marshall) forests had higher N concentration than forest floors of black spruce (*Picea mariana* (Mill.) BSP.) forest (Flanagan and Van Cleve 1983). Beech (*Fagus sylvatica* L.) stands in Germany had higher forest floor microbial N and net N mineralization rates than Norway spruce (*Picea abies* (L.) Karst.) stands growing on comparable soil (Zhong and Makeschin 2004). Forest floors under deciduous and coniferous tree species in a mixed stands in Kentucky differed in pH, exchangeable Ca, Mg and K concentrations and mineralizable N; all being higher under yellow poplar (*Liriodendron tulipifera* L.) than under eastern hemlock (*Tsuga Canadensis* (L.) Carr.) (Boettcher and Kalisz 1990). In mixed stands in interior British Columbia several forest floor characteristics such as pH, total N, available P and extractable Ca, Mg and K concentrations were positively correlated with the proportion of deciduous tree species, mainly paper birch (Sanborn 2001). But the presence of deciduous trees does not always result in higher pH and nutrient concentrations. For example soils of beech and oak forests had lower N mineralization rates than soils of spruce-fir-beech or pine forests (Hackl et al. 2004), and forest floors under paper birch had lower NH$_4$-N concentration and N mineralization rates than those
under Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Thomas and Prescott 2000). In a 40-year-old plantation, no differences were found in soil N concentration and C/N ratio among 5 deciduous species and Norway spruce (Hagen-Thorn et al. 2004).

It is well established that tree species have different preferences in terms of site characteristics, including climate, moisture, and nutrient availability. Their occurrence, thus, often reflects distribution of these conditions within the landscape (Sollins 1998; Tateno and Takeda 2003) and forest types may display different qualities due to inherent differences in the sites occupied by different tree species.

Soil characteristics under different tree species planted on a relatively homogenous area are the best indicator of the actual effects of tree species on soil. While differences in N dynamics between stands of different tree species may be evident, it is usually not possible to divide them into deciduous and coniferous, as the differences within one group may be bigger than between these groups (Menyailo et al. 2002a; Menyailo et al. 2002b). Thus deciduous trees within mixedwood forests may not be assumed to have higher N availability and faster N cycling than coniferous trees. There is also uncertainty about the presumed faster decomposition of deciduous litter (Prescott 2002), as studies have reported no difference between the decomposition rate of deciduous and coniferous litter (Berg and Ekbohm 1991; Prescott et al. 2000) and that the initial faster rate of deciduous litter decomposition is often not sustained (Prescott et al. 2000).

Tree species have been also shown to affect soil conditions through belowground nutrient and C inputs. Although tree roots may contain only about 7-16% of nutrients retained in vegetation (Foster and Morrison 1976), turnover of fine roots is fast and may exceed the turnover of aboveground organic matter (Fogel and Hunt 1983). Living trees
also supply considerable quantities of C through rhizodeposition as a result of photosynthates translocation. Seedlings of basket willow translocated about 40% of assimilated C to below-ground pools and consequently increased microbial biomass by 30% (de Neergaard and Porter 2002). Pine (*Pinus ponderosa* Dougl. ex Laws.) seedlings translocated about 35% to microbial biomass associated with their rhizosphere (Norton et al. 1990). Paper birch increased levels of available C in the soil and consequently both microbial biomass C and N (Bradley and Fyles 1995) more than five other species. However, it is not clear whether the increased microbial biomass implies higher N availability for trees. Although the composition and quantity of root exudates is known to differ among tree species (Grayston et al. 1996), little is known about the differences between broadleaf and coniferous trees.

1.1.4 Effect of harvesting on N availability

1.1.4.1 Clearcutting

Forest harvesting, like other disturbances, modifies many properties of forest ecosystems. Nutrients stored in tree biomass are removed, nutrient uptake and transpiration by trees ceases, and changes in C and nutrient inputs and microclimate cause shifts in soil biota and understory vegetation, further affecting nutrient cycling and availability. Clearcutting has been shown to increase nitrate levels and net nitrification rates in many forest types (Frazer et al. 1990; Dahlgren and Driscoll 1994; Hope et al. 2003), which can lead to increased losses of N as well as accompanying cations (such as K\(^+\), Ca\(^{2+}\)) with possible negative effects on future site productivity.

The most abrupt change following harvesting is an immediate reduction in plant N uptake, which lessens the magnitude of inorganic N consumptive processes at the site.
(Vitousek 1981), leading to increased inorganic N concentrations in the soil (Burns and Murdoch 2005). Increased inorganic N concentration in soil may also arise through increased mineralization rates, which have been attributed to several causes. Soil moisture is often increased in harvested sites, due to reduced plant water uptake (Keenan and Kimmins 1993) and may contribute to higher microbial activity (Barg and Edmonds 1999). Nitrogen mineralization may be also increased as a result of higher soil temperature due to direct solar radiation after plant cover removal and sometimes also forest floor removal (Frazer et al. 1990). Higher temperature may stimulate microbial activity and also alter the microbial community composition leading to utilization of previously inaccessible substrates (Zogg et al. 1997; Zak et al. 1999). Verburg et al. (1999) reported faster N turnover at increased temperature in L and F forest floor layers. However, net mineralization did not increase because higher gross NH₄ mineralization was accompanied by higher NH₄ immobilization (Dalias et al. 2002). Microbial responses to temperature changes are complex, interacting with soil matric potential (Zak et al. 1999) and other site climatic conditions (Dalias et al. 2002). Soil pH may increase after harvesting (Smolander et al. 1998; Siira-Pietikäinen et al. 2001; Bock and Van Rees 2002) because the respiration and organic acids exudation by tree roots ceases, which may increase nitrification rates, as they are generally positively correlated with pH (Simard et al. 2001). Nitrogen mineralization may be enhanced by input of fresh organic matter from slash or decaying roots (Hendrickson et al. 1985; Smethurst and Nambiar 1990; Keenan and Kimmins 1993). Increased turnover of microbial N resulting from increased mortality of the microbial biomass dependent on root exudation may also contribute to increased N availability after harvest (Paul and Clark 1996). Although these
factors may increase inorganic N levels in short-term pulses, over a longer time N may actually be immobilized in slash material, which can act as a N sink for 10-15 years following harvesting (Covington 1981). Nitrate availability may be also elevated as a result of reduced microbial immobilization due to decreased C availability from above ground input and root exudation (Davidson et al. 1992) or increased ammonium production (Bradley 2001).

1.1.4.2 Variable-retention harvesting
Variable-retention harvesting refers to a silvicultural practice in which standing trees are left in the harvested area in a dispersed or aggregated form (Anonymous 2003). Variable-retention harvesting aims to emulate structural and functional attributes of natural disturbances. The retained trees are expected to facilitate conditions more similar to a forest than a clear-cut. Trees retained on site will keep taking up N, supplying C in litter and rhizodeposition, and maintaining temperature and moisture conditions more closely resembling those of forests. Retention of transpiring trees may also prevent a large increase in the amount of drainage water leaving the site, thereby reducing nitrate leaching after harvest (Feller 1997).

There is some evidence that partial harvesting systems, such as variable retention or green-tree retention, have a smaller effect on soil properties than clearcut harvesting. Sites harvested with green-tree retention have different microclimatic conditions than clear-cut sites (Lajzerowicz et al. 2004) and provide more favourable conditions for survival of mycorrhizal fungi (Amaranthus and Perry 1993). Available N levels and mineralization rates may not be significantly altered by partial cutting (Barg and Edmonds 1999). N levels in partial cuts usually lie between those of clear-cuts and
unharvested stands (Lapointe et al. 2005). The effects of partial harvesting on N mineralization and nitrification may depend on the slope, aspect and sampling season as was shown in German beech forest (Geßler et al. 2005). In another beech forest study, nitrate and ammonium concentrations and nitrate losses were higher in gaps compared to forest (Ritter et al. 2005; Ritter 2005). Group harvesting methods, which create gaps, usually cause more change in N cycling that does single-tree removal (Knight et al. 1991; Prescott et al. 2003).

1.1.5 Variable-retention harvesting compared to natural disturbance in boreal mixedwoods
Western boreal forests are characterized as ecosystems with frequent crown fires, mainly caused by lightning (Parminter 1991). Large numbers of frequent, small fires occur but the majority of the area is burned by few large fires, which can exceed 180 000 ha (Larsen 1989). Although fires in the boreal forests represent large-scale stand-initiating disturbance, they are not spatially homogenous in their effects. There may be patches of low impact in severely burned areas and between 3-15% of mature forests may be unburned within a single fire area (Delong and Tanner 1996). Snags as well as green trees remain within burned stands, which retain considerable structural diversity compared to clearcuts. Furthermore, although fire is the dominant disturbance agent in the boreal forest, secondary disturbance factors, such as windthrow and insect outbreaks, create small-scale heterogeneity and contribute to gap creation (Ruel and Pineau 2002; Hogg et al. 2002; Gauthier et al. 2005). Variable-retention harvesting might thus be expected to maintain the natural variability of ecosystem processes to some degree as it emulates some of the structural characteristics created by natural disturbances.
1.2 Rationale
With the changes in forestry towards sustainable management of the whole ecosystem rather than just maintenance of the timber supply, companies are being encouraged to harvest in a manner that is similar with disturbance regime in a given area. It is assumed that organisms are adapted to the conditions originating from the predominant disturbance; thus emulating the natural disturbance regime is expected to better maintain the ecological integrity of the forest ecosystem. This approach is often proposed as a precautionary measure in the absence of detailed information about the actual effects of disturbance and harvesting on ecosystem processes.

It has been suggested that clearcutting of boreal forests increases nitrification and soil nitrate levels with several negative consequences for further stand development and productivity, and eutrophication of recipient lakes. Elevated levels of nitrate in clearcuts were proposed to create unfavourable conditions for the regeneration of white spruce, which prefers to take up \( \text{NH}_4^-\text{N} \) (Kronzucker et al. 1997). A higher proportion of \( N \) in the mobile form of nitrate may lead to increased leaching losses, which will diminish site \( N \) capital and availability and pollute recipient streams and lakes.

In this thesis, I do not directly compare effects of harvesting on \( N \) availability to those of natural disturbance. Rather, my aim is to assess whether clearcutting does have the suggested negative effects on \( N \) availability and whether VR harvesting would mitigate these effects and maintain the characteristics of the natural forests.

It is important to assess whether VR harvesting fulfills these objectives, because it requires leaving a proportion of merchantable timber unharvested on the sites, and incurs
higher cost of harvesting. It is thus important to determine how much of the stand should be left in order to ensure non-detrimental effects.

In boreal mixedwood forests, maintenance of a deciduous component is currently encouraged because it is assumed that deciduous trees facilitate faster N cycling and higher N availability. The evidence for this assumption is, however, equivocal. A second aim of my study is therefore to assess whether N availability is related to the proportion of deciduous trees in mixedwood forests.

Finally, although N is the limiting nutrient in most temperate and boreal forests, P availability has been shown limiting in eastern North American forests with relatively high levels of N deposition (Tessier and Raynal 2003) and in wet boreal forests in Sweden (Giesler et al. 2002). I therefore studied if P is limiting even in an area relatively unaffected by N deposition, or becomes so after harvesting.

1.3 Objectives
Specific objectives and hypotheses tested in this thesis are:

1) **Assess the effect of forest type on soil N availability**
Hypothesis: N availability increases with the proportion of deciduous trees in boreal mixedwood forest

2) **Assess the effect of harvesting intensity on soil N availability**
Hypothesis: clearcutting creates a soil environment dominated by nitrate. variable-retention harvesting mitigates the effects of clearcutting

3) **Estimate gross mineralization and nitrification and characterize the nitrification pathway**
Hypothesis: nitrate production is increased by harvesting and is higher in deciduous- than coniferous-dominated forests
4) Assess the effect of harvesting on P availability and phosphatase activity and its relation to N and C availability
   Hypotheses: a) phosphatase activity is lower in harvested sites as a result of lower microbial biomass, or b) phosphatase activity is higher in harvested sites, potentially as a result of higher demand for P

5) Assess litterfall production decomposition in determining soil N availability
   Hypothesis: N input as litterfall is a better predictor of site N availability than is litter decomposition rate

1.4 Site description
   This study was a part of EMEND (Ecosystem Management Emulating Natural Disturbance) project, a large-scale silvicultural project in northern Alberta (Spence et al. 1999). The EMEND research study site is located approximately 90 km north-west of Peace River in the Clear Hills Upland and Lower Foothills Ecoregion (Beckingham et al. 1996). Approximate centre of the project is located at 56° 46' 13" north latitude and 118° 22' 28" west longitude. Elevation ranges from 677 m to 880 m a.s.l. Mean annual temperature in the nearest climatic station (Eureka River, 56° 29'N 118° 44' W, 665 m a.s.l.) is -0.3 °C, with mean January and July temperatures of -18.8°C and 14.6°C, respectively. Mean annual precipitation is 433 mm (Environment Canada 2004). Soils are primarily Gray Luvisols with minor occurrences of Brunisols, Gleysols, and Solonetzic soils derived from similar glacio-lacustrine and glacial till parent materials containing few coarse fragments (Kishchuk 2004). Soil texture in each of deciduous, mixed, and coniferous stands is clay loam (B. Kishchuk, unpublished data). Soils are generally well drained and exhibit little difference in pedogenetic properties across the study area (Kishchuk 2004).
Dominant tree species are trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* (L.) Mill.), and white spruce (*Picea glauca* (Moench) Voss). Black spruce (*Picea mariana* (Mill.) BSP.), balsam fir (*Abies balsamea* (L.) Mill.), lodgepole pine (*Pinus contorta* Loudon), and tamarack (*Larix laricina* (Du Roi) K. Koch) also occur at some sites (Table 1-1). Green alder (*Alnus crispa* (Ait.) Pursh), low-bush cranberry (*Viburnum edule* (Michx.) Raf.), and prickly rose (*Rosa acicularis* Lindl.) are the predominant bushes. Tall bluebell (*Mertensia paniculata* (Ait.) G Don), bunchberry (*Cornus canadensis* L.), feather moss (*Pleurozium schreberi* (Brid.) Mitt.), and step moss (*Hylocomium splendens* (Hedw.) DeNot.) are common ground layer species. Tree ages in the stands ranged from 70 to 125 years (Spence and Volney 1999).

Table 1-1. Tree species composition in the vicinity of the sampling spots in the uncut stands of deciduous-dominated, mixed and coniferous-dominated forests.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Deciduous</th>
<th>Mixed</th>
<th>Coniferous</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Picea abies</em></td>
<td>5.2</td>
<td>63.2</td>
<td>83.4</td>
</tr>
<tr>
<td><em>Picea mariana</em></td>
<td>0</td>
<td>0</td>
<td>0.2</td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td>78.0</td>
<td>31.1</td>
<td>11.0</td>
</tr>
<tr>
<td><em>Populus balsamifera</em></td>
<td>11.5</td>
<td>2.8</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Abies balsamea</em></td>
<td>0</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td><em>Pinus contorta</em></td>
<td>0</td>
<td>2.4</td>
<td>0</td>
</tr>
<tr>
<td><em>Larix laricina</em></td>
<td>0</td>
<td>0</td>
<td>4.0</td>
</tr>
<tr>
<td><em>Betula papyrifera</em></td>
<td>0.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Salix sp.</em></td>
<td>4.9</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Figure 1-2. Map of EMEND project area
(EMEND web site www.emend.rr.ualberta.ca/english/homepage_e.html)
Treatments
Mature deciduous-dominated, coniferous-dominated, and mixed stands were located within a 1000 ha area. “Deciduous-dominated” stands had more than 75% deciduous trees, “coniferous-dominated” stands had more than 75% coniferous trees, and “mixed” stands ranged between these two values. The stands occurred on the mesic sites, classified as low-bush cranberry ecosites (Beckingham et al. 1996). Portion of each forest type was harvested, with three levels of tree retention; 0%-clearcuts, 20% and 50% retention. Each stand, harvested and unharvested, was approximately 10 ha. Location of the individual stands is shown in Figure 1-2.

Sampling methodology
Six plots were randomly located within each stand (Fig. 1-3). The plots were 2 m wide and 40 m long, running in the east-west direction. I sampled in four out of the six tree

Figure 1-3. Sampling sites within the stands
plots (randomly selected). Within these plots a sampling site was randomly chosen by
generating a sheet of random numbers that indicated the distance of the sampling site
from the beginning of the plot. Each sampling site was assigned a unique identifier
consisting of a stand – plot – site numbers, and its GPS coordinates were recorded. One
sample was collected from each sampling site, unless indicated otherwise, and the
samples were analyzed separately (not bulked). Forest floor (F and H layer) and upper 7
cm of mineral soil were sampled at each sampling site. The samples were takes with a
soil sampling core with diameter of 4.7 cm.

Statistical analysis
The experimental design was a completely randomized split-plot (with multiple
measurements) with three replicates, where treatments were fixed. Split-plot was soil
layer for soil characteristics and litter type for litter decomposition. Data were analysed
using SAS statistical package version 8.02 (SAS Institute Inc. 2004). The GLM (general
linear model) procedure was used to assess differences among treatments, where one
stand was an experimental unit. The proper testing of each factor was set based on the
components of variance for appropriate model.

Completely randomized factorial split-plot model:

\[ y_{iqr} = \mu + R_{q} + F_{p} + RF_{qp} + E1_{(qp)} + L_{r} + RL_{qr} + FL_{pr} + RFL_{pqr} + E2_{(qpr)} + \varepsilon_{(iqpr)} \]

where:
R = retention level
F = forest type
RF = interaction of retention level and forest type
L = split-plot (e.g. litter type)
RL = interaction of retention level and litter type
FL = interaction of forest type and litter type
RFL = interaction of retention levels, forest type and litter type
Table 1-2. Components of variance for completely randomized factorial split-plot model

<table>
<thead>
<tr>
<th>Components of Variance</th>
<th>tested against</th>
</tr>
</thead>
<tbody>
<tr>
<td>( E(\text{MS}_{\text{main}}) )</td>
<td>( \text{num} \sigma^2_{\text{main}} + \text{um} \sigma^2_{E1} + \text{ma} \sigma^2_{E2} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_R) )</td>
<td>( \text{ntum} \sigma^2_R + \text{um} \sigma^2_{E1} + \text{ma} \sigma^2_{E2} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_F) )</td>
<td>( \text{nsmu} \sigma^2_F + \text{um} \sigma^2_{E1} + \text{ma} \sigma^2_{E2} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_{RF}) )</td>
<td>( \text{nsmu} \sigma^2_{RF} + \text{um} \sigma^2_{E1} + \text{ma} \sigma^2_{E2} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_{E1}) )</td>
<td>( \text{um} \sigma^2_{E1} + \text{ma} \sigma^2_{E2} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_L) )</td>
<td>( \text{nstm} \sigma^2_L + \text{ma} \sigma^2_{E2} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_{mainL}) )</td>
<td>( \text{nm} \sigma^2_{\text{mainL}} + \text{ma} \sigma^2_{E1} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_{RL}) )</td>
<td>( \text{ntmo} \sigma^2_{RL} + \text{ma} \sigma^2_{E1} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_{FL}) )</td>
<td>( \text{nsmo} \sigma^2_{FL} + \text{ma} \sigma^2_{E2} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_{RFL}) )</td>
<td>( \text{nmom} \sigma^2_{RFL} + \text{ma} \sigma^2_{E2} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_{E2}) )</td>
<td>( \text{ma} \sigma^2_{E2} + \sigma^2_{SE} )</td>
</tr>
<tr>
<td>( E(\text{MS}_{SE}) )</td>
<td>( \sigma^2_{SE} )</td>
</tr>
</tbody>
</table>

Note: R is retention level; F is forest type; L is litter type.

Table 1-3. Degrees of freedom and F-test formulas for different factors in completely randomized factorial split-plot model

<table>
<thead>
<tr>
<th>Source</th>
<th>Degrees of freedom</th>
<th>F-test</th>
<th>F_{critical value}</th>
<th>degrees of freedom</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main plot</td>
<td>11</td>
<td>( \text{MS}<em>{\text{main}}/\text{MS}</em>{E1} )</td>
<td>(11,24)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>3</td>
<td>( \text{MS}<em>R/\text{MS}</em>{E1} )</td>
<td>(3,24)</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>2</td>
<td>( \text{MS}<em>F/\text{MS}</em>{E1} )</td>
<td>(2,24)</td>
<td></td>
</tr>
<tr>
<td>RxF</td>
<td>6</td>
<td>( \text{MS}<em>{RF}/\text{MS}</em>{E1} )</td>
<td>(6,24)</td>
<td></td>
</tr>
<tr>
<td>E_1</td>
<td>24</td>
<td>( \text{MS}<em>{E1}/\text{MS}</em>{E2} )</td>
<td>(24,24)</td>
<td></td>
</tr>
<tr>
<td>Split-plot L</td>
<td>1</td>
<td>( \text{MS}<em>L/\text{MS}</em>{E2} )</td>
<td>(1,24)</td>
<td></td>
</tr>
<tr>
<td>Main x split-plot</td>
<td>11</td>
<td>( \text{MS}<em>{\text{main}}/\text{MS}</em>{E2} )</td>
<td>(11,24)</td>
<td></td>
</tr>
<tr>
<td>RxL</td>
<td>3</td>
<td>( \text{MS}<em>{RL}/\text{MS}</em>{E2} )</td>
<td>(3,24)</td>
<td></td>
</tr>
<tr>
<td>FxL</td>
<td>2</td>
<td>( \text{MS}<em>{FL}/\text{MS}</em>{E2} )</td>
<td>(2,24)</td>
<td></td>
</tr>
<tr>
<td>RxFxL</td>
<td>6</td>
<td>( \text{MS}<em>{RFL}/\text{MS}</em>{E2} )</td>
<td>(6,24)</td>
<td></td>
</tr>
<tr>
<td>E_2</td>
<td>24</td>
<td>( \text{MS}<em>{E2}/\text{MS}</em>{SE} )</td>
<td>(24,360)</td>
<td></td>
</tr>
<tr>
<td>Sample error</td>
<td>360</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>431</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: R is retention level; F is forest type; L is litter type.

1.5 Thesis structure
In Chapter 2, I describe the N dynamics in the three types of uncut mixedwood boreal forests typical in the study area. I assess whether natural forests differ in N availability and cycling and whether a trend can be observed towards higher N availability with a higher proportion of deciduous trees; thus addressing Objective 1. I also address
Objective 5 by testing whether N availability is more closely related to N litterfall input or to litter decomposition rates.

Chapter 3 deals with Objective 2 and assesses whether clearcutting in boreal mixedwood forests increases N availability and whether the effects of the VR harvesting are less severe. I also compare the effect of harvesting in the three forest types, and assess whether changes in litterfall input and/or litter decomposition are associated with harvesting (Objective 5).

In Chapter 4 I describe the nitrate cycle in deciduous- and coniferous-dominated stands, estimate the actual production of nitrate, and evaluate the effect of clearcutting, thus addressing Objective 3.

In Chapter 5 I evaluate whether harvesting affects the availability of P, estimate P solubilization by phosphatase activity and explore the relationship between availabilities of P, N, and C (Objective 4).

In Chapter 6 I synthesize the results of the individual chapters, draw conclusions and suggest directions of further research.
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Chapter 2: Nitrogen dynamics in coniferous, deciduous, and mixed boreal mixedwood forests

2.1 Introduction
Boreal forest represents about 30% of the total forested area on the Earth (Burton et al. 2003). It has large supplies of commercially utilisable timber, contains significant pools of C (Apps et al. 1993), and provides important habitats, particularly for large mammals (Thompson 1991). The North American boreal forest covers 5.12 mil km$^2$ (Kuusela 1992) and is a matrix of closed and open canopy forests and bogs. Species composition changes with latitude in favour of coniferous species at northern sites (Perry 1994), but dominant species also vary along an east-west gradient. Black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* (L.) Mill.) and paper birch (*Betula papyrifera* Marsh.) have transcontinental distribution, subalpine fir (*Abies lasiocarpa* Nutt.) and lodgepole pine (*Pinus contorta* Dougl. Ex. Loud) are limited to the western region while balsam fir (*Abies balsamea* (L.) Mill.) and jack pine (*Pinus banksiana* Lamb.) are more common in the east (Zasada et al. 1997).

Mixedwood forests, which have varying proportions of conifers and deciduous (broadleaf) species, depending on site conditions and disturbance history, are found throughout the North American boreal forest zone. In the western boreal forest, they usually occupy relatively nutrient-rich, fresh to moist sites (Kabzems et al. 1986). Maintenance of a deciduous component within boreal forests is currently favoured, partly

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1 A version of this chapter has been accepted for publication in Canadian Journal of Forest Research. Authors: Jerabkova, L., Prescott, C.E. and Kishchuk, B. Title: Nitrogen dynamics in coniferous, deciduous and mixed boreal mixedwood forests
in response to perceived benefits of deciduous species for cycling and availability of nutrients.

In general, deciduous forests are believed to have faster nutrient turnover than coniferous forests (Pastor 1987) and retention in or introduction of deciduous species to conifer stands has been recommended to improve nutrient availability (Comeau 1996; Zasada et al. 1997). It has also been suggested that successional change from deciduous to coniferous stands causes a decline in nutrient availability (Bormann and Sidle 1990), and that exclusion of the deciduous phase in stand development could eventually result in site impoverishment (Bergeron and Harvey 1997). Coniferous stands generally accumulate larger quantities of organic matter and have longer mean nutrient resident times than deciduous stands (Vogt et al. 1986), consistent with slower nutrient turnover.

Nitrogen (N) dynamics is of particular importance in boreal forests as productivity is largely limited by N availability (Mahendrappa and Salonius 1982). Comparisons of N availability in boreal coniferous and deciduous stands have not consistently demonstrated the expected greater N availability in deciduous stands. Boreal aspen stands in southern Quebec (Bauhus et al. 1998) and birch stands in Finland (Priha and Smolander 1999) had higher microbial N (an indicator of N availability - Myrold et al. 1989), compared to spruce stands. Stands of trembling aspen in Quebec had faster turnover and higher accumulation of NO$_3$-N compared to white spruce (Ste-Marie and Paré 1999). In contrast, higher NO$_3$-N concentrations and higher net nitrification were found under pine than under birch in Finnish boreal forests (Priha and Smolander 1999). While 49-year-old aspen stands in Quebec had faster potential net N mineralization and nitrification than white spruce stands, no differences where found between older stands of aspen and
spruce (Paré and Bergeron 1996). There was an indication of faster N turnover under birch compared to balsam fir in the Canadian eastern boreal forest, but it was inconsistent— in the first year N-mineralization rates were higher under birch but nitrification was similar; in the second year there was no difference in N mineralization but nitrification was higher in birch plots (Evans et al. 1998).

In this study we therefore addressed the question of whether deciduous stands have higher N availability and faster N turnover rates than coniferous stands. We compared N availability in natural mature stands with varying proportions of deciduous and coniferous species in western boreal mixedwood region, where white spruce and trembling aspen are the dominant species. We measured several indicators of N availability and turnover, such as pool size of nitrate and inorganic N, net mineralization and nitrification rates, in forest floor and mineral soil of each forest type. We hypothesized that soils supporting a greater proportion of deciduous trees would be accompanied by larger pools and proportions of NO3-N, inorganic N (NH4-N + NO3-N), microbial N, and faster N mineralization and nitrification rates.

The positive effect of deciduous trees on nutrient cycling is usually attributed to their high-quality litter causing faster litter decomposition and faster nutrient cycling (Pastor 1987; Scott and Binkley 1997). However, the decomposition rate, especially the initial rate, has been shown to be a poor predictor of N availability (Giardina et al. 2001). Prescott (2002) suggested that amount of N returned annually in litter may be more influential than its rate of decay in determining N availability at a site. Thus, we also hypothesized that N availability and turnover in boreal mixedwood forests was more closely related to the amounts of N added in litter than to litter decomposition rates. We
tested this by measuring annual litter N input and litter decomposition rates in plots of
each forest type and assessing their degree of correlation with N availability indicators.

2.2 Methods

Site description

This study was a part of the Ecosystem Management Emulating Natural Disturbance
(EMEND) project, a large-scale silvicultural project carried out in northern Alberta
(Spence et al. 1999). The EMEND research study site is located approximately 90 km
north-west of Peace River in the Lower Foothills sub-region of the Clear Hills Upland
eco-region Beckingham, 1996 626 /id}. Elevation ranges from 677 m to 880 m a.s.l.
Mean annual temperature in the nearest climatic station is -0.3 °C, with mean January and
July temperatures of −18.8°C and 14.6°C, respectively. Mean annual precipitation is 433
mm (Environment Canada 2004). Soils were primarily Gray Luvisols with minor
occurrences of Brunisols, Gleysols, and Solonetzie soils derived from similar glacio-
lacustrine and glacial till parent materials containing few coarse fragments (Kishchuk
2004). Soil texture in each of deciduous, mixed, and coniferous stands was clay loam (B.
Kishchuk, unpublished data). Soils were generally well drained and exhibited little
difference in pedogenetic properties across the study area (Kishchuk 2004). Tree ages in
the stands ranged from 70 to 125 years (Spence and Volney 1999). Dominant tree species
were trembling aspen, balsam poplar, and white spruce. Black spruce, balsam fir, and
lodgepole pine also occurred at some sites. Green alder (Alnus crispa (Ait.) Pursh), high-
bush cranberry (Viburnum edule (Michx.) Raf.), and prickly rose (Rosa acicularis Lindl.)
were the predominant shrubs. Tall bluebell (Mertensia paniculata (Ait.) G Don),
bunchberry (Cornus canadensis L.), feather moss (Pleurozium schreberi (Brid.) Mitt.),
and step moss (*Hylocomium splendens* (Hedw.) DeNot.) were common ground layer species.

**Sampling and soil analysis**

Within a 1000 ha area, three replicates of mature deciduous-dominated, coniferous-dominated, and mixed stands were located. Each stand was approximately 10 ha. The “Deciduous-dominated” stands had more than 75% deciduous trees, “coniferous-dominated” stands had more than 75% coniferous trees by number of stems, and “mixed” stands ranged between these two values. In each of the stands, six samples of the F+H layer of the forest floor and the upper 7 cm of mineral soil were collected from randomly selected plots in June and August 2002. Samples from each plot were analyzed separately.

The following nitrogen availability indicators were measured or calculated: \( \text{NH}_4\text{-N} \), \( \text{NO}_3\text{-N} \), soluble inorganic N (SIN), and net rates of N mineralization and nitrification (Binkley and Hart 1989). Net rates of ammonification, nitrification and mineralization were assessed through a 6-week in-situ buried-bag incubation (Hart et al. 1994) between June and August 2002. Net ammonification was calculated as \( \text{NH}_4\text{-N} \) accumulated after 6 weeks minus \( \text{NH}_4\text{-N} \) at the beginning of the incubation; net nitrification as \( \text{NO}_3\text{-N} \) at the end minus \( \text{NO}_3\text{-N} \) at the beginning; net mineralization as inorganic N (\( \text{NH}_4\text{-N} + \text{NO}_3\text{-N} \)) at the end minus inorganic N at the beginning. We also measured microbial N (Binkley and Hart 1989) as another pool of N potentially available to plants (Hodge et al. 2000) through microbial biomass turnover.

Percentage of SIN that is \( \text{NO}_3\text{-N} \) was used to describe relative importance of nitrate as an alternative way to express the \( \text{NH}_4\text{-N} / \text{NO}_3\text{-N} \) ratio used in other studies (Walley et
Similarly, percentage of soluble N that is SIN was used to describe the relative importance of inorganic N analogous to SON / SIN ratio (Northup et al. 1995). This index has not been traditionally used, but it shows the relative contribution of readily available N to the soluble N pool and we believe that these relative indices can be useful in comparisons among sites across broad gradients. Soluble N is defined as soluble inorganic N plus soluble organic N; labile N is defined as soluble N plus microbial N.

Samples were kept on ice while being transported to the laboratory and kept at 4 °C until processing. A portion of each sample was oven-dried at 105°C for 24 hours to measure gravimetric moisture content and another part of the sample was air-dried prior to total N and C analysis. Soluble N, DOC and microbial biomass C and N were analyzed on field-moist samples. Samples were sieved immediately before extraction through a 4-mm mesh sieve to remove coarse mineral and organic fragments (Hart et al. 1997; Brierley et al. 2001). The high clay content made it impossible to pass moist samples through a 2-mm sieve.

For soluble inorganic N (NH4-N and NO3-N) analysis, approximately 10 g fresh mass of sieved soil and 6 g fresh mass of sieved forest floor were extracted with 50 mL of 0.5 M K2SO4. The suspensions were shaken for 1 hour on a reciprocal shaker and then allowed to settle at 4°C for 30 min. They were then gravity-filtered through pre-leached Fisher Q2 filter and filtrate then the vacuum-filtered through a 0.45 µm Duvapore PVDF membrane filter. A portion of the resulting filtrate was set aside and frozen for NH4-N and NO3-N determination. Ammonium and nitrate were analyzed by colorimetric methods on Technicon Autoanalyser II (Technicon Industrial Systems 1973; Technicon Industrial Systems 1977). Another portion of the filtrate (ca 10 mL) was used for the
analysis of soluble organic C, measured as total organic C, after adjustment for inorganic C, by automated persulphate oxidation on an Astro 2000 DOC analyzer Schreurs, 1978 548 /id}. Total soluble N was measured as nitrate after digestion of the filtrates with potassium persulfate Cabrera, 1993 110 /id}. Ten mL of 0.5 M persulfate oxide were added to 5 mL of filtrate and autoclaved for 50 min. Soluble organic N was calculated as the difference between total soluble and inorganic soluble N, adjusted for water loss during autoclaving.

Microbial biomass N and C were estimated using the chloroform-fumigation-extraction method (Horwath and Paul 1994). Samples were incubated with chloroform for 48 hours (Jenkinson and Powlson 1976) to ensure complete lysis of the microbial cells. Microbial N was calculated as total soluble N after the fumigation minus total soluble N before the fumigation and microbial C as total organic C after fumigation minus total organic C before the fumigation, respectively (Martikainen and Palojarvi 1990). No conversion coefficient to account for the incomplete recovery of microbial N and C was used as the primary goal was to compare among forest types. Total N and C of air-dried samples were analyzed on a Leco CN 2000 analyzer.

For extractable phosphorus (P) analysis, approximately 10 g fresh mass of soil and 6 g fresh mass of forest floor were extracted with added 40 mL of Bray-1 solution (Kuo 1996). Samples were shaken for 1 hour on a reciprocal shaker and then settled at 4 °C for 30 min. They were then gravity-filtered through pre-leached Fisher Q2 filters. Phosphorus in the filtrate was determined using the molybdate-blue method on a Technicon Autoanalyzer (Olsen and Sommers 1982).
pH was measured with an Accumet AP62 portable pH/mV meter (Fisher Scientific) in fresh samples suspended in 0.01 M CaCl$_2$ in ratios of 1:2 by fresh weight for mineral soil and 1:4 for forest floor (Kalra and Maynard 1991). Preliminary trials showed independence of pH values in dry soil suspension ratios up to 1:50, and we were thus able to use fresh mass ratios. Bulk density of the mineral soil was determined by core sampling in 2000; bulk density of forest floor was determined by quadrat sampling in 2002. Bulk density values were used to calculate nutrient and C content and concentration on the volume basis.

*Vegetation description*
To characterize the vegetation structure in the vicinity of the sampling plots, trees were measured and understory vegetation was described within 10-m radius circle plot centered on the sampling plot, at 4 out of 6 sampling plots in each stand. Diameter of trees larger than 10 cm was measured at 1.30 m height. Understory vegetation was described by coverage (<1; 1-5; 5-25; 25-50; 50-75; >75 %) of vegetation groups (alder, other shrubs, low shrubs, grass, herbs, moss).

*Litter input and decomposition*
Overstory litterfall was collected in 50 x 50-cm litter traps (fiberglass mesh with 1.5 mm openings stapled into a plywood frame) for one year (2002-2003) at 4 of the 6 sampling plots in each stand; one trap per plot. Litter was air-dried, sorted into needles, leaves, twigs and "other" faction, which was mostly cones. Nitrogen concentration of each of these fractions was measured on a Leco CN 2000 analyzer after grinding and used to calculate annual aboveground litter input for each stand.
To measure rates of litter decomposition, standard samples of aspen and spruce litter were incubated on-site in litter bags for 1 year (2003-2004) and weight loss determined. This litter was collected in October 2002 from one place within the experimental area. Two grams of air-dried litter were placed into mesh bags with 1.5-mm openings, which were double-layered to minimize the spillage of spruce needles. Both types of litter were placed out at all sampling plots, so the influence of both site and litter could be distinguished (one bag of one litter type at each sampling plot). The litter bags were placed on the top of the forest floor and pinned by a metal flag. The bags were collected after one year, air-dried, weighed and analyzed for C and N concentrations and moisture content. Litter masses were adjusted for oven-dried mass. Average decomposition of on-site litter was calculated as weighted average of decomposition rates of aspen and spruce based on their proportions in the litterfall.

Statistical analysis
The experimental design was a completely randomized split-plot (with multiple measurements) with three replicates, where treatments were fixed. The split-plot factor was the soil layer for soil characteristics and litter type for litter decomposition. Data were analysed using SAS statistical package version 8.02 (SAS Institute Inc. 2004). The GLM (general linear model) procedure was used to assess differences between forest types, where one stand was an experimental unit. Factor analysis and canonical correlation (Tabachnick and Fidell 2001) were used to explore interactions among soil variables and vegetation characteristics, and multiple linear regression was applied to identify actual predictors of the soil variables. These analyses were based on individual sampling plot data. None of the data fulfilled the requirements of normality and equal variances for analysis of variance, and several transformations did not solve this problem,
so the data were ranked. The ranked values were normalized (Blomm 1958) to enable parametric statistical tests as for original data. The significance level was set at $\alpha=0.1$ for analysis of variance, to account for high within-stand variability in most soil N measurements, and $\alpha=0.05$ for other analyses. Bonferroni adjustment was used for multiple means comparison, no adjustment was applied experiment wide.

Extractable NH$_4$-N, NO$_3$-N, and SON values are presented as the average of the June and August 2002 samplings, so that they could be used in the analyses with data measured only once. Although there were some differences in these values between the sampling dates, the trend across the forest types was the same.

2.3 Results
Forest floors in the deciduous-dominated stands had the highest total N concentration and lowest C/N ratio of the forest types (Table 2-1). Deciduous forest floors also had higher NH$_4$-N, inorganic N and microbial N concentration, although the difference in the latter was not significant (Table 2-1). Similar trends were seen when expressed as content, but only the differences in NH$_4$-N and inorganic N were significant (Table 2-1). Nitrate concentrations were low at all sites, often below detection levels, and did not differ among forest types. For the mineral soil samples, there were no differences between forest types for any of the N availability indices (Table 2-2). The deciduous stands had the highest pH and extractable P concentrations, both in forest floor and mineral soil (Table 2-3).

Rates of net N mineralization were highest in the forest floor of mixed stands (Table 2-4). The amount of SIN accumulated per g of forest floor during the field incubation was also higher in mixed stands. There were no differences among forest
types in the rate of net nitrification and NO$_3$-N accumulation during the incubation. There was also no difference in the percentage of NO$_3$-N from total inorganic N accumulated during incubation.

Deciduous stands had a higher proportion of labile N in the microbial biomass (p=0.08) in the forest floor, and inorganic N (SIN) formed a larger proportion of the total soluble N pool (Fig. 2-1). However, the proportion of SIN that was NO$_3$-N in mineral soil was higher (p=0.025) in coniferous stands.

*Relation of N availability indices to vegetation*

Tree species composition in the sampling plots in the three forest types is shown in Fig. 2-2. Forest floor N values were more strongly correlated with vegetation characteristics than were mineral soil N values (Table 2-5). In keeping with our hypothesis, the proportion, number and basal area (data not shown) of deciduous trees were all positively correlated with forest floor soluble N, SIN, NH$_4$-N, microbial N pools and pH and negatively correlated with the forest floor microbial C/N ratio (Table 2-5). The proportion of deciduous trees was also positively correlated with percentage of SIN from soluble pool and inorganic N accumulated during field incubation. Coverage of alder correlated positively with NH$_4$-N, microbial N and accumulated NH$_4$-N, and grass coverage with nitrification and accumulated nitrate. Moss cover was negatively correlated with ammonium, microbial N and percentage of SIN from soluble N. These trends were confirmed by factor analysis of the forest floor.

The first vegetation factor, representing “deciduousness”, included number, basal area and proportion of deciduous trees. The second factor, representing “dense coniferous stands”, consisted of total tree numbers and basal area, number and basal area of
coniferous trees and moss cover. The third factor representing “soil N availability” was positively associated with SIN, NH$_4$-N, microbial N and negatively with percentage of SON from labile pool and microbial C/N ratio. The “N availability” factor correlated positively with “deciduousness” and negatively with “dense coniferous stands”. The trend was similar but weaker when both soil layers were analyzed together, but there were no significant correlations for mineral soil.

We also assessed whether N availability indices could be predicted from stand characteristics. No common predictors existed for both forest floor and mineral soil data, so the layers were again analyzed separately. In the forest floor, microbial N and NH$_4$-N concentrations and proportion of soluble N made up by SIN could be reliably predicted from stand characteristics. NH$_4$-N concentration was predicted by soil pH and moss cover (NH$_4$-N = 1.23 pH – 0.04 moss cover + 1.31; R$^2$ = 0.58; p < 0.0001); microbial N concentration by moisture content, proportion of deciduous trees and moss cover (microbial N = 0.21 moisture + 0.03 proportion deciduous – 0.67 moss cover; R$^2$ = 0.57; p < 0.0001). The proportion of soluble N that was SIN was associated with low soil soluble C/N ratio and low moss cover, which together explained 60% of the variation (SIN proportion of soluble N = - 0.434 soluble C/N - 0.49 moss cover; R$^2$ = 0.60; p < 0.0001). In the mineral soil, 66% of the variation in NH$_4$ concentrations could be explained by total basal area (NH$_4$ = 0.76 + 1.24 basal area; R$^2$ = 0.66; p < 0.0001).

**Litter input and decomposition**

There was no significant difference in total litter mass production or N content between the three stand types (Fig. 2-3). However, foliar litter input (leaves and needles) was significantly greater in deciduous than coniferous stands both in mass (p=0.029) and N.
content (p=0.046). The foliar litterfall flux of N was positively correlated with forest floor soluble N (r=0.64), SIN (r=0.65) (Fig. 2-4a), NH$_4$-N (r=0.59), microbial N (r=0.56) and SIN as proportion of soluble N (r=0.46), and was negatively correlated with microbial C/N ratio (r=-0.47) in the forest floor.

Aspen leaf litter decomposed significantly faster (p=0.064) than spruce needles during the 1-year incubation, but there were no differences in the weight loss of either litter type among the three forest types. Litter decomposition was only weakly correlated with soil available N (Fig. 2-4b) and the trends were different for aspen and spruce litter. Decomposition rate of aspen litter was weakly correlated with NH$_4$-N (r=0.33) and microbial N (r=0.27) concentrations in the forest floor. While a decomposition rate of spruce litter was negatively correlated with forest floor SIN (r=-0.33) and NH$_4$-N (r=-0.37) concentration.

2.4 Discussion
Most measures of soil N availability were consistent with our first hypothesis of higher N availability in deciduous stands. Higher ammonium and soluble inorganic N concentration in the forest floor of deciduous stands has also been found in boreal forest in Quebec (Côté et al. 2000). The higher proportion of soluble N consisting of SIN also supports the hypothesis of relatively higher N availability in deciduous stands, as a low proportion of SIN can be indicative of sites limited by N (Northup et al. 1995). The tendency for a greater soil microbial N concentrations in deciduous forests also indicates higher N availability as the soil microbial biomass is considered by some to be a relatively labile pool of N (Myrold 1987; Wardle 1992). However, Martikainen and Palojarvi (1990) suggested that microbial N is rather unavailable. Forest floors in the
Deciduous stands had higher total N concentration but similar total N capital than in coniferous stands, reflecting less organic matter accumulation (Hannam et al. 2004). The same difference between deciduous and coniferous forests was reported in birch/aspen and black spruce stands in Alaska (Troth et al. 1976).

Deciduous stands did not have higher nitrate concentrations or net nitrification rates despite having soil characteristics generally favourable to nitrification, such as higher pH, higher ammonium concentrations, and lower soil C/N ratios (Ste-Marie and Paré 1999). The lack of differences could reflect sensitivity of the extraction method as NO₃⁻-N concentrations were very low. However, we also found no difference in amounts of NO₃⁻-N collected on ion exchange probes incubated at some of these sites (unpublished data). Paré and Bergeron (1996) also found no differences in net nitrification in mature aspen and spruce stands, and in which NO₃⁻-N levels were also very low. In Finland, Priha and Smolander (1999) found higher NO₃⁻-N levels and a higher net nitrification rate in pine forest soil compared to birch, despite lower pH. Thus, at least in boreal forests, deciduous forest floors should not be assumed automatically to be "nitrate environments" (sensu Kronzucker et al. 1997).

The positive correlations between the pools of soil available N and the amount of N returned in litter supported our second hypothesis that soil N availability is more closely related to input of N in litterfall than to decomposition rate. Correlations between litter N content and net N mineralization rates have been reported within (Vitousek et al. 1982; Nadelhoffer et al. 1983; Ferrari 1999) and across forest types (Reich et al. 1997). Thus we suggest that litterfall inputs of N may be a better indicator of N availability in forests than are rates of litter decomposition.
Faster decomposition of aspen leaves than coniferous needles during the first year is consistent with other studies (Alban 1982; Prescott et al. 2000a). This difference may, however, be short-lived, as other studies indicate that, in the later stages, the decomposition rate of leaf litter (including aspen) slows down more than that of needle litter, with rates converging after 3 years (Berg and Ekbohm 1991; Moore et al. 1999; Prescott et al. 2000b; Prescott et al. 2004). As we found also no correlation between soil and forest floor N availability and average decomposition rate of on-site litter, our results do not support the hypothesis that deciduous litter results in higher N availability because of faster decomposition.

Faster decay of spruce needles on sites with low N availability may be related to their higher lignin concentrations than aspen leaves, as inorganic N has been shown to inhibit ligninolytic activity (Carreiro et al. 2000; DeForest et al. 2004). In our study, the sites with low inorganic N and faster spruce litter decomposition, were often spruce sites. The negative relationship between N availability and litter decomposition may then reflect a “home-field advantage” (Hunt et al. 1988), where processes and organisms involved in the decomposition are specific for each litter type, resulting in faster decay of particular litter at the sites where it is naturally dominant litter type.

The higher forest floor pH in aspen stands is in keeping with other comparisons of spruce and aspen (Bauhus et al. 1998) and deciduous and coniferous forests in general (Raulund-Rasmussen and Verje 1995; Priha and Smolander 1999; Hagen-Thorn et al. 2004). The higher forest floor pH of aspen stands is often associated with higher Ca concentration (Brais et al. 1995). This results from calcium being redistributed in the soil profile, such that the forest floor is enriched and deeper mineral soil depleted of Ca
(Alban 1982). This was evident in this study as exchangeable calcium concentrations were higher in forest floors of deciduous stands, but lower in the deepest mineral soil sampled (10-17 cm) compared to coniferous stands (Kishchuk 2002). The higher pH might also contribute to the observed higher availability of P in the deciduous stands, but aspen litter is known to have higher P concentrations (Flanagan and Van Cleve 1983).

Although the differences in N cycling among forest types are consistent with other studies of spruce and aspen, we cannot assume that the differences are directly and solely attributable to stand composition. Because we studied natural forests, the possibility exists that the patterns reflect other site factors such as slope position (Prescott et al. 2000b; Chen et al. 1998) and soil texture (Reich et al. 1997; Levula et al. 2003), affect species composition and N cycling characteristics. However, soil moisture contents did not differ among the forest types and there is no consistent trend in the distribution of aspen- and spruce-dominated stands within the studied landscape with respect to topography (slope position, slope and aspect). There was also little difference among forest types in soil texture (Kishchuk 2004). Slope position or soil texture are thus not likely to be cause of the differences in N availability among forest types.

There were also no differences in total and available N and other major chemical properties among the forest types in the deeper soil layers (Kishchuk, 2002 113 /id, but nitrogen availability in upper layers was directly related to the proportion of deciduous trees. These findings suggest that the differences detected in the upper soil layers and forest floor reflect the influence of the vegetation rather than inherent differences in the soils at the sites.
The negative correlation between cover of moss and N availability is consistent with the documented ability of feather and step moss to immobilize inorganic N (Weber, 1981). The positive correlation between N availability and cover of alder and grass suggest that these plants may increase N availability. However, our experimental design does not allow us to determine if understory vegetation composition was contributing to differences in N availability, responding to the differences, or simply associated with site conditions unrelated to N availability.

The higher rates of net N mineralization in the mixed stands coincide with their having the highest basal area, volume and tree size of the forest types (Spence and Volney 1999). This may indicate a mixture effect resulting in higher productivity of mixed stands, similar to in mixed stands of spruce and aspen in eastern Alberta (MacPherson et al. 2001).

Some N availability indices (nitrification rates, proportion of SIN) increased with stand openness, but adjustment for tree numbers or basal area through analysis of covariance did not significantly affect the outcome of the comparisons. Stand density is thus not likely to be a main influence on the N dynamics.

Management implications
Our results suggest that, maintaining a deciduous component in coniferous stands may result in a higher proportion of soil N being in the available form. A presence of deciduous trees in a spruce forest appear particularly beneficial for the spruce as higher levels of NH₄-N were observed under deciduous species, and spruce is believed to prefer ammonium as a N source. Hypothetically, perpetuation of pure coniferous stands may shift the soil N pool towards larger proportion of relatively unavailable forms. As this
study only presents short-term results we can not speculate about the long-term consequences and how reversible the changes might be. As no difference was found in nitrate availability and net nitrification it does not seem that one forest type would be more prone to N losses. Litter N input is a better indicator of N availability than decomposition rate. Understory vegetation may serve as a valuable indicator of N availability, and its active or passive role in N cycling should be more closely investigated.
### 2.5 Tables and Figures

Table 2-1. Concentration [µg g⁻¹] and content [mg m⁻²] of total C, and several forms of N in the forest floors in the three forest types, SON is soluble organic N.

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Total C [g g⁻¹]</th>
<th>Total N [mg g⁻¹]</th>
<th>C/N</th>
<th>NO₃-N [µg g⁻¹]</th>
<th>NH₄-N [µg g⁻¹]</th>
<th>SON [µg g⁻¹]</th>
<th>Microbial N [µg g⁻¹]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous</td>
<td>0.411 (0.02) a</td>
<td>21.51 (0.7) a**</td>
<td>19.2 (0.7) a**</td>
<td>0.34 (0.27) a</td>
<td>100.40 (5.05) a**</td>
<td>132.29 (7.74) a</td>
<td>942.23 (0.02) a</td>
</tr>
<tr>
<td>Mixed</td>
<td>0.427 (0.02) a</td>
<td>17.84 (0.83) ab</td>
<td>24.8 (0.8) ab</td>
<td>1.55 (0.27) a</td>
<td>63.50 (4.83) b</td>
<td>205.31 (7.40) a</td>
<td>575.44 (0.83) ab</td>
</tr>
<tr>
<td>Coniferous</td>
<td>0.389 (0.03) a</td>
<td>12.19 (1.17) b</td>
<td>32.4 (1.2) b</td>
<td>0.65 (0.28) a</td>
<td>50.86 (4.98) b</td>
<td>159.17 (7.40) a</td>
<td>422.86 (0.27) a</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Content [g m⁻²]</th>
<th>[mg m⁻²]</th>
<th>[mg m⁻²]</th>
<th>[mg m⁻²]</th>
<th>[mg m⁻²]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous</td>
<td>2566.18 (209.42) a</td>
<td>2566.18 (11.88) a</td>
<td>2.15 (4.04) a</td>
<td>610.10 (12.61) a</td>
<td>626.20 (79.21) a</td>
</tr>
<tr>
<td>Mixed</td>
<td>2578.53 (247.79) a</td>
<td>2578.53 (14.06) a</td>
<td>9.36 (4.04) a</td>
<td>383.87 (40.75) b</td>
<td>959.20 (727.41) a</td>
</tr>
<tr>
<td>Coniferous</td>
<td>2970.83 (310.62) a</td>
<td>2970.83 (20.58) a</td>
<td>5.17 (4.17) a</td>
<td>405.88 (72.0) b</td>
<td>900.20 (75.74) a</td>
</tr>
</tbody>
</table>

Note: Each value is the least squares mean of three replicates of forest and layer combinations with standard error in the brackets. Different letters indicate significant differences among the forest types; * indicates difference at p < 0.1, ** difference at p < 0.05.
Table 2-2. Concentration [μg g$^{-1}$] and content [mg m$^{-2}$] of total C, and several forms of N in the upper 7 cm of mineral soil in the three forest types, SON is soluble organic N.

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Total C [g g$^{-1}$]</th>
<th>Total N [mg g$^{-1}$]</th>
<th>C/N</th>
<th>NO$_3^-$N [μg g$^{-1}$]</th>
<th>NH$_4^-$N [μg g$^{-1}$]</th>
<th>SON [μg g$^{-1}$]</th>
<th>Microbial N [μg g$^{-1}$]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous</td>
<td>0.023 (0.028)a</td>
<td>2.17</td>
<td>11.3 (1.0)a</td>
<td>0.11</td>
<td>3.57</td>
<td>13.13</td>
<td>45.70</td>
</tr>
<tr>
<td>Mixed</td>
<td>0.026 (0.027)a</td>
<td>1.91</td>
<td>13.7 (0.97)a</td>
<td>0.19</td>
<td>2.17</td>
<td>15.38</td>
<td>62.37</td>
</tr>
<tr>
<td>Coniferous</td>
<td>0.038 (0.021)a</td>
<td>2.99</td>
<td>13.4 (0.93)a</td>
<td>0.44</td>
<td>2.23</td>
<td>18.47</td>
<td>52.98</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Total C [g m$^{-2}$]</th>
<th>Total N [mg m$^{-2}$]</th>
<th>C/N</th>
<th>NO$_3^-$N [mg m$^{-2}$]</th>
<th>NH$_4^-$N [mg m$^{-2}$]</th>
<th>SON [mg m$^{-2}$]</th>
<th>Microbial N [mg m$^{-2}$]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous</td>
<td>1864.47</td>
<td>157.60</td>
<td>7.62</td>
<td>259.56</td>
<td>741.80</td>
<td>3 326.73</td>
<td></td>
</tr>
<tr>
<td>Mixed</td>
<td>(233.2)a</td>
<td>(16.97)a</td>
<td>(4.04)a</td>
<td>(42.00)a</td>
<td>(78.07)a</td>
<td>(702.62)a</td>
<td></td>
</tr>
<tr>
<td>Coniferous</td>
<td>1753.94</td>
<td>127.09</td>
<td>12.68</td>
<td>144.39</td>
<td>802.30</td>
<td>4 147.65</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(288.67)a</td>
<td>(16.38)a</td>
<td>(4.04)a</td>
<td>(40.75)a</td>
<td>(75.74)a</td>
<td>(909.75)a</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2856.54</td>
<td>218.26</td>
<td>29.53</td>
<td>148.43</td>
<td>989.20</td>
<td>3 522.85</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(223.60)a</td>
<td>(15.67)a</td>
<td>(4.04)a</td>
<td>(39.45)a</td>
<td>(75.74)a</td>
<td>(702.62)a</td>
<td></td>
</tr>
</tbody>
</table>

Note: Each value is the least squares mean of three replicates of forest and layer combinations with standard error in the brackets. Different letters indicate significant differences among the forest types; * indicates difference at p < 0.1, ** difference at p < 0.05.
Table 2-3. pH, gravimetric moisture, extractable P and microbial C concentrations in the forest floor and upper 7 cm of mineral soil in the three forest types

<table>
<thead>
<tr>
<th>Forest type</th>
<th>pH&lt;sub&gt;(CaCl₂)&lt;/sub&gt; [g·g&lt;sup&gt;-1&lt;/sup&gt;]</th>
<th>Moisture [g·g&lt;sup&gt;-1&lt;/sup&gt;]</th>
<th>Extractable P [µg·g&lt;sup&gt;-1&lt;/sup&gt;]</th>
<th>Microbial C [µg·g&lt;sup&gt;-1&lt;/sup&gt;]</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Forest floor</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deciduous</td>
<td>5.59 (0.12)a**</td>
<td>235.14 (12.65)a</td>
<td>46.15 (4.27)a</td>
<td>4373.53 (357.52)a</td>
</tr>
<tr>
<td>Mixed</td>
<td>4.89 (0.12)b</td>
<td>201.03 (12.65)a</td>
<td>43.01 (4.27)a</td>
<td>4653.12 (357.52)a</td>
</tr>
<tr>
<td>Coniferous</td>
<td>4.44 (0.12)b</td>
<td>244.72 (12.65)a</td>
<td>42.91 (4.27)a</td>
<td>3999.19 (380.61)a</td>
</tr>
<tr>
<td><strong>Mineral soil</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deciduous</td>
<td>4.83 (0.13)a**</td>
<td>36.20 (12.65)a</td>
<td>18.10 (4.42)a</td>
<td>276.40 (397.05)a</td>
</tr>
<tr>
<td>Mixed</td>
<td>4.23 (0.13)b</td>
<td>41.91 (12.65)a</td>
<td>8.70 (4.28)ab</td>
<td>455.84 (397.05)a</td>
</tr>
<tr>
<td>Coniferous</td>
<td>4.71 (0.13)ab</td>
<td>75.46 (12.65)a</td>
<td>8.03 (4.55)b</td>
<td>348.68 (447.50)a</td>
</tr>
</tbody>
</table>

Note: Each value is the least squares mean of three replicates of forest and layer combinations with standard error in the brackets. Different letters indicate significant differences among the forest types; * indicates difference at p < 0.1, ** difference at p<0.05.

Table 2-4. Rates of net N mineralization and nitrification in the forest floor and upper 7 cm of mineral soil in the three forest types

<table>
<thead>
<tr>
<th>Mineralization</th>
<th>Concentration [µg·g&lt;sup&gt;-1&lt;/sup&gt;·d&lt;sup&gt;-1&lt;/sup&gt;]</th>
<th>Content [mg·m&lt;sup&gt;-2&lt;/sup&gt;·d&lt;sup&gt;-1&lt;/sup&gt;]</th>
<th>Concentration [µg·g&lt;sup&gt;-1&lt;/sup&gt;·d&lt;sup&gt;-1&lt;/sup&gt;]</th>
<th>Content [mg·m&lt;sup&gt;-2&lt;/sup&gt;·d&lt;sup&gt;-1&lt;/sup&gt;]</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Forest floor</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deciduous</td>
<td>1.81 (0.51)ab</td>
<td>1.13 (0.68)a</td>
<td>0.98 (0.33)a</td>
<td>0.62 (0.24)a</td>
</tr>
<tr>
<td>Mixed</td>
<td>3.58 (0.50)a*</td>
<td>2.17 (0.68)a</td>
<td>1.04 (0.32)a</td>
<td>0.64 (0.23)a</td>
</tr>
<tr>
<td>Coniferous</td>
<td>0.92 (0.50)b</td>
<td>0.73 (0.66)a</td>
<td>0.12 (0.32)a</td>
<td>1.0 (0.23)a</td>
</tr>
<tr>
<td><strong>Mineral soil</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deciduous</td>
<td>0.16 (0.57)a</td>
<td>1.15 (0.75)a</td>
<td>0.03 (0.32)a</td>
<td>0.22 (0.27)a</td>
</tr>
<tr>
<td>Mixed</td>
<td>0.17 (0.50)a</td>
<td>1.12 (0.66)a</td>
<td>0.08 (0.32)a</td>
<td>0.50 (0.23)a</td>
</tr>
<tr>
<td>Coniferous</td>
<td>0.30 (0.52)a</td>
<td>2.01 (0.68)a</td>
<td>0.04 (0.32)a</td>
<td>0.27 (0.24)a</td>
</tr>
</tbody>
</table>

Note: Each value is the least squares mean of three replicates of forest and layer combination with standard error in the brackets. Different letters indicate significant differences among the forest types; * indicates difference at p < 0.1, ** difference at p<0.05.
Table 2-5. Correlations between soil N variables and characteristics of vegetation in the immediate vicinity of sampling plots in all forest types. FF is forest floor, min is upper mineral soil, accum NO₃ is NO₃-N accumulated after 6-wks incubation, accum SIN is soluble inorganic N accumulated after 6-wks incubation.

<table>
<thead>
<tr>
<th></th>
<th>total trees</th>
<th>total conifers</th>
<th>total deciduous</th>
<th>% deciduous</th>
<th>alder</th>
<th>low shrubs</th>
<th>grass</th>
<th>moss</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soluble N</td>
<td>FF</td>
<td>0.00</td>
<td>-0.4</td>
<td>0.51</td>
<td>0.53</td>
<td>-0.34</td>
<td>0.09</td>
<td>-0.44</td>
</tr>
<tr>
<td></td>
<td>min</td>
<td>0.12</td>
<td>0.21</td>
<td>-0.20</td>
<td>-0.27</td>
<td>0.22</td>
<td>-0.24</td>
<td>0.15</td>
</tr>
<tr>
<td>Inorganic N</td>
<td>FF</td>
<td>-0.16</td>
<td>-0.56</td>
<td>0.49</td>
<td>0.60</td>
<td>0.32</td>
<td>-0.52</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>min</td>
<td>-0.31</td>
<td>-0.35</td>
<td>0.11</td>
<td>0.12</td>
<td>0.15</td>
<td>-0.53</td>
<td>0.18</td>
</tr>
<tr>
<td>NH₄-N</td>
<td>FF</td>
<td>-0.25</td>
<td>-0.63</td>
<td>0.48</td>
<td>0.58</td>
<td>0.43</td>
<td>-0.56</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>min</td>
<td>-0.29</td>
<td>-0.38</td>
<td>0.17</td>
<td>0.17</td>
<td>0.19</td>
<td>-0.56</td>
<td>0.17</td>
</tr>
<tr>
<td>NO₃-N</td>
<td>FF</td>
<td>-0.19</td>
<td>-0.10</td>
<td>-0.06</td>
<td>-0.06</td>
<td>0.19</td>
<td>-0.31</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>min</td>
<td>-0.18</td>
<td>0.19</td>
<td>-0.37</td>
<td>0.44</td>
<td>-0.31</td>
<td>0.14</td>
<td>0.19</td>
</tr>
<tr>
<td>Microbial N</td>
<td>FF</td>
<td>-0.06</td>
<td>-0.53</td>
<td>0.56</td>
<td>0.47</td>
<td>0.39</td>
<td>-0.22</td>
<td>-0.00</td>
</tr>
<tr>
<td></td>
<td>min</td>
<td>0.16</td>
<td>0.05</td>
<td>0.1</td>
<td>-0.14</td>
<td>-0.18</td>
<td>0.05</td>
<td>0.15</td>
</tr>
<tr>
<td>Microbial C/N</td>
<td>FF</td>
<td>0.19</td>
<td>0.50</td>
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<td>-0.34</td>
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</tr>
<tr>
<td></td>
<td>min</td>
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<td>0.28</td>
<td>-0.18</td>
<td>-0.15</td>
<td>-0.16</td>
<td>-0.03</td>
<td>-0.29</td>
</tr>
<tr>
<td>Nitrification</td>
<td>FF</td>
<td>-0.50</td>
<td>-0.32</td>
<td>0.31</td>
<td>0.29</td>
<td>0.20</td>
<td>-0.30</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>min</td>
<td>-0.27</td>
<td>-0.30</td>
<td>0.19</td>
<td>0.00</td>
<td>0.31</td>
<td>-0.17</td>
<td>0.30</td>
</tr>
<tr>
<td>Accum NO₃</td>
<td>FF</td>
<td>-0.48</td>
<td>-0.22</td>
<td>0.31</td>
<td>0.30</td>
<td>0.43</td>
<td>-0.32</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>min</td>
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<td>-0.36</td>
<td>0.05</td>
<td>0.02</td>
<td>0.24</td>
<td>-0.19</td>
<td>0.31</td>
</tr>
<tr>
<td>Accum SIN</td>
<td>FF</td>
<td>-0.23</td>
<td>-0.39</td>
<td>0.33</td>
<td>0.46</td>
<td>0.23</td>
<td>-0.32</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>min</td>
<td>-0.45</td>
<td>-0.36</td>
<td>0.05</td>
<td>0.02</td>
<td>0.24</td>
<td>-0.19</td>
<td>0.32</td>
</tr>
<tr>
<td>SIN/soluble N</td>
<td>FF</td>
<td>-0.36</td>
<td>-0.54</td>
<td>0.24</td>
<td>0.42</td>
<td>0.32</td>
<td>-0.42</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>min</td>
<td>-0.45</td>
<td>-0.51</td>
<td>0.19</td>
<td>0.24</td>
<td>0.28</td>
<td>-0.49</td>
<td>0.18</td>
</tr>
<tr>
<td>pH</td>
<td>FF</td>
<td>-0.27</td>
<td>-0.64</td>
<td>0.60</td>
<td>0.62</td>
<td>0.33</td>
<td>-0.60</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>min</td>
<td>-0.28</td>
<td>-0.35</td>
<td>0.19</td>
<td>0.27</td>
<td>0.08</td>
<td>-0.27</td>
<td>-0.07</td>
</tr>
</tbody>
</table>

Note: "Total trees" = total number of trees per ha, "total conifers" = total number of coniferous trees per ha, "total deciduous" = total number of deciduous trees per ha, "% deciduous" = proportion of deciduous trees from total number of trees, "alder, low shrubs, grass, moss" = percent coverage of each group.

Numbers in bold are r-values significant at p<0.05.
Fig. 2-1. Distribution of N (%) within the labile pool (total soluble N and microbial N) in forest floor and upper 7 cm of mineral soil in deciduous, mixed and coniferous stands. SON is soluble organic N, micrN is microbial N.
Fig. 2-2. Tree density and species composition in the vicinity of sampling spots; a) number of trees per ha b) basal area per ha. (Each column represents the least squares mean of three replicates of forest and tree type combinations with bars indicating standard error. There were no significant differences between forest types.

Fig. 2-3. Canopy litter Annual mass (a) and mean N content (b) in the three forest types (g·m⁻²). The values are means of 3 stands for each forest type.
Fig. 2-4. Relationship between concentration of soluble inorganic N (SIN) in the forest floor and a) N input in foliar litter and b) decomposition rate in the three forest types.
2.6 References


Chapter 3: Effect of variable-retention harvesting on soil nitrogen availability in boreal mixedwood forests

3.1 Introduction

Clear-cut harvesting of forests is often associated with increased availability and losses of nutrients, especially N in the forms of nitrate or inorganic N (Bradley et al. 2000; Prescott et al. 2003). Net rates of N mineralization and nitrification often rise after clear-cutting (Fisk and Fahey 1990; Frazer et al. 1990) but may also remain unchanged (Barg and Edmonds 1999) or even decrease (Chang et al. 1995). Soluble organic N (SON) concentrations may temporarily increase after harvesting as a result of organic matter input from slash, but are likely to decline after longer periods (Hannam and Prescott 2003). Microbial biomass N has also been found to decrease after harvesting (Chang et al. 1995). Total microbial biomass may be reduced (Bradley et al. 2000; Siira-Pietikäinen et al. 2001), remain unchanged (Smolander et al. 1998; Barg and Edmonds 1999) or increase (Sundman and Huhta 1978) after harvesting.

Variable-retention harvesting (VR), in which a portion of the trees are left standing, has been suggested as an environmentally acceptable alternative to clear-cut harvesting. Sites harvested through variable retention have been shown to have microclimatic conditions, available N levels and mineralization rates between those of clear-cuts and unharvested stands (Barg and Edmonds 1999; Lajzerowicz et al. 2004; Lapointe et al. 2005). The spatial pattern of retention, i.e. dispersed or aggregated, also influences the effects of harvesting on N availability.

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1 A version of this chapter has been submitted for publication in Canadian Journal of Forest Research Authors: Jerabkova, L., Prescott, C.E. and Kishchuk, B. Title: Effect of variable-retention harvesting on soil nitrogen availability in boreal mixedwood forests
and losses (Siira-Pietikäinen et al. 2001). Nitrate concentrations in the soil or soil solution are not usually elevated in single-tree removal treatments (Prescott et al. 2003) (even when as much as 60% of trees were removed; (Knight et al. 1991), but usually increase when canopy gaps are created (Bauhus and Barthel 1995; Prescott et al. 2003).

Clearcut harvesting is common in western boreal mixedwoods but concerns about N losses and effects on future stand productivity has prompted introduction of VR harvesting in these forests. Boreal mixedwood forests of western Canada consist of varying proportions of deciduous tree species; mainly trembling aspen (*Populus tremuloides* Michx.); and coniferous species; mainly white spruce (*Picea glauca* (Moench) Voss), typically occurring on relatively nutrient-rich sites (Kabzems et al. 1986). The cold climate and low soil pH of unharvested boreal forests are believed to cause slow N mineralization and nitrification, and the risk of leaching after harvesting is thought to be low as a consequence of a general N limitation and efficient ammonium and nitrate cycling (Tamm 1991). The effects of clearcut harvesting in boreal mixedwoods have been variable. Patch clearcuts of trembling aspen in Saskatchewan did not have higher nitrate levels or nitrification rates than forests (Maynard and MacIsaac 1998), whereas clearcutting of mixed aspen-spruce stands has led to increased net nitrification and narrowing of the NH₄-N / NO₃-N ratio (Walley et al. 1996). In mixed stands in northern Alberta, Carmosini et al. (2002) found higher NH₄-N production and immobilization in harvested sites, while NO₃-N production and immobilization levels were low and were not changed by harvesting. In contrast, Bock and Van Rees (2002) reported minimal changes to forest floor and mineral soil properties and nutrient content following harvest of a western boreal mixedwood forest.
Variable-retention harvesting increases the costs of harvesting. So it is important to know how well VR fulfills its objective of retaining some of the “forest characteristics” and diminishing some of the potential adverse effects of clear-cutting. In this study we compared the effects of clear-cut and VR harvesting of boreal mixedwood forests on N availability in the forest floor and mineral soil. We measured concentrations of nitrate, ammonium, soluble organic N and microbial N to estimate available and potentially available N pools in uncut, 50% and 20% retention, and clear-cuts of deciduous- and coniferous-dominated stands. Litter decomposition and N mineralization rates were measured to indicate whether rates of processes involved in cycling and availability of N have been altered. We hypothesized that: 1) clear-cuts will have higher nitrate and inorganic N concentrations, a greater proportion of inorganic N as NO₃-N, a greater proportion of soluble N as inorganic N, greater rates of net mineralization and nitrification, and lower SON and microbial biomass than uncut forests; 2) treatments with 50% retention will resemble forests (because only individual trees were removed), while 20% retention will resemble clear-cuts (because gaps were created); and 3) harvesting effects on N availability indicators will be greater in deciduous than coniferous forests, because N is usually more available and cycles faster in deciduous forests, making them more responsive.

### 3.2 Methods

This study was a part of the Ecosystem Management Emulating Natural Disturbance (EMEND) project, a large alternative silvicultural project in northern Alberta. The broad objective of this project is to determine which forest harvest and regenerative practices best maintain biotic communities and functional ecosystem integrity relative to the mixed-wood
landscapes that have originated through natural disturbances. The study site is approximately 90 km north-west of Peace River in the Lower Foothills sub-region of the Clear Hills Upland eco-region (Beckingham et al. 1996). Elevation ranges from 677 m to 880 m a.s.l. Mean annual temperature at the nearest climatic station is -0.3 °C, with mean January and July temperatures of -18.8°C and 14.6°C, respectively. Mean annual precipitation is 433 mm (Environment Canada 2004). The soils are fine-textured, well-drained Gray Luvisols and Brunisols on glacio-lacustrine and glacial deposits (Kishchuk 2004). Tree ages in the stands ranged from 70 to 125 years (Spence and Volney 1999). Dominant tree species are trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss). Black spruce (*Picea mariana* (Mill.) BSP.), balsam fir (*Abies balsamea* (L.) Mill.) and lodgepole pine (*Pinus contorta* Loudon) also occur at some sites. Green alder (*Alnus crispa* (Ait.) Pursh), high-bush cranberry (*Viburnum edule* (Michx.) Raf.) and prickly rose (*Rosa acicularis* Lindl.) are the dominant understory shrubs.

Ten-hectare stands were clear-cut or VR-harvested during winter 1998-99 by a conventional whole-tree, two-pass shelterwood method. Three canopy-retention levels, 0% (clear-cut), 20% and 50%, were used in addition to an uncut control (100%). Felling and skidding occurred in 5-m-wide machine corridors, spaced 20 m (center-to-center) apart, leaving a 15-m-wide retention strip between each corridor. Machine corridors accounted for 25% of net compartment area and thus resulted in 75% retention. Lower retention levels (20%, 50%) were achieved by systematic tree removal from the retention strips and was done from the machine corridors, minimizing soil disturbance. Debris from the de-limbing process was piled on landings. Harvesting was not followed by any site preparation in this study. Site preparation
techniques would normally be applied to these sites; however, this was not feasible within the variable retention treatments, nor was it applied to the clearcut treatment for consistency. Only natural regeneration was allowed within the study area. Within each forest type, three replicates of clear-cut, 20% and 50% partial cut and control stand were sampled. “Deciduous-dominated” stands had at least 75% deciduous trees, “coniferous-dominated” stands had at least 75% coniferous trees, and “mixed” stands were between these values.

In each stand (10 ha), six samples of the F+H layer from the forest floor and the upper 7 cm of mineral soil were collected from randomly selected plots in June and August 2002. Samples from each plot were analyzed separately and all plots were sampled each time. Samples were kept on ice while transported to the laboratory and stored at 4°C until processing. A portion of each sample was oven-dried at 105°C for 24 hours to measure gravimetric moisture content. Soluble C and N and microbial biomass C and N were analyzed on field-moist samples. Samples were sieved immediately before extraction though a 4 mm mesh sieve to remove coarse mineral and organic fragments (Hart et al. 1997; Brierley et al. 2001). The high proportion of clay made it impossible to pass moist mineral soil though a 2-mm sieve.

The following N availability indicators were measured or calculated: 0.5 M K₂SO₄ NH₄-N, NO₃-N, soluble inorganic N (SIN), and net rates of N mineralization, ammonification and nitrification (Binkley and Hart 1989). Net rates of ammonification, nitrification and mineralization were assessed through a 6-week in-situ buried-bag incubation (Hart et al. 1994) between June and August 2002. Net ammonification was calculated as NH₄-N accumulated after 6 weeks minus NH₄-N at the beginning of the incubation; net nitrification as NO₃-N at the end minus NO₃-N at the beginning; net mineralization as inorganic N (NH₄-N + NO₃-N) at the end.
minus inorganic N at the beginning. We also determined microbial N (Binkley and Hart 1989) as it is another pool of N potentially available to plants (Hodge et al. 2000) through microbial biomass turnover.

The percentage of SIN that is NO$_3$-N was used to describe the relative importance of nitrate (an alternative way to express the NH$_4$-N / NO$_3$-N ratio used in other studies such as (Walley et al. 1996)). Similarly, the percentage of soluble N that is SIN was used to describe relative importance of inorganic N (analogous to SON / SIN ratio; (Northup et al. 1995). This index shows the relative contributions of readily available N to the soluble N pool, which we believe is useful when comparing among sites across broad N availability gradients. Soluble N is defined as soluble inorganic N plus soluble organic N; labile N is defined as soluble N plus microbial N.

For soluble inorganic N (NH$_4$ and NO$_3$) analysis, approximately 10 g (fresh mass) of soil and 6 g (fresh mass) of forest floor were extracted with 50 mL of 0.5 M K$_2$SO$_4$. Samples were shaken for 1 hour on a reciprocal shaker and then settled at 4°C for 30 min. They were then gravity-filtered through pre-leached Fisher Q2 filter and vacuum-filtered through a 0.45 μm Duvapore PVDF membrane filter. A portion of the filtrate was set aside for NH$_4$-N and NO$_3$-N determination and frozen until analysis. Ammonium and nitrate were analyzed on Technicon Autoanalyser II (Technicon Industrial Systems 1973; Technicon Industrial Systems 1977). Another portion of the filtrate was used for analysis of soluble organic C, measured as total organic C by automated persulphate oxidation on an Astro 2000 DOC analyzer (Schreurs 1978). Total soluble N was measured as nitrate after digestion of the filtrates with potassium persulphate (Cabrera and Beare 1993). Ten milliliters of 0.5 M persulphate oxide were added to
5 mL of filtrate and autoclaved for 50 min. Soluble organic N was calculated as the difference between total soluble and soluble inorganic N, adjusted for water loss during autoclaving.

Microbial biomass N and C were estimated by the chloroform-fumigation-extraction method (Horwath and Paul 1994). Samples were incubated with chloroform for 48 hours (Jenkinson and Powlson 1976) to ensure complete lysis of microbial cells. Microbial N and C were calculated as total extractable N after the fumigation minus total extractable N before the fumigation and total organic C after minus total organic C before the fumigation, respectively (Martikainen and Palojarvi 1990). No conversion coefficient was used as we could not confirm which of the coefficients would be most appropriate and because the primary goal was to compare among the treatments. pH was measured with an Accumet AP62 portable pH/mV meter (Fisher Scientific) in fresh samples suspended in 0.01 M CaCl₂ in ratios 1:2 by fresh weight for the mineral soil and 1:4 for the forest floor (Kalra and Maynard 1991). Bulk density of the mineral soil was determined by core sampling in 2000; bulk density of forest floor was determined by quadrat sampling in 2002.

Overstory litter was collected in four 50 cm x 50 cm litter traps (fiberglass mesh with 1.5 mm openings stapled into a plywood frame), for one year, at 4 of the 6 sampling plots in each stand. Litter was air-dried, sorted into needles, leaves, twigs and “other”, which consisted mainly of cones and cone bracts. The N concentration of each of these components was measured on Leco CN 2000 analyzer and total N content of annual aboveground litter input was calculated for each stand. To measure rates of litter decomposition, samples of aspen and spruce foliar litter collected from a single location within the experimental area were incubated on-site in litter bags. Two grams of air-dried litter were placed into fiberglass mesh bags with 1.5-mm openings,
which were double-layered to minimize spillage of spruce needles (Prescott et al. 2000b). Both types of litter were placed at all sites, so the influence of both site and litter could be distinguished. The litter bags were placed on the top of the forest floor and pinned by a metal flag. The bags were collected after one year, air-dried, weighed and analyzed for C and N concentrations. Litter masses were adjusted for oven-dried mass.

The experimental design was a completely randomized, factorial split-plot with multiple measurements, where treatments were fixed. Retention level and forest types were the two factors. The split-plot was soil layer for soil characteristics and litter type for litter decomposition. Data were analyzed using SAS statistical package version 8.02 (SAS Institute Inc. 2004). The GLM procedure was used to assess differences among forest types, where one stand was an experimental unit. Treatment effects were tested at the stand level (n=3) and the six samples from each stand were treated only as sub-samples. None of the data fulfilled the requirements of normality and equal variances for analysis of variance, and several transformations did not solve this problem, so the data were ranked. The ranked values were normalized (Blomm 1958) to enable statistical tests as for original data. The significance level was set at α=0.1, to accommodate the substantial variability common in soil nitrogen measures. Bonferroni adjustment was used for multiple means comparison; no adjustment was applied experiment-wide.

3.3 Results
We detected little effect of harvesting on N availability in any of the forest types, four years after harvest. Most of the indicators of N availability – concentrations of nitrate (Table 3-1) and ammonium (Table 3-2), and net N mineralization and nitrification rates (Fig. 3-1) were similar
in clear-cut and uncut forests. Nitrate concentrations were very low, ranging 0-3.95 μg g⁻¹; ammonium concentration ranged 51.83-110.63 μg g⁻¹ in the forest floor, and 1.88-10.11 μg g⁻¹ in the mineral soil.

The proportion of soluble N that was inorganic N was higher in the forest floors and mineral soil of clear-cuts compared to uncut stands on one occasion (June) (Fig. 3-2); this was the result of decreased SON concentrations (Table 3-3) and occurred only in forest floors of mixed stands and mineral soil of coniferous-dominated stands. No effects of harvesting on any measured variable were apparent in deciduous-dominated stands. Microbial biomass N, C and C/N ratio (Fig. 3-3) were also not significantly changed by harvesting. No threshold effect of harvesting could be determined as most indices were similar in the two retention levels (20% and 50%), clear-cuts and uncut stands.

Soil gravimetric moisture and pH did not vary among harvesting treatments (Table 4). Litter decomposition rates were not affected by harvesting in any forest type (Fig. 3-4a), whereas litter input decreased with increasing intensity of tree removal (Fig. 3-4b). Annual litter input was significantly lower in clear-cuts and 20% retention (except in coniferous stands) than in uncut stands. Litter input in the 50% retention treatment was not significantly different from that in the uncut forest treatment.

3.4 Discussion
The lack of significant changes in N availability in harvested sites means we had to reject all out hypotheses. Little effect of harvesting in boreal aspen, mixed and coniferous forests has, however, been reported in other studies (Silkworth and Grigal 1982; Maynard and MacIsaac
Nitrate availability and nitrification are generally little affected by harvesting in boreal forests, unless the sites have been fertilized (Paavolainen and Smolander 1998), burned (Pietikäinen and Fritze 1995), trenched (Walley et al. 1996) or scalped (Frey et al. 2003). Where elevated soil nitrate concentrations without site preparation have been reported, it has usually been shortly after harvest; e.g. 0.5 (Carmosini et al. 2003) and 1-4 years (Lapointe, 2005), and levels decline with time since harvest.

Studies about net N mineralization rates are less consistent, showing no change (Smith et al. 2000) a decline (Walley et al. 1996; Hassett and Zak 2005), or an increase 10 to 21 years after the harvest (Simard et al. 2001; Brais et al. 2002), and there does not seem to be a clear trend with the time since harvest among the studies. The effects of harvesting on N availability in these studies are not clearly differentiated based on harvesting method, geographic region or forest type. The only distinguishing factor seems to be the degree of site disturbance, especially in the case of nitrate. This is consistent with the suggestion (Bock and Van Rees 2002; Frey et al. 2003) that site preparation may have a greater influence on N availability and seedling regeneration than does harvesting in boreal forests.

Nitrate concentration across the forest types and harvesting treatments were similar to those reported by Westbrook (2004), Maynard and McIsaac (1998), and Smith et al. (2000). Ammonium concentrations were comparable to Carmosini (2002), and slightly higher than those reported by Westbrook (2004) in similar forests.

The increase in SIN as a proportion of soluble N was not accompanied by an increase in SIN concentrations or increased N mineralization, rather, it was due to a decrease in SON concentration. Decreased levels of SON have been reported after clear-cutting of western
redcedar – western hemlock forest (Hannam and Prescott 2003), gap creation in pine forest (Parsons et al. 1994) or removal of grass (Chapman et al. 2001). The decrease in SON in the clear-cuts is probably a consequence of the reduction in input in throughfall and above- and below-ground organic matter input resulting from removal of a portion of the vegetation. Subsequent retention of SON in the soil may also be reduced in clear-cuts (Hannam and Prescott 2003), but this was not assessed in our study.

The lack of difference between the 50% and 20% retention treatments was not in agreement with our hypothesis that N availability would be elevated in the 20% retention which, unlike the 50% retention, created gaps. Other studies have reported a threshold gap size at which N availability increased (Parsons et al. 1994; Prescott et al. 2003). Although several neighbouring trees were cut in the 20% retention treatment, these gaps may not have reached the threshold size. Also N availability was measured at random locations throughout the cutovers in this study, whereas in other studies it was measured in the centre of the gap. Nevertheless, there were no differences between smaller openings in 20% and larger openings in 50% retention treatments, similar to Ritter et al. (2005) who did not find a relationship between gap size and N availability in Danish beech forests.

There was no change in litter decomposition rates with full or partial tree removal. Other studies in BC forests have documented that litter does not decompose faster in clear-cuts than in forests (Prescott 1997; Prescott et al. 2000a; Hope et al. 2003). The decomposition rates in the harvested sites may have remained similar to those in the forests as a result of unchanged site conditions. Soil moisture and pH were not altered by harvesting, although both have been previously reported to increase after clear-cutting (Keenan and Kimmins 1993; Siira-Pietikäinen
et al. 2001; Bock and Van Rees 2002). Although canopy litter input was reduced in the harvested sites, the corresponding increase in rates of nitrification, caused by lower N immobilization due to decline in C availability (Davidson et al. 1992), did not occur.

Since harvesting did not affect N availability in any forest type, the hypothesis that deciduous forests would be affected by harvesting more than coniferous forests was not fulfilled. Lapointe et al. (2005) also did not find greater effects of harvesting in deciduous stands in the eastern boreal mixedwood forest. Mladenoff (1987) found a greater increase in N availability in gaps under coniferous compared to deciduous species in a northern maple-hemlock forest.

Because we sampled during the fourth season after harvest, it is possible that there was a short-term pulse of available N that we did not detect. This is particularly likely in the deciduous-dominated forests, as other studies in deciduous forests indicate that the concentration and proportion of soil nitrate, and nitrification rates usually increase immediately after harvest and decline to pre-harvest levels within five years (Fisk and Fahey 1990; Titus et al. 1997; Idol et al. 2003). In coniferous forests, the effects of harvesting on soil nitrate levels and nitrification rates, are often delayed but then sustained for several years, with the maximum effect evident 3-4 years after harvest (Bradley et al. 2002; Prescott et al. 2003; Hope et al. 2003). At EMEND, nitrate concentrations in the forest floor of deciduous clearcuts were elevated relative to levels in uncut forests during the first growing season after harvest, while the other two forest types remained unchanged (Kishchuk 2002; Lindo and Visser 2003) (Figure 3-5). Nitrification rates were unchanged, indicating that elevated nitrate levels in the deciduous clearcuts were a consequence of cessation of nitrate uptake by trees. During the third season after harvest nitrate levels in the deciduous clearcuts were not significantly higher than in uncut stands, and net
nitrification rates were significantly lower in the deciduous clearcuts (Figure 3-5). Nitrate levels were elevated in the coniferous clearcuts during the third growing season after harvest, but there was not difference in the size of the inorganic N pool (Lindo and Visser 2003).

High variability of N measurements within forest stands is very common in nutrient studies in forest ecosystems, making it more difficult to discern an effect of treatment among the overall high variability. We thus believed that there is more to be learned if we discuss also less significant trends rather than adhering strictly to usual but arbitrary value of $\alpha=0.05$. We also considered important, from the management perspective, to avoid falsely concluding that harvesting has no effect when it actually has (i.e. to minimize type II error). By setting the $\alpha$-level to a higher (0.1) value, we allowed for smaller effect of harvesting to be considered significant, and we are thus more confident in concluding that there were almost no effects of harvesting on N availability.

In conclusion, our results indicate that changes in N cycling and availability following harvesting of these boreal mixedwood forests are small and short-lived. Variable-retention harvesting as opposed to clear-cutting boreal mixed-woods therefore may not be justified on the basis of nutritional concerns. However, it is important to point out that the harvesting operations caused minimal disturbance to the forest floor, and were not followed by any site preparation or vegetation control. Other studies reporting little effect of harvesting on N availability have also had minimal disturbance to the forest floor (Crow 1985; Maynard and MacIsaac 1998). Revegetation is known to be important in retaining N within harvested temperate forests (Vitousek and Matson 1984; Reiners 1992; Iseman et al. 1999). Thus, while harvesting of boreal forests per se does not appear to cause large changes in N cycling and availability, site
preparation following harvest, especially practices that delay site re-establishment of vegetation, may increase N availability and subsequent loss.
### 3.5 Tables and figures

**Table 3-1. Nitrate (NO₃-N) concentration [μg g⁻¹] in the forest floor and upper 7 cm mineral soil under four retention levels in the three forest types**

<table>
<thead>
<tr>
<th>Tree retention level (%)</th>
<th>June</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Deciduous</td>
<td>Mixed</td>
</tr>
<tr>
<td>0</td>
<td>1.06 (0.67)</td>
<td>3.83 (0.69)</td>
</tr>
<tr>
<td>20</td>
<td>1.17 (0.67)</td>
<td>2.28 (0.65)</td>
</tr>
<tr>
<td>50</td>
<td>1.34 (0.69)</td>
<td>0.07 (0.70)</td>
</tr>
<tr>
<td>100</td>
<td>0.00 (0.65)</td>
<td>1.26 (0.65)</td>
</tr>
</tbody>
</table>

**Forest floor**

<table>
<thead>
<tr>
<th>Mineral soil</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
</tr>
<tr>
<td>0</td>
</tr>
<tr>
<td>20</td>
</tr>
<tr>
<td>50</td>
</tr>
<tr>
<td>100</td>
</tr>
</tbody>
</table>

Note: Each value is the least squares mean of three replicates of forest type, retention level and layer combinations with standard error in the brackets. There were no significant differences among the retention levels for a given forest type on a given sample date.
Table 3-2. Ammonium (NH$_4$-N) concentration [µg g$^{-1}$] in the forest floor and upper 7 cm mineral soil under four retention levels in the three forest types

<table>
<thead>
<tr>
<th>Tree retention level (%)</th>
<th>June</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Deciduous</td>
<td>Mixed</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>81.54 (6.63)</td>
<td>65.17 (6.63)</td>
</tr>
<tr>
<td>20</td>
<td>82.13 (6.63)</td>
<td>55.56 (6.42)</td>
</tr>
<tr>
<td>50</td>
<td>67.43 (6.42)</td>
<td>83.93 (6.91)</td>
</tr>
<tr>
<td>100</td>
<td>110.63 (6.42)</td>
<td>57.64 (6.42)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Forest floor</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
</tr>
<tr>
<td>20</td>
</tr>
<tr>
<td>50</td>
</tr>
<tr>
<td>100</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mineral soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
</tr>
<tr>
<td>20</td>
</tr>
<tr>
<td>50</td>
</tr>
<tr>
<td>100</td>
</tr>
</tbody>
</table>

Note: Each value is the least squares mean of three replicates of forest type, retention level and layer combinations with standard error in the brackets. There were no significant differences among the retention levels for a given forest type on a given sample date.
Table 3-3. Soluble organic N (SON) concentration [µg g\(^{-1}\)] in the forest floor and upper 7 cm mineral soil under four retention levels in the three forest types

<table>
<thead>
<tr>
<th>Tree retention level (%)</th>
<th>June</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Deciduous</td>
<td>Mixed</td>
</tr>
<tr>
<td></td>
<td>(µg g(^{-1}))</td>
<td>(µg g(^{-1}))</td>
</tr>
<tr>
<td></td>
<td>79.65 (9.72)</td>
<td>78.41 (9.72)a**</td>
</tr>
<tr>
<td></td>
<td>77.66 (10.02)</td>
<td>134.79 (9.41)ab</td>
</tr>
<tr>
<td></td>
<td>86.40 (10.02)</td>
<td>173.79 (10.93)b</td>
</tr>
<tr>
<td></td>
<td>96.09 (10.16)</td>
<td>157.55 (9.72)b</td>
</tr>
<tr>
<td></td>
<td>11.33 (10.02)</td>
<td>7.70 (9.72)</td>
</tr>
<tr>
<td></td>
<td>8.66 (10.02)</td>
<td>13.69 (10.02)</td>
</tr>
<tr>
<td></td>
<td>16.50 (9.72)</td>
<td>11.72 (10.62)</td>
</tr>
<tr>
<td></td>
<td>10.07 (10.02)</td>
<td>12.38 (9.41)</td>
</tr>
</tbody>
</table>

Note: Each value is the least squares mean of three replicates of forest type, retention level and layer combinations with standard error in the brackets. Different letters indicate significant differences among the retention levels for a given forest type on a given sample date; * indicates difference at p < 0.1, ** difference at p<0.05.
### Table 3-4. pH and gravimetric moisture in the forest floor and upper 7 cm of mineral soil under four retention levels in the three forest types

<table>
<thead>
<tr>
<th>Tree retention level (%)</th>
<th>pH(_{\text{CaCl}_2})</th>
<th>Moisture [g g(^{-1})]</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Deciduous</td>
<td>Mixed</td>
</tr>
<tr>
<td>0</td>
<td>5.96 (0.12)</td>
<td>5.18 (0.12)</td>
</tr>
<tr>
<td></td>
<td>(20.87)</td>
<td>(20.20)</td>
</tr>
<tr>
<td>20</td>
<td>5.92 (0.12)</td>
<td>5.25 (0.12)</td>
</tr>
<tr>
<td></td>
<td>(20.87)</td>
<td>(20.20)</td>
</tr>
<tr>
<td>50</td>
<td>5.92 (0.12)</td>
<td>5.16 (0.13)</td>
</tr>
<tr>
<td></td>
<td>(20.20)</td>
<td>(20.43)</td>
</tr>
<tr>
<td>100</td>
<td>5.59 (0.12)</td>
<td>4.89 (0.12)</td>
</tr>
<tr>
<td></td>
<td>(20.20)</td>
<td>(20.20)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mineral soil</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
</tr>
<tr>
<td>0</td>
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<tr>
<td></td>
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<td>20</td>
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<td></td>
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<tr>
<td>100</td>
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<td></td>
</tr>
</tbody>
</table>

Note: Each value is the least squares mean of three replicates of forest type, retention level and layer combinations with standard error in the brackets. There were no significant differences among the retention levels for a given forest type on a given sample date (p < 0.1).
Figure 3-1. Net nitrification rates (a) and net ammonification rates (b) during 6-week in-situ incubation in the forest floor and upper 7 cm of mineral soil in deciduous-dominated, mixed, and coniferous-dominated forests at four retention levels (0-100%).

Note: Each column is the least squares mean of three replicates of forest type, retention level and layer combinations with standard error indicated by the error bars. There were no significant differences among the retention levels for a given forest type on a given sample date (p < 0.1).
Figure 3-2. Proportion of soluble N as soluble inorganic N (SIN) from in the forest floor and 7 cm of upper mineral soil of deciduous-dominated, mixed, and coniferous-dominated forests at four retention levels (0-100%) in a) June and b) August.

Note: Each column is the least squares mean of three replicates of forest type, retention level and layer combinations with standard error indicated by the error bars. Different letters indicate significant differences among the retention levels for a given forest type on a given sample date; * indicates difference at \( p < 0.1 \), ** difference at \( p<0.05 \).
Figure 3-3. Microbial N (a) and microbial C/N (b) in the forest floor and 7 cm of upper mineral soil of deciduous-dominated, mixed, and coniferous-dominated forests at four retention levels (0-100%).

Note: Each column is the least squares mean of three replicates of forest type, retention level and layer combinations with standard error indicated by the error bars. There were no significant differences among the retention levels for a given forest type on a given sample date (p < 0.1).
Figure 3-4. Decomposition of foliar litter of aspen and spruce during the first year (a), and annual mass of canopy litter (b) in deciduous-dominated, mixed, and coniferous-dominated forests at four retention levels (0-100%).

Note: Each column is the least squares mean of three replicates of forest type, retention level and layer combinations with standard error indicated by the error bars. Different letters indicate significant differences among the retention levels for a given forest type on a given sample date; * indicates difference at p < 0.1, ** difference at p<0.05.
Figure 3-5. Inorganic N (NO$_3$-N and NH$_4$-N) concentrations in the forest floor clearcuts and uncut stands of deciduous- and coniferous-dominated forests, one, three and four years after the harvest. The first and third year data are from Kishchuk (2002) and Lindo and Visser (2003).
3.6 References


Chapter 4: Post-harvest soil nitrate dynamics in boreal mixedwood forests

4.1 Introduction

Kronzucker et al. (1997; 2003) suggested that the succession from deciduous to coniferous tree species in boreal forests is associated with a change in the soil N environment from being dominated by nitrate early in succession to being dominated by ammonium later in succession. The predominance of nitrate after disturbance, such as clear-cutting, was hypothesized to encourage colonization of species such as aspen, which prefer nitrate, and cause regeneration failure of species such as white spruce, which prefer ammonium. Several empirical studies have, however, contradicted this hypothesis, reporting active nitrate production in both deciduous and coniferous forests (Davidson et al. 1992; Stottlemyer and Toczydlowski 1999) and minimal change in nitrate production following clear-cutting (Carmosini et al. 2002).

Elevated nitrate concentrations in soil solution and drainage waters after clear-cut harvesting (Frazer et al. 1990; Smolander et al. 1998) were thought to result from stimulation of autotrophic nitrifiers by enhanced ammonium levels resulting from elevated N mineralization rates. Reports of substantial nitrification in coniferous forests and microbial nitrate immobilization led to the alternative hypotheses that reduced heterotrophic assimilation, possibly resulting from a decline in available C, was the cause of elevated nitrate in clear-cuts (Davidson et al. 1992; Hart et al. 1994). Bradley (2001) proposed a third alternative - that the reduced

1 A version of this chapter has been submitted for publication in Soil Biology and Biochemistry. Authors: Jerabkova, L. and Prescott, C.E. Title: Post-harvest soil nitrate dynamics in boreal mixedwood forests
Nitrate immobilization was caused by higher ammonium production and availability to heterotrophic organisms.

Using a boreal mixedwood forest dominated by trembling aspen and white spruce, we tested the Kronzucker et al. (1997) hypothesis. If the Kronzucker et al. (1997) hypothesis is correct, we would have found nitrate as the dominant inorganic N form in deciduous forests and in clear-cuts of both forest types, and ammonium dominating in mature coniferous forests. We will also determine if nitrification is primarily autotrophic or heterotrophic in these ecosystems, and examine the effect of increasing C availability on production and consumption of nitrate.

4.2 Methods
The research site is located approximately 90 km north-west of Peace River, Alberta in the Clear Hills Upland and Lower Foothills Ecoregion (Beckingham et al. 1996) within the EMEND (Ecosystem Management Emulating Natural Disturbance) project. Elevation ranges from 677 m to 880 m a.s.l. Mean annual temperature at the nearest climatic station is -0.3°C, with mean January and July temperatures of -18.8°C and 14.6°C, respectively. Mean annual precipitation is 433 mm (Environment Canada 2004). The soils are fine-textured, well-drained Luvisols that have developed on glacio-lacustrine and glacial till deposits (Kishchuk 2004). Tree ages in the uncut stands ranged from 70 to 125 years (Spence and Volney 1999). Dominant tree species were trembling aspen (Populus tremuloides Michx.), balsam poplar (Populus balsamifera (L.) Mill.) and white spruce (Picea glauca (Moench) Voss). Green alder (Alnus crispa (Ait.) Pursh), high-bush cranberry (Viburnum edule (Michx.) Raf.) and prickly rose (Rosa acicularis Lindl.) were the dominant understory shrubs. Stands were harvested during the winter of 1998-99 by a
conventional whole-tree clear-cut method. Tree tops and branches were piled on landings, and there was no site preparation.

In August 2003, we sampled three replicates of clear-cuts and uncut stands of “deciduous-dominated” and “coniferous-dominated” forests, each ca 10 ha. “Deciduous-dominated” stands were more than 75% deciduous trees and “coniferous-dominated” stands were more than 75% coniferous trees. In each stand, six samples each of the F+H layer of the forest floor and the upper 7 cm of mineral soil were collected from randomly selected points. Samples from each plot were analyzed separately, unless otherwise specified.

Soluble nitrogen and soluble organic carbon (SOC) concentrations were measured on field-moist samples. Samples were sieved through a 4-mm mesh sieve immediately before extraction. Approximately 10 g fresh mass of soil and 6 g fresh mass of forest floor was extracted with 50 mL of 0.5 M \( \text{K}_2\text{SO}_4 \). Samples were shaken for 1 hour on a reciprocal shaker and then settled at 4°C for 30 min. They were then gravity-filtered through pre-leached Fisher Q2 filter and vacuum-filtered through a 0.45 μm Duvapore PVDF membrane filter. A portion of the filtrate was used for analysis of soluble organic C, measured as total organic C by automated persulfate oxidation on an Astro 2000 DOC analyzer (Schreurs 1978). Total soluble N was measured as nitrate after digestion of the filtrates with potassium persulfate (Cabrera and Beare 1993). Ten mL of 0.5 M potassium persulfate was added to 5 mL of filtrate and autoclaved for 50 min. Total soluble N was adjusted for water loss during autoclaving.

Nitrogen availability was measured as NO\(_3\)-N and NH\(_4\)-N supply rate onto PRSTM ion exchange probes (Western Ag Innovations Inc., Saskatoon, Canada). The probes were incubated
for 6 weeks in forest floor and mineral soil in four of the six sampling points in each plot. When taken out, they were cleaned with de-ionized water, inserted into clear plastic bags, kept moist and cold and shipped to Western Ag Innovations (Saskatoon, Sask.) for analysis.

Gross rates of N mineralization and nitrification were assessed in the field using the $^{15}$N dilution method according to Hart et al. (1994). At each of the six sampling plots, two cores of forest floor and mineral soil were injected with ($^{15}$NH$_4$)$_2$SO$_4$ to measure gross ammonification and two were injected with K$^{15}$NO$_3$ to measure gross nitrification. The solution was distributed throughout the core by five injections by a side-port needle attached to a 1 mL gas-tight syringe. Each core was injected with 5 mL of $^{15}$N enriched solution (30 mg $^{15}$N L$^{-1}$; 99% atom enrichment). The solution was prepared to contain ca 2 μg of $^{15}$N per cm$^3$ of soil. A portion of one of the two injected cores was immediately extracted into 0.5M K$_2$SO$_4$ and kept on ice until filtered (the same day). The remaining soil was kept in a plastic bag and used to determine the moisture content and total mass of soil in the core. The second core was incubated in a closed plastic vial in the forest floor or mineral soil for 24 hours, after which it was similarly extracted. The samples were shaken for 1 hour, gravity-filtered through pre-leached Fisher Q2 filter, and frozen until analysis. A portion of the filtrate was analyzed for NH$_4$-N and NO$_3$-N on a Technicon Autoanalyser II (1973; Technicon Industrial Systems 1977). The rest of the filtrate (40 mL) was prepared for $^{15}$N analysis by the diffusion method according to Brooks et al. (Brooks et al. 1989). Filter paper discs with $^{15}$N were analyzed on a Europa Integra IRMS analyzer at UC Davis. Gross NH$_4$-N and NO$_3$-N production rates were calculated by equations according to Kirkham and Bartholomew (1954) as given by Davidson et al. (1991):
\[
m = \frac{N_0 - N_t}{t} \times \frac{\log(H_0 N_t / H_t N_0)}{\log(N_0 / N_t)}
\]

where \( m \) is N (NO₃-N or NH₄-N) gross production rate; \( N_0 \) is initial concentration of N pool (\(^{14+15}\)N); \( N_t \) is post-incubation concentration of N pool (\(^{14+15}\)N); \( H_0 \) is initial concentration of \(^{15}\)N; \( H_t \) is post-incubation concentration of \(^{15}\)N; \( t \) is the length of incubation in days.

Gross NH₄-N and NO₃-N consumption was calculated by the "difference method" suggested by Hart et al. (1994) where N consumption (\( c \)) is calculated as the difference between gross production rate and net N turnover rate without the addition of the labeled N:

\[
c = m - \frac{N_t - N_0}{t}
\]

The "difference method" has been proposed instead of calculating the consumption rate by Kirkham and Bartholomew's (1954) equations, because addition of N was shown to stimulate N consumption (Stark and Hart 1997). I calculated the consumption also by the differential equations and the results showed higher N consumption than production although samples without added labeled N showed measurable net rates of N mineralization and nitrification. I thus used the "difference method" as a better approximation to N cycling rates in undisturbed conditions.

The proportion of nitrification carried out by autotrophic microorganisms was estimated using laboratory incubation with acetylene inhibition (Bollmann and Conrad 1997). Field-moist samples, collected in June 2004, were sieved through a 4-mm sieve and weighed into plastic vials with a rubber septum in the lid. Acetylene (1.3 ml) was injected into one set of samples to block autotrophic nitrification, while N₂ was injected into the second (control) set. The vials were
incubated at 27°C for 24 hours. After incubation, samples were extracted with 0.5 M K$_2$SO$_4$, shaken for 1 hour and gravity-filtered through pre-leached Fisher Q2 filter paper. The filtrate was analyzed colorimetrically for NO$_3$-N (Technicon Industrial Systems 1977).

Gross autotrophic and heterotrophic nitrification and their relation to C supply were measured during a second laboratory incubation. Forest floor samples were sieved through a 4-mm sieve and six samples from each site were composited to form two sub-samples for incubation. For each sub-sample, one vial received 2 mL of K$^{15}$NO$_3$ (30 mg $^{15}$N l$^{-1}$) and 1 mL of water and was immediately extracted with 100 mL of 0.5 M K$_2$SO$_4$. Two vials received 2 mL of K$^{15}$NO$_3$ and 1 mL of water and were incubated at 27°C for 24 hours. Acetylene was injected into the headspace of one vial and N$_2$ was injected into the other as a control. Two vials received 2 mL of K$^{15}$NO$_3$ and 1 mL of sucrose (5.76 mgC l$^{-1}$) and were incubated at 27°C for 24 hours. This addition increased the C concentration by approx. 3.2 mg C g$^{-1}$ soil, which has previously been shown to elicit an increase in microbial activity in similar forest floors (S. Visser personal communication). Again acetylene was injected into the headspace of one vial and N$_2$ was injected into the other. After the incubation, samples were extracted with 100 mL 0.5 M K$_2$SO$_4$, shaken for 1 hour and gravity-filtered through pre-leached Fisher Q2 filter paper. A portion of the filtrate was colorimetrically analyzed for NO$_3$-N and the rest was prepared for $^{15}$N analysis by the diffusion method (Brooks et al. 1989).

The experimental design was a completely randomized factorial split-plot with multiple measurements, where treatments were fixed. Retention level and forest types were the two factors and soil layer represented the split-plot. Data were analyzed using SAS statistical package version 8.02 (SAS Institute Inc. 2004). The GLM procedure was used to assess the effect of
forest type or harvesting, where one stand was an experimental unit. When the data did not fulfill the requirements of normality and equal variances for analysis of variance, and several transformations did not solve this problem, the data were ranked. The ranked values were normalized (Blomm 1958) to enable statistical tests as for original data.

4.3 Results
The results of this study were inconsistent with the Kronzucker et al. (1997) hypothesis. Ammonium was the dominant inorganic N-form at all sites; nitrate accounted for less than 10% of the inorganic N (based on concentration) or 35% (based on supply rate) at any site. Deciduous forests did not have higher availability of NO$_3$-N measured as concentration and supply rate (Table 4-1) or nitrate gross production rates (Fig. 4-1) than coniferous forests. Nitrate availability, measured as soil NO$_3$-N concentration and NO$_3$-N supply rates (Table 4-1), was not higher in clear-cuts than in uncut forests of either type and clear-cuts did not have a narrower soil extractable NH$_4$-N/NO$_3$-N ratio than uncut forests.

Rates of gross nitrate production were not significantly different in clear-cuts than in uncut forests. Although soil nitrate concentrations were low, nitrate was produced at all sites, including the mature coniferous forests (Fig. 4-1). Gross rates of nitrate immobilization were similar to nitrate production rates and were not affected by harvesting. Total gross N$_4$-N production was not affected by harvesting (Fig. 4-2). Nitrification accounted for 5-10% of gross mineralized N.

The laboratory incubations confirmed the lack of differences in gross NO$_3$-N production between clear-cut and uncut forests (Fig. 4-3). Nitrate production and consumption during the laboratory incubations was slightly higher (p=0.12) in deciduous than coniferous forest soils.
Nitrification was mainly (about 70%) heterotrophic, but autotrophic nitrification occurred in both forest types. The proportion of nitrification carried out by heterotrophic organisms was not altered by harvesting.

Addition of available C as sucrose increased heterotrophic nitrate production (Fig. 4-3a), but more than doubled consumption of nitrate (Fig. 4-3b), resulting in increased net immobilization of nitrate. Carbon availability in the field, measured as soluble organic C (SOC) concentration and soluble C/N ratio was lower in the coniferous clear-cuts (Table 4-2) than uncut stands.

4.4 Discussion
Our results refuted the hypothesis that harvesting of boreal mixedwoods creates a “nitrate environment” dramatically different from that of mature forests (Kronzucker et al. 1997). Changes in soil N availability 4-5 years after harvesting were minimal and NH₄-N remained the dominant inorganic form of N. Similar findings have been reported in other northern forests (Prescott 1997; Prescott et al. 2003; Hope et al. 2003; Hannam and Prescott 2003) and boreal forests (Westbrook and Devito 2004), where even if the proportion of nitrate increased it never became more abundant than ammonium (Walley et al. 1996; Carmosini et al. 2002; Lapointe et al. 2005).

The hypothesis that the dominance of aspen in cutovers is a consequence of higher nitrate availability in harvested sites (Kronzucker et al. 1997) was also not supported, as the number of aspen suckers increased with increasing harvesting intensity, while N availability remained unchanged. Furthermore, we found no evidence that boreal forests dominated by aspen have higher nitrate availability and production than do spruce-dominated forests. Other studies in
boreal and northern temperate forests have also reported little change in nitrate production rates after clear-cutting (Carmosini et al. 2003; Westbrook and Devito 2004; Grenon et al. 2004).

Bradley's (2001) hypothesis that nitrate immobilization declines as a result of higher NH$_4$-N availability also did not apply in this ecosystem, as NH$_4$-N production was not elevated in the harvested sites. In other studies where ammonium production was increased after harvesting in aspen-spruce mixedwoods (Carmosini et al. 2002) and montane spruce-fir forests (Grenon et al. 2004), nitrate immobilization was not suppressed. Thus increased NH$_4$-N availability did not result in higher NO$_3$-N availability.

Although soluble C concentration declined in our coniferous clearcuts, consistent with Hart et al. (1994), there was no evidence of reduced nitrate immobilization or increased nitrate availability. Nitrification at our sites was responsive to labile C supply and, as expected, mainly heterotrophic nitrification responded to C addition. The stronger stimulation of nitrate immobilization than production when abile C was added agrees with the findings from alder and aspen forest soils (Clein and Schimel 2002). The tendency towards a greater increase in heterotrophic nitrification with C addition in coniferous compared to deciduous forest floors may indicate stronger C limitation in the coniferous forest floors. Aspen forest floors at our sites had a higher proportion of C within labile compounds than spruce forest floors (Hannam et al. 2004). Another deciduous tree, birch (*Betula pendula*), has been shown to produce a higher quantity of labile C in root exudates than spruce (Sandness et al. 2005); it would be interesting to know if the same was true of aspen.

The dominance of nitrification by heterotrophic organisms is consistent with findings from other northern (Klingensmith and Van Cleve 1993; Grenon et al. 2004) and dry coniferous
forests (Jordan et al. 2005), but not from some coniferous temperate forests (Stark and Hart 1997; Mintie et al. 2003), where nitrate was produced by autotrophic nitrifiers. Although shifts to dominance by autotrophic nitrification have been reported following harvesting in mixed coniferous (Pedersen et al. 1999) and hardwood forests (Duggin et al. 1991), we did not find an increase in autotrophic activity 4 years after harvesting. The detection of autotrophic nitrification at coniferous sites with soil pH of 4.7 or less confirms the occurrence of autotrophic activity in fairly acidic conditions. Although a pH of about 5 was previously reported as a critical level below which autotrophic nitrification does not occur (Adams 1986), autotrophs have been found important nitrifiers in acid forest soils with pH as low as 4.0 (Stams et al. 1990; Tietema et al. 1992).

Gross nitrification rates were not related to soil pH as might be expected based on the increased nitrification and nitrifier numbers after liming (Klemendtsson et al. 1999; Bäckman et al. 2003) or the soil C/N ratio. This lack of correlation is, however, consistent with the results of the Booth et al. (2005) review.

In conclusion, our results refute the suggestion that boreal aspen forests and clear-cuts are “nitrate environments”. Some nitrate was produced, mostly by heterotrophs, but in both coniferous and deciduous-dominated forests, and ammonium was the dominant form of inorganic N in all environments.
### 4.5 Tables and figures

**Table 4-1.** Supply rate of nitrate and ammonium in the forest floor and upper 7 cm of mineral soil in uncut and clearcut sites in deciduous- and coniferous-dominated boreal mixedwood forests.

<table>
<thead>
<tr>
<th></th>
<th>NO$_3$-N (µg 10cm$^2$ 6wk$^{-1}$)</th>
<th>NH$_4$-N (µg 10cm$^2$ 6wk$^{-1}$)</th>
<th>NH$_4$ / NO$_3$ (µg 10cm$^2$ 6wk$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Deciduous</td>
<td>Coniferous</td>
<td>Deciduous</td>
</tr>
<tr>
<td><strong>Forest floor</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncut</td>
<td>3.78 (0.64)</td>
<td>3.87 (0.64)</td>
<td>11.96 (1.80)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>3.47 (0.64)</td>
<td>2.82 (0.64)</td>
<td>7.4 (1.80)</td>
</tr>
<tr>
<td><strong>Mineral soil</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncut</td>
<td>2.83 (0.64)</td>
<td>5.17 (0.64)</td>
<td>7.11 (1.80)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>3.40 (0.64)</td>
<td>2.87 (0.64)</td>
<td>6.9 (1.80)</td>
</tr>
</tbody>
</table>

Note: Each value is the LS mean of three replicates of forest type, retention level and layer combinations with standard error in the brackets. There were no differences between the clearcuts and uncut stands (p < 0.05). Coniferous-dominated forests had overall higher NH$_4$-N supply rates but not at any single retention level and layer combination (p < 0.05).
Table 4-2. Soluble organic C concentration and soluble C/N ratio in the forest floor and upper 7 cm of mineral soil in uncut and clearcut sites in deciduous- and coniferous-dominated forests.

<table>
<thead>
<tr>
<th></th>
<th>Soluble organic C [mg*g⁻¹]</th>
<th>Soluble C/N ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Deciduous June</td>
<td>Coniferous</td>
</tr>
<tr>
<td><strong>Forest floor</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncut</td>
<td>1.82 (0.24)</td>
<td>2.43 (0.22)a</td>
</tr>
<tr>
<td>Clearcut</td>
<td>1.76 (0.21)</td>
<td>1.80 (0.21)b</td>
</tr>
<tr>
<td><strong>Mineral soil</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncut</td>
<td>0.09 (0.23)</td>
<td>0.45 (0.21)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>0.12 (0.22)</td>
<td>0.15 (0.21)</td>
</tr>
</tbody>
</table>

Note: Each value is the LS mean of three replicates of forest type, retention level and layer combinations with standard error in the brackets. Different letters indicate significant differences between the clearcuts and uncut stands (p < 0.05).
Figure 4-1. NO$_3$-N gross production (a) and consumption (b) in the forest floor and upper 7 cm of mineral soil of the uncut stands and clearcuts in deciduous- and coniferous-dominated forests. (Each column is the LS mean of three replicates of forest type, harvesting treatment and layer combinations with standard error indicated by the error bars. There were no significant differences among the treatments.)
Figure 4-2. NH$_4$-N gross production (a) and consumption (b) in the forest floor and upper 7 cm of mineral soil of the uncut stands and clearcuts in deciduous- and coniferous-dominated forests. (Each column is the LS mean of three replicates of forest type, harvesting treatment and layer combinations with standard error indicated by the error bars. There were no significant differences among the treatments.)
Figure 4-3. Gross nitrification rates (a) and gross nitrate consumption rates (b) without and with addition of labile C (sucrose) during a 24-hour laboratory incubation of the forest floor of un-cut and clear-cuts in deciduous- and coniferous-dominated forests. (Each column is the LS mean of three replicates of forest type, harvesting treatment and layer combinations with standard error indicated by the error bars. There were no significant differences among the treatments.)
4.6 References


Chapter 5: Effect of clear-cut harvesting on phosphorus availability and phosphatase activity in boreal mixedwood forests

5.1 Introduction
The productivity of most forest ecosystems is limited by either N and/or P availability (Wardle et al. 2004). While N availability often increases following forest harvesting (Bradley et al. 2000), several studies have reported a post-harvest decline in available P (Schmidt et al. 1996; Lindo and Visser 2003; Whitson et al. 2005). The decline in P availability has been attributed increased microbial and plant demand for P under conditions of increased N availability (Olander and Vitousek 2000). A negative relationship between P supply and phosphatase activity (Tadano et al. 1993) and a positive effect of N availability on phosphatase activity (Zou et al. 1995) have been observed. Thus, a decline in soil available P after harvesting might be expected to be accompanied by an increase in phosphatase activity. Alternatively, harvesting may cause an overall reduction in soil microbial biomass and activity due to lower litter inputs, which would lead to reduced phosphatase activity in clearcuts compared to mature stands (Hassett and Zak 2005).

In the boreal mixedwood forest of Alberta, Canada, Lindo and Visser (2003) found lower soil available P in clearcuts than in mature coniferous stands. We assessed whether the reduction in soil available P was accompanied by increased phosphatase activity, and if this pattern appeared to be related to P supply, and N and C availability.

5.2 Methods
This study was part of the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment, located approximately 90 km north-west of Peace River in
Alberta, Canada. The soils are fine-textured, well-drained Luvisols and Brunisols that have developed on glacio-lacustrine and glacial till deposits (Kishchuk 2004). Dominant tree species are trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L. Mill.) and white spruce (*Picea glauca* (Moench) Voss). Stands were harvested during the winter of 1998-99 using conventional whole-tree harvesting methods; debris from the de-limbing process was piled on the landing. There was no site preparation.

We sampled three replicates of clearcut and uncut stands of “deciduous-dominated” and “coniferous-dominated” forests. In each stand, six samples of the F+H layer of the forest floor and the upper 7 cm of mineral soil were collected from randomly selected sampling plots. In June 2003 (four years after harvest), 10 g (fresh mass) of soil or 6 g (fresh mass) of forest floor were extracted with 40 mL of Bray-1 solution (Kuo 1996), shaken for 1 hour, and filtered for extractable P analysis. Phosphate-P in the filtrate was determined by the molybdate-blue method on a Technicon Autoanalyzer (Olsen and Sommers 1982). Phosphorus supply rate was assessed by PRSTM ion exchange probes (Western Ag Innovations, Saskatoon). The probes were incubated for 6 weeks (between June and August, 2003) in the forest floor and mineral soil at 4 of the 6 sampling plots. After removal from the soil, the probes were cleaned with distilled water, kept moist and cool, and shipped to Western Ag Innovations (Saskatoon, Canada) for analysis. The PRSTM probes were also used to assess supply rate of ammonium, nitrate, aluminum and iron ions. Acid and alkaline phosphatase activity were measured in six fresh samples of forest floor and mineral soil collected from each stand in June 2004 (five years after harvest) using the colorimetric estimation method (Tabatabai 1994).
sample was oven-dried at 105°C for 24 hours to measure gravimetric moisture content, allowing phosphatase activity to be was calculated on an oven-dry basis. Water holding capacity of the soil was estimated according to Alef and Nannipieri (1995). pH was measured with an Accumet AP62 portable pH/mV meter (Fisher Scientific) using fresh samples suspended in 0.01 M CaCl₂ at soil:solution ratios of 1:2 (fresh weight) for mineral soil and 1:4 for forest floor (Kalra and Maynard 1991). Microbial biomass C was estimated by the chloroform-fumigation-extraction method (Horwath and Paul 1994). Soluble inorganic N (NH₄-N and NO₃-N) was measured in 0.5 M K₂SO₄ extracts that were gravity-filtered through pre-leached Fisher Q2 filter paper. Ammonium and nitrate were analyzed by a colorimetric method on a Technicon Autoanalyser II (Technicon Industrial Systems 1973; Technicon Industrial Systems 1977).

The experimental design was a completely randomized factorial split-plot with multiple subsamples, where treatments were fixed. Forest types and harvesting were the two factors in the main treatments and the soil layer was the split-plot. Data were analysed using the SAS statistical package, version 8.02 (SAS Institute Inc. 2004).

5.3 Results
Extractable P concentrations and P-supply rates tended to be higher in the soils of deciduous forests (Figure 5-1a and b) than in the soils of coniferous forests. Concentrations of extractable phosphorus in clearcut sites did not differ from those in uncut stands of either stand type (Figure 5-1a). Phosphorus supply rate in the forest floor of deciduous clearcuts was actually significantly higher than in uncut stands (Figure 5-1b).
The soil reaction was acid (pH range 4-6), phosphatase activity was dominated by acid phosphatase. Acid phosphatase activity was not significantly altered by harvesting (Figure 5-2a). Overall, alkaline phosphatase represented about 30% of total phosphatase activity, but this varied with forest type and harvesting. Alkaline phosphatase activity was consistently higher in clearcuts, although differences were only significant in deciduous stands, and was significantly greater in deciduous forest floors than in coniferous forest floors (Figure 5-2b).

While alkaline phosphatase activity was not related to levels of available P, it was positively correlated with levels of inorganic N (NO$_3$-N + NH$_4$-N) ($r=0.39$; $p<0.001$) in the forest floor (Figure 5-3). Phosphatase activity was also not related to soil moisture across all the treatments (gravimetric moisture content and water holding capacity), but was positively correlated with gravimetric moisture content within each forest type (assessed by ANCOVA; $p=0.035$).

5.4 Discussion
The results indicated that clearcutting did not result in lower levels of available phosphorus (per soil mass or volume). Ratios of N / P supply rates (Figure 5-4) also showed that proportion of phosphorus N relatively was not decreased. The values of N/P ratios were lower at all clearcuts but the difference was not significant. However, the ratios of N/P supply rates of deciduous stands were significantly lower than those of coniferous stands consistent with results of higher phosphorus availability in deciduous stands compared to coniferous stands.

Extractable PO$_4$-P concentration in uncut forests was positively correlated with soluble organic C concentrations (assessed by ANCOVA; $p=0.032$). This is consistent
with the suggestion that higher levels of available C may enable faster P solubilization, and that higher concentrations of organic C may increase P availability through the complexation of metal ions, which would otherwise bind with P (Whitson et al. 2005). The supply rates of iron and aluminum were, however, not affected by harvesting or forest type at these sites (Table 1). Reduced supply of available C could have been the reason for the lower phosphate concentration in coniferous clearcuts two years after harvest (Lindo and Visser, 2003), which did not persist in the present study, probably because of the recovery of understory vegetation and aspen regeneration.

Phosphatase activity expressed per g of microbial biomass C showed the same trend as per g dry mass (Table 5-2 and Figure 5-2). Acid phosphatase activity was not affected by harvesting or forest type, but alkaline phosphatase activity was higher in clearcut sites and deciduous forests. The higher activity per unit microbial biomass may be a result of greater microbial efficiency or a change in composition of microbial community. Although Hassett and Zak (2005) attributed reduced phosphatase activity in an aspen cutover to decreased microbial biomass rather than to changes in microbial composition or activity, we did not detect any significant change in microbial biomass (Table 5-3). Acid phosphatase activity expressed per unit of microbial biomass C was not affected by forest type or harvesting. The higher alkaline phosphatase activity per g in deciduous forest floors could have been partly the result of a greater proportion of alder in deciduous stands. The presence of alder (Selmants et al. 2005) and other N-fixing species (Zou et al. 1995; Giardina et al. 1995) has been shown to be associated with increased phosphatase activity.
In conclusion, clearcutting in boreal mixedwoods did not result in reduced soil available phosphorus concentrations measured 4 years after harvest, although it had after 2 years. Contrary to expectations, phosphorus supply rate and alkaline phosphatase activity were actually higher in the clearcuts than in the uncut forests. Deciduous- and coniferous-dominated stands responded similarly, although harvesting effects were stronger in aspen stands. Forest floor and mineral soils showed the same trends. There was no conclusive evidence that clearcutting would reduce microbial biomass or activity at these sites.

5.6 Tables and figures

Table 5-1. Iron and aluminum supply rate in the forest floor and upper 7 cm of mineral soil in uncut and clearcut sites in deciduous- and coniferous-dominated forests.

<table>
<thead>
<tr>
<th></th>
<th>Fe^{2+} [µg*10 cm^{-2}*6 wks^{-1}]</th>
<th>Al^{3+} [µg*10 cm^{-2}*6 wks^{-1}]</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Deciduous</td>
<td>Coniferous</td>
</tr>
<tr>
<td>Forest floor</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncut</td>
<td>2.85 (1.35)</td>
<td>2.10 (1.35)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>2.80 (1.35)</td>
<td>6.85 (1.35)</td>
</tr>
<tr>
<td>Mineral soil</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncut</td>
<td>7.76 (1.35)</td>
<td>6.30 (1.35)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>8.68 (1.35)</td>
<td>16.04 (1.35)</td>
</tr>
</tbody>
</table>

Note: Each value is the LS mean of three replicates of forest type, retention level and layer combinations with standard error in the brackets. There were no significant differences between clearcuts and uncut stands or between deciduous and coniferous forests (p < 0.05).
Table 5-2. Activity of acid and alkaline phosphatase in the forest floor and upper 7 cm of mineral soil in uncut and clearcut sites in deciduous- and coniferous-dominated forests, expressed per mass of soil and microbial biomass C.

<table>
<thead>
<tr>
<th></th>
<th>Acid phosphatase [ng p-NP* g micr C⁻¹*h⁻¹]</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>acid</td>
<td>alkaline</td>
</tr>
<tr>
<td></td>
<td>Deciduous</td>
<td>Coniferous</td>
</tr>
<tr>
<td><strong>Forest floor</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncut</td>
<td>0.92 (1.45)</td>
<td>1.63 (1.57)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>1.49 (1.55)</td>
<td>1.16 (1.86)</td>
</tr>
<tr>
<td><strong>Mineral soil</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncut</td>
<td>4.39 (1.63)</td>
<td>1.58 (2.07)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>3.30 (1.55)</td>
<td>5.74 (2.19)</td>
</tr>
</tbody>
</table>

Note: Each value is the LS mean of three replicates of forest type, retention level and layer combinations with standard error in the brackets. Different letters indicate differences between clearcuts and uncut stands (p<0.05). Deciduous-dominated forests had overall higher alkaline activity but not at any single retention level and layer combination (p < 0.05). p-NP is p-nitrophenol used as an indicator of phosphatase activity.
Table 5-3. Soil water-holding capacity and microbial biomass C in the forest floor and upper 7 cm of mineral soil in uncut and clearcut sites in deciduous- and coniferous-dominated forests.

<table>
<thead>
<tr>
<th></th>
<th>Deciduous</th>
<th>Coniferous</th>
<th>Deciduous</th>
<th>Coniferous</th>
<th>Deciduous</th>
<th>Coniferous</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Gravimetric moisture [g*g⁻¹]</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest floor</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncut</td>
<td>152.53 (10.13)</td>
<td>196.04 (10.13)</td>
<td>19.80 (2.53)</td>
<td>24.16 (2.53)</td>
<td>4.37 (0.32)</td>
<td>4.00 (0.34)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>199.48 (10.13)</td>
<td>266.11 (10.13)</td>
<td>26.97 (2.62)</td>
<td>31.65 (2.62)</td>
<td>2.92 (0.35)</td>
<td>3.78 (0.36)</td>
</tr>
<tr>
<td>Mineral soil</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncut</td>
<td>30.08 (10.13)</td>
<td>42.41 (10.13)</td>
<td>25.84 (2.70)</td>
<td>34.22 (2.53)</td>
<td>0.28 (0.36)</td>
<td>0.35 (0.40)</td>
</tr>
<tr>
<td>Clearcut</td>
<td>42.42 (10.13)</td>
<td>41.62 (10.46)</td>
<td>43.18 (2.53)</td>
<td>48.03 (2.62)</td>
<td>0.24 (0.35)</td>
<td>0.12 (0.38)</td>
</tr>
</tbody>
</table>

Note: Each value is the LS mean of three replicates of forest type, retention level and layer combinations with standard error in the brackets. There were no significant differences between clearcuts and uncut stands or between deciduous and coniferous forests (p < 0.05).
Figure 5-1. Concentration of extractable phosphorus (a) and phosphorus supply rate (b) in the forest floor and upper 7 cm mineral soil in clearcuts and uncut deciduous- and coniferous dominated forests (different capital letters indicate harvesting effect; different lower-case letters indicate forest type effect, where there are no letters there were no significant differences; bars represent standard errors; p<0.05).
Figure 5-2. Activity of acid phosphatase (a) and alkaline phosphatase (b) in the forest floor and upper 7 cm of mineral soil in clearcuts and uncut deciduous- and coniferous dominated forests (capital letters indicate harvesting effect; lower-case letters indicate forest type effect; bars represent standard errors).

Figure 5-3. Relation of alkaline phosphatase activity to the concentration of inorganic N in the forest floor in clearcuts and uncut deciduous- and coniferous dominated forests.
Figure 5-4. Ratio of inorganic N/P supply rates in the forest floor and upper 7 cm of mineral soil in clearcuts and uncut deciduous- and coniferous dominated forests (capital letters indicate harvesting effect; lower-case letters indicate forest type effect; bars represent standard errors).
5.2 References


Chapter 6: Discussion and conclusions

6.1 Synthesis of results
To summarize in relation to the 5 objectives of this study (Chapter 1.3), the major findings are:

Objective 1

- Deciduous-dominated forests had higher soil inorganic N levels than coniferous forests but there was no evidence of faster decomposition, mineralization and nitrification in deciduous forests.
- Nitrate was not more important in N dynamics of deciduous than coniferous forests.
- Forest floor and upper mineral soil inorganic N concentrations were positively correlated with the proportion of deciduous trees

Objective 2

- Clearcutting did not increase N availability (nitrification or nitrate levels) and so does not pose a threat with respect to creation of soil nitrate environment.
- Ammonium remained the dominant inorganic N form at all sites in these forests.
- Effects of variable-retention harvesting did not differ from either uncut forests or clearcuts.
- Although the overall effect of harvesting on N availability was very small, some effects were greater in forests dominated by coniferous trees than in deciduous-dominated forests.

Objective 3

- Clearcutting did not increase nitrate production and neither was it higher in deciduous forests.
• Nitrate was produced by both autotrophic and heterotrophic soil organisms, but heterotrophic activity dominated.

• Nitrification was responsive to manipulation of available C levels in laboratory, but changes in soil C quality in the field treatments were not associated with significant changes in nitrate production and consumption.

Objective 4

• Phosphorus availability was higher in deciduous than coniferous-dominated stands.

• Phosphorus availability was not reduced by clearcutting 4 years after harvest, but phosphatase activity was elevated in the clearcuts.

Objective 5

• Aboveground litter input of N was a better indicator of soil N availability than litter decomposition rate.

The hypothesis that soil N availability increases with the proportion of deciduous trees in boreal mixed-wood forest was partially supported. Soils of deciduous forests had higher NH$_4$-N and inorganic N concentrations and these N availability indices were positively related to proportion of deciduous trees. However, the hypothesis that deciduous stands have higher nitrate production and availability was not supported by the data. Nitrate levels and net nitrification rates were low at all forest types, as has also been shown in boreal mixedwood studies (Carmosini et al. 2002). The high spatial variability of nitrate has also been noted before (Maynard and MacIsaac 1998).

The higher inorganic N and NH$_4$-N levels in deciduous forests correlated with the litterfall input of N. Other characteristics of deciduous litter, such as higher pH and higher Ca$^{2+}$ concentration, could also positively affect available soil N. However, I did
not find higher net ammonification or mineralization rates in the deciduous stands, nor was NH$_4$-N production higher. In this context, the higher soil NH$_4$-N concentration in deciduous stands could be a result of lower plant uptake. Lower NH$_4$-N supply rate in deciduous stands measured by ion-exchange probes supports this possibility. In a laboratory hydroponic solution study, aspen was shown to have a higher potential for NO$_3$-N uptake than white spruce, but it showed lower uptake of NH$_4$-N (Hangs et al. 2003). Nitrogen could also be taken up as NO$_3$⁻ by aspen from soil solution but a portion of it recycled back to soil as NH$_4$⁺ or amino acids, which were quickly mineralized back to NH$_4$⁺. When labeled $^{15}$NO$_3$⁻ was added to soil with live roots of tomato at least 18% of the labeled N appeared in the NH$_4$⁺ pool within 1 day (Burger and Jackson 2004). This could be a potential pathway in deciduous forests as aspen was observed to prefer to take up NO$_3$⁻ and NH$_4$⁺ was recycled quickly with high efflux in hydroponic culture (Kronzucker et al. 2003). My experimental design does not allow me to confirm or reject this possibility.

Some of the N availability trends were predictable from the proportion of deciduous trees while other seemed to be non-additive effects of the species combination, and were highest in the mixed stands. For example, rates of net N mineralization and stand biomass were highest in the mixed stands, which may suggest higher productivity of mixed forests. The higher productivity of mixtures of ecologically complementary species have been well documented (Smith and Long 1992; Kelty 1992; Mård 1996; MacPherson et al. 2001) and could be attributed to competition reduction (Vandermeer 1989), where white spruce and trembling aspen exhibit spatial, temporal and qualitative differentiation in the resource use, leading to more efficient utilization of site resources.
These two species are at least partially spatially separated in their resource use by root stratification, as aspen have deeper roots than white spruce (La Roi et al. 1988). Competition is also reduced by species having differing phenologies. For examples spruce gains a large proportion of carbon during spring and autumn periods when aspen is without leaves and light interception is low (Constabel and Lieffers 1996). Qualitative differentiation in resource use (Waring and Schlesinger 1985) may also occur in nutrient uptake as spruce and aspen are thought to prefer different N forms; NH₄⁺ and NO₃⁻ respectively (Kronzucker et al. 2003). The higher productivity of mixed stands may also be caused by a facilitation effect of one or more of the species. The presence of aspen was shown to increase productivity of the black spruce component in mixed stands with aspen proportions lower than 41% (Légaré et al. 2004). A possible mechanism for this, which should be tested, is the possible effect of deciduous litter on the decomposition of coniferous organic matter, due to the higher proportion of easily leachable compounds in deciduous litter (Berg et al. 1996).

My post-harvest measurements supported the conclusions of others (Silkworm and Grigal 1982; Tamm 1991; Maynard 1997; Bock and Van Rees 2002; Piirainen et al. 2002; Westbrook and Devito 2004) that harvesting boreal forests does not greatly change N dynamics. The concern that spruce seedlings experience inadequate N nutrition on clearcuts because of the shift to nitrate domination (Kronzucker et al. 1997) was unfounded according to my results. The soil inorganic N pool in the clear-cut sites, both deciduous- and coniferous-dominated was dominated by ammonium. Vegetation competition (Hangs et al. 2004) and adequate seedbed conditions (Awada et al. 2004) are
probably more important than the form of available N form for conifer regeneration on harvested boreal sites.

This supports findings from other studies in boreal forests (Carmosini et al. 2002; Westbrook and Devito 2004; Lapointe et al. 2005) that the soil inorganic N pool does not become dominated by nitrate after harvest. In the forest floor, which is an important rooting medium of boreal species, nitrate played a minor role in the N cycle even after harvesting. The ratio of gross NO$_3$-N production to gross NH$_4$-N production, suggested as a measure of the potential for NH$_4$-N to be transformed to NO$_3$-N rather than immobilized (Tietema and Wessel 1992), ranged between 0.07 - 0.11. Nitrate was more important in the mineral soil (0.2-3), as reported earlier in the aspen boreal forests (Fyles and McGill 1987). Cycling of nitrate was very fast with an estimated mean residence time of a nitrate molecule in the nitrate pool of less than one day, similar to that in a mixed coniferous forest (Hart et al. 1994). Ammonium turnover was slower, with an average mean residence time of 2-4 days, corresponding to its larger pool.

Nitrate immobilization is important in the retention of nitrate on site. Although I did not measure N leaching but based on the negligible soil concentration values, it is likely to be small. Even in a temperate hardwood forest that received substantial N deposition, N leaching was negligible due to high nitrate immobilization (Vervaet et al. 2004). Immobilization (biotic and abiotic) was probably the main fate of NH$_4$-N as gross nitrification only accounted for 5-10% of NH$_4$-N production.

The hypothesis that harvesting would have a stronger effect on N cycling in deciduous forests was not supported. Although the overall effects of harvesting were small, they were more apparent in coniferous and mixed stands. The stronger response of
coniferous forests to harvesting could reflect the different composition of soil biota and primary pathways of energy and nutrient flow, as different groups are likely to respond differently to the same perturbation. Fungi have been shown to be more strongly affected by clearcutting than bacteria at some forests (Siira-Pietikäinen et al. 2001), so the higher proportion of fungi at coniferous sites (higher C/N ratio) would lead to bigger changes at these sites. Clearcutting of coniferous forests is also followed by greater changes in vegetation composition with likely changes in quality of C inputs and nutrient acquisition. Aspen forests are more similar to clearcuts in species composition and changes that occur after harvesting are largely structural (Macdonald et al. 2001). Thus some of the changes after harvest may reflect changes in vegetation and influences of a newly established plant community as well as effects of changes in microclimate associated with the tree removal. Coverage of some understory vegetation groups was correlated with N availability. The contribution of nutrients originating from understory vegetation is higher than would be estimating based on their biomass (Alban and Perala 1990) and understory is thought to be important in the post-disturbance retention of N on site (Reiners 1992; Iseman et al. 1999). Whether the understory affected N availability or just indicated site N availability status could not be distinguished in this study. The gradients within monitored mixedwood stands were too small to indicate any plant species as a simple and reliable indicator of N status and availability based on presence or absence. Sites were differentiated rather by relative abundance of similar species. Moss cover was the most reliable indicator of N availability, being associated with low levels of ammonium and low rates of ammonification.
6.2 Strengths and weaknesses of the project and potential sources of uncertainty

The effect of harvesting was assessed simultaneously in three forest types, thus it could be determined whether harvesting has the same effect in different forest types or whether any effects are specific to one forest type. Both N availability and actual production were measured. The measurements were carried out in both forest floor and mineral soil layers, while in many studies one or the other layer is disregarded. The experiment at EMEND was replicated and the results should be applicable to western boreal forests under comparable conditions. The harvesting was done by the usual operational techniques so the results of this study are directly applicable to operational practices.

However, most of the measurements were done only once or twice and did not capture seasonal trends, which might be different in deciduous and coniferous forests. For example, microbial biomass C and N has been shown to fluctuate widely during the year (Zhong and Makeschin 2004). Also some of the measurements that were compared were done at different times. Measurements were taken only during the growing season, but microbial activity and leaching may occur during winter when there is no plant uptake. The values may thus not reflect yearly average values, although measurements during growing season should provided good indication of N availability relative to demand in the different forest types and harvesting treatments, and allow comparisons of forest types and harvesting treatments to be made.

The 10-ha blocks representing forest types were artificially delineated in the continuum of the mixedwood landscape. Substantial variability existed within the stands with deciduous patches in coniferous stands and vice-versa. Although diverse microsites were included within the study, the results are likely representative of the whole stand,
variations within the stands are not explicit. There were distinct microsites characterized by high soil moisture where processes might occur at rates that are quite different from the rest of the stand.

There were no actual measurements of leaching losses, and N status of the regenerating trees was not assessed. However, I showed that the commonly held belief that N leaching increases after harvesting because of increased nitrification does apply in these boreal forests. Thus any increased losses would result only from lower plant uptake and/or increased water flux in the clearcuts.

The effect of harvesting was assessed after 4 years, which did not capture short-term pulses immediately following harvesting. However these measurements were supplemented with earlier measurements of N availability at the same experimental sites (see chapter 3).

Although differences in N cycling among forest types correlated with the proportion of deciduous trees, other factors such as soil, topography and stand age may contribute to differences among forest types. Although the effect of site cannot be completely ruled out in this experimental design, the similar soil characteristics at depth, similar soil texture and topographic position suggest that vegetation had the prevalent effect on forest floor and upper soil characteristics (see chapter 2). Differences in the stand characteristics could also reflect their age or successional stage. Succession in western boreal mixedwoods is traditionally assumed to proceed from fire-disturbed sites, through aspen-dominated stands and mixed stands towards spruce-dominated stands. Only spruce and mixed stands are expected to be sustained on the site in the long term. However, Cumming et al. (2000) suggested that pure aspen stands can also be maintained.
in the absence of stand-replacing fire. Gap dynamics leading to the development of uneven-aged aspen stands has been described in northern Alberta, starting in stands as young as 40 years (Cumming et al. 2000). The aspen sites in my study had mature trembling aspen (80-100 years old), but usually did not have a spruce understory. The three replicates of mixed stands might have been of different ages. In one mixed stand, more than 15% of the trees had diameters larger than 40 cm, which has been proposed as an indicator of old-growth characteristics in boreal mixedwoods (Lee et al. 2000). As reliable information about the disturbance history to infer the previous development of the stands was not available, I considered stands in this study to be different forest types, based on tree cover.

I sampled randomly throughout the cutblocks, to attempt to represent average conditions of the site. It is possible that there were microsites with higher N availability, which might have been captured if systematic sampling had occurred across the cutblocks. In VR treatments, the samples were taken only in the retention strips where machinery did not enter, thus the overall effects of harvesting operations may have been underestimated. However, the samples from clearcuts (where machines traveled) also did not indicate any effect of harvesting for most variables, so this probably did not affect the results. Nitrate values were also close to detection levels, so subtle differences might have existed but were not captured with the method used.

Although soil N availability correlated with aboveground litter inputs, it may also have been affected by belowground inputs, which were not identified in this study. The vegetation may have influenced soil pH as a result of the release of H⁺ or OH⁻ ions in association with cation or anion uptake (Marschner et al. 1986). Aspen is thought to
preferentially use NO₃-N (Kronzucker et al. 2003), which would increase pH in deciduous forest floors, by releasing more OH⁻ ions. Spruce is believed to rely more on NH₄-N (Gessler et al. 1998), which would decrease pH in coniferous stands, by releasing more H⁺ ions. Soil reaction may affect N cycling, as soil pH was positively correlated with NH₄-N and SIN concentration in this study and with net nitrification rates in other boreal sites (Paavolainen and Smolander 1998; Ste-Marie and Paré 1999).

6.2.1 Measurements of N availability

As already mentioned, the size of the soluble N pool at any one time gives limited information about availability over time. Rates of net N mineralization and nitrification are better measures of N availability since they reflect soil processes over several weeks, but they still only show the net balance of several processes. Measurement of rates of gross N mineralization and nitrification is the only method which provides data about the turnover rate and actual production and consumption rates of NH₄ and NO₃. It does not, however, indicate how much N may become available for plant uptake.

Nitrogen supply rate measured by ion-exchange probes, on the other hand, does not show the actual magnitude of production and consumption, but estimates actual supply of N to plant root. The ion supply rate is assumed to be a more dynamic assessment of nutrient supply and it has been shown to correlate with plant nutrient uptake for N, P and K (Huang 1991; Schoenau and Huang 1991). Measurements of nitrate supply rates have been found to correlate with soil solution concentration of nitrate (with r² between 0.35-0.98 Ziadi et al. (1999). In this case, soil extractions and supply rate measurements yielded similar results for availability of NO₃-N, and for differences in P availability between forest types, but had conflicting results with respect to the effect of harvesting
on P and the availability of NH₄-N in different forest types. As supply rate measurements integrate more of the factors involved in nutrient availability, such as moisture (Qian and Schoenau 1996), and vegetation competition (Binkley 1984), they are more difficult to interpret (Qian and Schoenau 2002). Higher NH₄-N supply rates in spruce stands could reflect higher fluxes and faster cycling or it could actually be a result of higher uptake of NH₄-N in aspen sites, if the vegetation was a stronger competitor, as nutrient supply rate measured in the presence of roots is considered “net supply rate” (supply rate minus plant uptake).

Another methodological problem rated to estimation of microbial biomass by the chloroform-fumigation-extraction method also does not give the actual size of the microbial biomass C and N pools, as the efficiency of recovery is less than 100%. I did not use any coefficient to adjust for this because although “usual” values are commonly used they may vary in different conditions. The use of a conversion coefficient not tested under these conditions could introduce error.

Estimates of gross mineralization and nitrification by the ¹⁵N dilution method are based on several assumptions. If these are not fulfilled, turnover rates will be over- or underestimated. Assumptions of no remineralization, zero-order kinetics and no isotopic discrimination are expected to be fulfilled during short-term (1-2 day) incubations with ¹⁵N enrichment (Murphy et al. 2003). The requirement of homogeneous enrichment of the N pool is, however, probably not fulfilled and microsites with different availability of NH₄-N and NO₃-N likely occur within the incubated samples. It is also not clear how precisely the measured turnover rates reflect actual rates in the field in the presence of vegetation. Nitrogen production in the absence of roots is expected to be lower than in
their presence as labile C and N sources from root exudation are excluded (Burger and Jackson 2004). On the other hand, live roots may compete with nitrifiers for NH\textsubscript{4}-N (Norton and Firestone 1996), so at least autotrophic nitrification could be lower in the presence of plant roots. Thus while the gross N mineralization and nitrification rates estimated by the $^{15}$N dilution method in this study offer a reliable comparison among the different treatments, although they may not accurately measure the actual rates.

### 6.3 Management implications

Clearcutting did not have a significant effect on N availability in these forests, regardless of domination by coniferous or deciduous trees. Retention of live trees within cutblocks of western boreal mixedwoods may thus not be necessary for reasons pertaining to N dynamics and potential N losses.

In this study, disturbance of the forest floor was minimal and vegetation regrowth was fast. In studies that have shown elevated N availability, vegetation control and/or site preparation have often been a common factor. Forest floor disturbance seems to have greater consequences than harvesting itself for soil N availability and N leaching risk, and should be minimized during harvesting operations. Regrowth of vegetation should be encouraged following harvest, as it may have an important role in nutrient retention.

One of the distinct differences between the forest types was the higher proportion of inorganic N from the soluble N pool in deciduous stands. It might be desirable to maintain mixed stands or rotate stands with dominance of deciduous and coniferous species. Presence of aspen following spruce-dominated stands may lead to mineralization of part of the organic N reserve while subsequent spruce stand may take advantage of this
mobilization. Perpetuation of pure coniferous stands may shift the soil N pool towards larger proportion of relatively unavailable forms.

6.4 Conclusions and recommendations
The widely held assumption that deciduous forests as nitrate-rich environments in contrast to coniferous forests does not seem to apply to western boreal mixedwoods. The differences in N cycling between the forest types are subtle, involving small differences in the relative abundances of different N forms (e.g. microbial N, inorganic N). The mechanisms leading to these subtle differences still need to be clarified and implications for long-term site productivity investigated.

Concerns about a change to nitrate domination of the soil inorganic N pool after forest harvesting are largely unsubstantiated. There has been some elevation of nitrate and increase in the NO$_3$/NH$_4$ reported immediately after harvest in some studies and the factors contributing to this change should be further investigated.

Variable-retention harvesting in western boreal forests is not justified by concerns about changes in soil N availability. However, its suitability for specific objectives, such as better conifer regeneration, should be further explored.

Nitrification is an active process in boreal mixedwood forests. Both NH$_4$-N and NO$_3$-N immobilization are important mechanisms for N retention in these forest soils. The role of C availability in controlling N immobilization and retention in these forests should be further investigated. Immobilization may have been biotic or abiotic, both have been suggested to cause fast and substantial removal of nitrate from soil solution (Berntson and Aber 2000; Fitzhugh et al. 2003).
Microbial biomass and activity (measured as microbial biomass C and N phosphatase activity, N production and consumption) was not significantly reduced in the harvested sites. This might be because of the partial compensation for the reduced C input from the trees by quickly regenerating aspen and understory vegetation.

6.4.1 Further research
As mixed stands had the highest rates of N mineralization and highest stand biomass that could indicate potential higher productivity, mechanisms that might lead to higher productivity in mixed stands should be tested. For example, temporal compatibility in nutrient dynamics between trembling aspen and white spruce may reduce competition, as Lapointe et al. (2005) found N mineralization in aspen stands was higher in spring, whereas in coniferous stands it was higher in autumn. Another intriguing possibility is a priming effect of aspen-derived soluble C to decomposition of spruce organic matter, or a positive effect of higher Ca content of aspen litter on decomposition of spruce organic matter.

Litter decomposition rates showed differences in relation to soil N availability among aspen- and spruce-dominated stands and there was an indication of a possible “home field” advantage. Detailed study of the decomposition pathways (channels of energy and nutrients) should be conducted under spruce and aspen. If the processes and organisms involved are identified, the outcomes of a disturbance might be better predictable on a finer scale. This could include estimation of the proportion of nitrification carried out by fungi and bacteria, as they are also likely to respond differently to disturbance events.
It should be assessed how VR harvesting affects C rhizodeposition of the remaining trees. As C exudation has been shown to correlate with photosynthesis, below-ground C input per tree might be increased as a result of increased light. Composition of the exudates might be altered at the same time, and both these factors would have consequences for soil biota and associated processes.

The chemical composition of the SON pool should be characterized. Coniferous forests had a higher proportion of SON and also a trend towards a larger SON pool than deciduous forests. However, little is known about the composition and thus accessibility of this pool for microbial transformation and plant uptake by the two forest types.

The proportion soluble N that was SIN was a distinct characteristic of the three forest types. The use of the relative abundance of SIN (SON) as an indicator of N availability and site fertility should be explored along productivity gradients under single and multiple tree species.

Although data from the ion-exchange probes were useful for among-sites comparisons, they were difficult to relate to other measurements and contributed to contradicting results for NH₄-N. Further use of ion-exchange membranes in forestry research should be carried out to facilitate interpretation of the results.

Seasonality of N mobilization and immobilization by microbial biomass should be explored, in the light of recent evidence of high microbial activity during winter (Lipson et al. 1999; Grogan and Jonasson 2003); this could have implications for timing of management operations.
Understory coverage correlated with several N availability indices in uncut stands. The role of the understory in N retention in harvested sites should be further assessed. Understory plants were shown to immobilize 10 x more N than microbes (Burger and Jackson 2004) but they also compete with the tree seedlings for nutrients (Robinson et al. 2001; Hangs et al. 2002). Suggestions for understory management that optimize N retention and promote availability to target species are needed.
6.1 References


