University of Alberta

Effects of soil compaction and organic matter treatments on soil nutrient cycling in boreal forest ecosystems

by

Xiao Tan ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **'Effects of soil compaction and organic matter treatments on soil nutrient cycling in boreal forest ecosystems'** submitted by **Xiao Tan** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy** in **Soil Science**.

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Abstract

Forest harvesting and site preparation may cause soil compaction, organic matter removal, or organic materials being mixed with mineral soil in boreal forest ecosystems. By altering soil environmental conditions (e.g., aeration porosity, soil temperature and moisture content, etc.), severe compaction and organic matter manipulation (whole tree harvesting plus forest floor removal, referred to below as forest floor removal, or forest litter addition) may affect soil biological/biochemical properties and processes, thereby affecting tree growth. In a boreal aspen (*Populus tremuloides* Michx.) forest long-term soil productivity site near Dawson Creek, British Columbia, Canada, lower microbial biomass, enzyme (protease and phosphatase) activities, and net nitrification rates were found in the compacted soil due to poor soil aeration porosity, indicating that microorganisms such as nitrifiers and enzymes were sensitive to soil compaction. Forest floor removal reduced microbial biomass, enzyme activities, and N and P availability by reducing water content and substrate availability, while net N mineralization and nitrification rates increased due to increased soil temperature. Nitrogen loss may occur as reflected in the higher aspen foliar $\delta^{15}N$ and lower foliar N concentrations. Forest litter addition, however, increased microbial biomass and N transformation rates under controlled soil conditions. By altering soil biological/biochemical properties and processes, and increasing understory vegetation cover and species richness, soil compaction and forest floor removal had a negative effect on aspen and white spruce (*Picea glauca* [Moench] Voss)

growth in the short-term. Consequently, it is desirable to minimize the extent of soil compaction and forest floor removal to sustain soil and forest productivity in boreal forest ecosystems.

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Chapter 1. Introduction and literature review

1. Introduction

The boreal forest is a remarkably biologically diverse and dynamic domain, extending over 15 million square kilometers and accounting for one third of this planet's total forest area, and about one-third of Canada's land mass (Boreal Forest Network, 2006). Boreal forests play an important role as a source of forest products, a habitat for a wide range of plants and animals, and in mitigating climate change. In boreal forest ecosystems, management practices such as timber harvesting, thinning, mechanical site preparation, and fertilization are employed both extensively and intensively (Ballard, 2000; Prescott et al., 2000; Thibodeau et al., 2000; Strengbom et al., 2001). Boreal forest ecosystems have several important features which could challenge forest management activities 1) long cold winters and short growing seasons; 2) low soil temperature (a growth-limiting factor for vegetation and soil organisms that has been frequently cited as a rational for the wide spread use of site preparation before planting); and 3) a thick forest floor (Messier et al., 1995; Prescott et al., 2000).

Few management activities can be done without causing soil and site disturbances. Society's concern about the effects of management activities on forest productivity led to the initiation of the Long-term Soil Productivity (LTSP)

study on national forest lands (Powers et al., 1990) (Fig. I -1). Two key properties affected directly by management are soil porosity and site organic matter content. These two soil properties regulate critical soil processes through their roles in water and gas exchange, physical restrictions on rooting, microbial activities, and nutrient availability (Powers et al., 1990) (Fig. I -2).

Soil compaction is defined as an arrangement and bringing of the solid particles of the soil closer together and consequently causing an increase in bulk density (Greacen and Sands, 1980). Soil compaction occurs naturally from rainfall, growth of plant roots, foot traffic from both humans and animals, the weight of vegetation, and soil itself (Greacen and Sands, 1980; Kozlowski, 1999). However, the main forces causing soil compaction arise from heavy forestry machinery (tractors, skidders, disc-trenchers, etc.) used to harvest forests, drag logs, and prepare sites for stand regeneration (Kozlowski, 1999). The total area of land disturbed, e.g., landings, and primary and secondary skid trails by forest harvesting, was found to be as high as 18-26% of the total harvested area in 1950's (Steinbrenner and Gessell, 1955), and can be expected to be higher in recent years due to more demand on timber products and more intensive forest management practices (Fox, 2000). The highest degree of compaction typically happens in the top 30 cm of the soil profile, which normally contains most of the root mass (Wingate-Hill and Jakobson, 1982). In Canada, boreal forest soils may remain compacted for several decades (Corns, 1988). Although soils may

eventually recover from compaction by natural processes such as freezing and thawing and wetting and drying, severely compacted soils may not recover for a very long time. Growth reduction may occur during the early years that could be critical in determining overall forest productivity. Effects of soil compaction on soil physical properties such as soil bulk density and strength, pore size distribution, soil aeration porosity, water infiltration capacity, saturated hydraulic conductivity, and water runoff and soil erosion have been studied extensively (Corns, 1988; Orlander et al., 1990; Soane, 1990; Zabowski et al., 1994; Miller et al., 1996). These changes may have marked effects on soil biological and biochemical properties, soil processes, nutrient availability, and finally on crop yields. In the USA alone, it was estimated that soil compaction accounted for an annual loss in crop values of $ 1.2 billion in 1971 (Kozlowski, 1999).

Organic matter treatments are referred to as organic matter removal or organic materials mixed with mineral soil throughout this thesis. Ground-based harvesting and site preparation disturb site organic matter by removing trees, piling and burning slash, scalping forest floor, and mixing organic materials with mineral soil to bring nutrient retention (McMinn and Hedin, 1990). Generally, harvesting and site preparation may increase or decrease the amount of organic matter depending on harvesting intensity, either stem-only harvesting, or whole-tree harvesting, or all above-ground biomass removal (whole-tree harvesting plus forest floor removal), or how much organic matter is mixed with mineral soil as a

result of scarifying effects of harvesting equipments and the use of an assortment of plows, choppers, crushers in site preparation (McKinnon et al., 2002). Organic matter removal off site may intensify nutrient export (Morris et al., 1983; Stevens et al., 1988; Zabowski et al., 1994). For example, in a 50-year old Sitka spruce (*Picea sitchensis* (Bong.) Carrière) stand studied by Stevens et al. (1988), N, P, K, and Ca in bolewood and whole tree amounted to 128, 12.3, 38, 151 and 428, 43.5, 144, 279 kg ha^{-1}, respectively. Concerns about nutrient removals by forest operations have centered on whether harvesting losses can be replenished by natural processes or cause progressive nutrient depletion. Organic matter removal during harvesting or site preparation can also affect soil thermal behavior and soil moisture content due to the disappearance of mulching effect (Robert and Dong, 1993; Zabowski et al., 1994; Henderson, 1995). In mechanical site preparation, techniques such as mounding or mixing, that mixes organic materials with mineral soil have been reported to create more favorable microclimatic conditions for seedling growth (Orlander et al., 1990). Organic matter addition to soil may improve soil structure, reduce soil compactibility, and increase water content (Larson and Allmaras, 1971; Ross and Malcolm, 1982; Soane, 1990). Management of site organic matter in boreal forests entails two rather divergent considerations: 1) to maintain site organic matter and nutrient capitals to promote long-term site productivity; and 2) to manipulate site organic matter to enhance short-term productivity such as seedling growth by increasing

rates of organic matter decomposition and nutrient mineralization, improving seedbed conditions, and reducing vegetative competition (Prescott et al., 2000).

Soil microorganisms and enzymes play important roles in nutrient cycling in forest soils. Alteration of biological and biochemical properties and processes can have significant effects on nutrient availability, with implications on tree growth in a short-term, and for prediction on long-term soil productivity. We have a poor understanding of how soil compaction and organic matter treatments affect biological and biochemical properties and processes or how such changes could affect nutrient availability for plant uptake and thus forest productivity in boreal forest ecosystems. Understanding these soil properties and processes will improve our ability to predict management effects on boreal forest soils and to design better management systems. With these considerations in mind, I proposed to study the effects of soil compaction and organic matter treatments on soil biological and biochemical properties and processes, and tree growth in boreal forest ecosystems.

2. Literature review

The objective of this literature review was to provide the necessary background information to hypothesize that soil compaction and organic matter treatments would influence soil microbial properties and processes (C and N

transformations), enzyme activities, foliar $\delta^{13}C$ and $\delta^{15}N$, understory vegetation composition and structure, and tree growth in boreal forest ecosystems.

2.1. Soil microbial properties and processes

Soil microorganisms play an important role in soil nutrient cycling (Jenkinson and Rayner, 1977). Soil processes such as decomposition of organic matter and mineralization of nutrients are largely regulated by soil microorganisms and are fundamentally important not only for tree growth but also for forest ecosystem function (Tamm, 1991). Soil microbial biomass is a small but comparatively labile part of the organic matter in soil, acts as a source or sink of available nutrients, and may show a quick response to disturbances caused by forest management practices (Bosatta and Agren, 1993). The main effects of soil compaction on microbial biomass may result from changes in soil aeration status such as the loss of continuous biopores and O_2 deficiency. As most microorganisms live under aerobic conditions, a lower microbial biomass and N mineralization rates in compacted soil could be attributed to microbial deficiency of C assimilation due to O_2 deficiency (Dick et al., 1988; Kaiser et al., 1991; Whalley et al., 1995; Li et al., 2003). Anaerobic conditions could limit the activities of some microbes such as nitrifiers and result in the lower rates of nutrient transformations such as nitrification, and also cause gaseous losses of nitrogen due to increasing denitrification rates (Tobert and Wood, 1992).

However, portions of boreal forests are frequently subjected to periods of water logging after harvesting and microbial communities may become adapted to the changed environment following harvesting and show tolerance or resilience to soil compaction (Shestak and Busse, 2005). Startsev et al. (1998) found that Luvisolic soils had greater decomposition and respiration rates after compaction, an indication that soil biota had adapted to the low soil aeration and periodic anaerobic conditions. Microbial biomass may be larger and N mineralization rates lower in the compacted soil resulting from the protection of microbial organisms and organic materials against predation of mesofauna such as nematodes and protozoas once soil compaction reduces the accessible pore space for mesofauna (Breland and Hansen, 1995). Effects of soil compaction on microbial properties and N transformations are very complex depending on soil texture, water content, and organic matter content (Greacen and Sands, 1980). Furthermore, the effects of soil compaction are sometimes confounded during harvesting by the mixing of surface organic material with mineral soil. More research is needed to clarify the effects of soil compaction on soil microbial properties and processes in boreal forest ecosystems under either field or controlled (such as laboratory incubation) conditions.

Organic matter removal alters soil microclimatic conditions such as soil temperature and moisture content, which may have a dramatic effect on soil microbial activity, microbial access to substrate pools, organic matter

decomposition, and soil N cycling in northern boreal forest soils, where the rate and degree of decomposition would be less than optimal (Hendrickson et al., 1985; Prescott et al., 2000). Zabowski et al. (1994) suggested that organic matter removal can lead to increased temperature and reduced soil moisture content with concomitant negative effects on biological activity. Organic matter removal may also dramatically intensify nutrient export and reduce the amount of substrate for microbial utilization before trees return significant amounts of nutrients to the soil (Zabowski et al., 1994). Residue retention has been found to increase microbial biomass and N mineralization rates due to the increased C availability for microbial metabolism (Piatek and Allen, 1999; Mendham et al., 2002; O'Connell et al., 2004). Vitousek and Matson (1984) report that microbial immobilization of mineral N is the dominant process controlling leaching loss of N during management practices that remove organic matter from a site and thereby reduce the potential for immobilization. In the early stage of stand development, nutrient loss may reduce tree growth; however, in the late stage, N leached from surface soil may be available to trees as their roots explore deeper parts of the soil profile and trees start to return nutrients to soil. As noted above, confusion remains concerning the exact effects of organic matter removal on microbial properties and processes and thus nutrient availability, particularly the long-term effects on forest productivity in the boreal regions.

Considering nutrient export or loss following organic matter removal, mechanical site preparation such as mounding or mixing organic material with mineral soil after harvesting has been extensively applied to boreal forests (McMinn and Hedin, 1990). Soil mixing may improve environmental conditions such as aeration and drainage, expose more organic matter surface areas for microbial decomposition, and increase nutrient mineralization and mobilization (Ross and Malcolm, 1982). Addition of fresh residues to soil has been found to stimulate soil organic matter decomposition by providing available C for microbial activity in the early stage (Bingeman et al., 1953; Salonius, 1983; Orlander et al., 1990). However, adding and mixing organic material with mineral soil may have negative effects on nutrient availability as the incorporation of C substrate into the soil may increase microbial N immobilization (Vitousek et al., 1992; Messier et al., 1995). The extent to which N in the added litter is mineralized or immobilized mainly depends on the quality of substrate available to the decomposer (McClaugherty and Berg, 1987). In addition, Messier et al. (1995) found that mixing may control competing vegetation rather than stimulating decomposition rates. Much more work is needed to better understand the mechanisms on how mixing affect microbial activities and nutrient transformations in boreal forest soils.

2.2. Soil enzyme activities

Soil enzymes are proteins that act as catalysts without undergoing permanent alteration and cause chemical reactions to proceed at faster rates (Dick, 1994). Enzymes are mainly produced by microorganisms, but soil animals and plants can also contribute enzymes to soils. Enzymes such as dehydrogenase, protease, and phosphatase are specific activators and play important roles in soil C, N, and P cycling through their catalysis during the decomposition of organic compounds, breakdown of organic N and P esters to inorganic N and P, and formation of soil organic matter (Kiss et al., 1975). Enzyme activities may be correlated with microbial activities and have been used to understand the complex decomposition process. Soil enzyme activities are very sensitive to both natural and human-induced disturbances and can be used as a potential biochemical/biological indicator of soil fertility (Dick et al., 1988). By altering soil microclimatic conditions and changing total porosity, O_2 content, diffusion rate, and water infiltration rate, soil compaction may affect enzyme activities and nutrient availability (Zahir et al., 2001). A positive correlation has been found between soil enzyme activities and the numbers of pores ranging from 30 to 200 μm which are considered the most important pores in soil-water-plant systems and maintaining a good soil structure (Sequi et al., 1985; Pagliai and De Nobili, 1993). Soil compaction has been found to reduce soil enzyme activities due to reduced O_2 diffusion rate (Glinski et al., 1986; Dick et al., 1988; Pagliai and De Nobili, 1993), or increase soil enzyme activities due to favorable conditions for colonization with decomposer microflora on the basis of the closer contact of

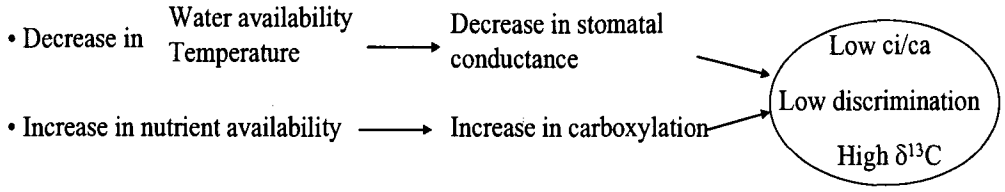
mineral and plant particles (Buck et al., 2000). Little information exists about the effects of soil compaction on enzyme activities in boreal forest soils.

By changing soil microclimatic conditions such as temperature and moisture content, and substrate availability, organic matter removal would be expected to change enzyme activities. However, effects of organic matter removal on enzyme activities have been rarely studied. Postharvest forest management practices such as different levels of organic matter removal or broadcast burn of the logging slash and forest litter have been found to reduce the activities of extracellular enzymes (e.g., glucosidase, cellobiohydrolase, phenol oxidase, etc.) involved in litter decomposition resulted from changes in soil water potential and in the quality and biochemical composition of litter (Waldrop et al., 2003; Hassett and Zak, 2005). Staddon et al. (1998) did not find any differences in the activities of phosphatase and arylsulfatase between uncut forest and clearcut plus scarification treatments in either the forest floor or mineral soils. Effects of soil compaction and organic matter removal on soil enzyme activities are very complex. Evidence of this was provided by Quilchano and Marañón (2000), who found that site factors (forest species composition, soil texture) and sampling date were greater determinants of the variation in dehydrogenase activities than management factors such as shrub-clearing. Dick et al. (1988) also indicated that sites with different climatic regimes or soil types may respond to compaction differently in relation to biological properties such as biomass and

enzyme activities. Before soil enzyme activities can be used as an indictor of soil disturbances, systematic studies across ecosystem and long-term soil productivity sites are needed to identify the most appropriate enzyme assays of soil quality.

2.3. Foliar $\delta^{13}C$ and $\delta^{15}N$

Stable isotope information has been the most informative in studies focused on water, carbon, and nitrogen that influence and limit plant growth (Dawson et al., 2002). Carbon isotope composition ($\delta^{13}C$) can be used as an indicator of environmental changes and is a useful index for assessing plant water use efficiency (Dawson et al., 2002). Discrimination has been observed to vary in response to soil moisture content, temperature, and nitrogen availability, and so on (Högberg et al., 1993; Panek and Waring, 1995; Gomez et al., 2002a). $\delta^{13}C$ variation affected by stress could be summarized by the following diagram:



(ci/ca is intercellular to atmospheric CO_2 concentrations)

Soil compaction and organic matter removal may reduce the rate of photosynthesis of plants due to both stomatal and non-stomatal inhibition by

altering soil water status, temperature, and nutrient availability (Greacen and Sands, 1980; Kozlowski, 1999). Stomatal closure reduces photosynthesis by inhibiting the diffusion of CO_2 to the mesophyll. Non-stomatal inhibition of photosynthesis may be involved in decreased carboxylating enzymes, capacity for electron transfer and chlorophyll content (Kozlowski and Pallard, 1997). Variation in $\delta^{13}C$ can be a useful index to explain tree growth differences under soil compaction and organic matter removal. Trees utilizing C3 pathway are likely to have a good correlation between $\delta^{13}C$ and water status (Waring and Silvester, 1994). For example, white spruce (*Picea glauca* (Moench) Voss) is an ideal species to test $\delta^{13}C$ technique because guard cells begin to close at xylem water potentials of -1.6 MPa, thus reducing C isotope discrimination (Coates et al., 1994). There are very few studies focusing on the effects of soil compaction and organic matter removal on foliar $\delta^{13}C$. After observing a significant correlation between leaf $\delta^{13}C$ and ponderosa pine (*Pinus ponderosa*) growth, and midday stem water potentials, Gomez et al. (2002a) suggested that leaf $\delta^{13}C$ can be used to measure retrospective water status and to assess the impact of soil compaction on tree growth.

The ratio between the two stable isotopes of nitrogen, ^{15}N and ^{14}N, varies in the biosphere as a result of isotope fractionation in soil physical, chemical, and biological processes (Högberg, 1997). The $\delta^{15}N$ of soil total N is dominated by the isotopic signature of stable N, which is not likely to change over decades,

while biologically active pools such as plants may be the good integrators of $\delta^{15}N$ of available N sources and N isotopic fractionation accompanying N fluxes in soil-plant systems (Högberg, 1997). Measurement of foliar N isotope ratios has been found to be useful in the assessment of plant N status and soil N dynamics (Garten Jr. and Van Miegroet, 1994). Some soil-mediated processes may lead to changes in plant $\delta^{15}N$ values include 1) N uptake by mycorrhizal fungi and plants; 2) changes in soil microbial activity resulting from alterations in plant attributes; and 3) nitrification. Nitrification has been associated with fairly large isotope effects during the first step of the reaction: $NH_4^+ \rightarrow NO_2^-$ controlled by *Nitrosomonas* (Yoshida, 1988); and (4) enhanced denitrification rates under anaerobic conditions in a wide range of forest and soil types, and climatic environments (Garten Jr. and Van Miegroet, 1994; Högberg, 1997). As discussed earlier, soil compaction and organic matter removal may affect soil microbial properties, enzyme activities, soil N mineralization and nitrification, and N losses due to leaching or denitrification, and may affect N source status which could be reflected in foliar $\delta^{15}N$. Choi et al. (2005) found that organic matter removal increased foliar $\delta^{15}N$ in both lodgepole pine (*Pinus contorta* Dougl. Ex. Loud.) and Douglas-fir (*Pseudotsuga menziesii*) stands on a calcareous soil. They attributed the higher foliar $\delta^{15}N$ to the altered isotope composition of N available for plant uptake because forest floor is the principle reservoir of nutrients in boreal forests and suggested that foliar $\delta^{15}N$ may provide

insights into the effects of soil compaction and organic matter removal on soil N status and dynamics.

2.4. Understory vegetation composition and structure

The establishment of understory vegetation after soil disturbance plays an important role in enhancing nutrient retention, reducing soil erosion, and providing wildlife forage in forest ecosystems; however, it may affect crop tree growth in the early stage of succession due to competition for light, water, and nutrients between non-crop and crop plants (Coates et al., 1994). Based on a ten-year LTSP research summary, Powers et al. (2005) suggested that forest productivity may not be affected by soil compaction and organic matter removal when trees are free of understory competition. They suspected that crop trees would have the advantage of access to old root channels and root crown microsites without a competing understory. Levels of compaction and organic matter removal may determine the negative or positive influence of understory vegetation on tree growth. For example, light soil disturbance could stimulate the growth of bluejoint (*Calamagrostis canadensis*) grass that competes for nutrients and water with white spruce seedlings (Lieffers et al., 1993), while heavy soil compaction together with organic matter removal could cause the largest reductions in understory vegetation cover and richness and may affect forest productivity (Kranabetter, 1999). Very little information is available on the effect

of soil compaction and organic matter removal on understory vegetation composition and how understory vegetation affects crop tree growth. We do not know if changes in plant communities are simply a short-term response to soil disturbances, or reflect more fundamental and profound changes to soil quality and forest productivity.

2.5. Tree growth

Effects of soil compaction on transport, absorption, and transformation of nutrients are influenced by altering soil aeration status, hydraulic properties, and diffusive transport of nutrients from the soil to plant roots (Lipiec and Stępniewski, 1995). Effects of soil compaction on tree growth vary from beneficial to detrimental, with the latter being much more common (Kozlowski, 1999). Severe compaction typically leads to physiological dysfunction in plants by altering water and nutrient availability through restricting root penetration, reducing diffusion coefficients as a result of increased tortuosity of pores (Nambiar and Sands, 1992; Sheriff and Nambiar, 1995), and causing nutrient losses such as denitrification and leaching (Tobert and Wood, 1992); however, if soil air, water and nutrients are in plentiful supply, moderate soil compaction may benefit tree growth due to the closer contact between soil particles and roots (Gomez et al., 2002b), and greater water retention and hydraulic conductivity in the case of increased diffusion rate and mass flow of mineral nutrients (Kemper

et al., 1971; Miller et al., 1996). Growth reduction has been reported in economically significant forest species such as radiata pine (*Pinus radiata),* lodgepole pine, and ponderosa pine (Sands and Bowen, 1978; Conlin and van den Driessche, 1996; Gomez et al., 2002b and c). Gomez et al. (2002c) found the effects of soil compaction on ponderosa pine growth to be detrimental, insignificant, and beneficial on clayey, loamy, and sandy soils, respectively. They suggest that the effects of soil compaction on tree growth depend on soil texture and tree species itself. For example, Douglas-fir reaches its best growth on well-aerated soil and does not survive on compacted soil while soil with underlying hardpan supports lodgepole pine growth (Lotan and Critchfield, 1992). Further studies are needed to investigate the effects of soil compaction on different tree species in different soil textures within boreal forest ecosystems.

Organic matter removal may dramatically intensify nutrient export and result in decreased nutrient availability, and may also change soil water availability and temperature by eliminating the mulching effects of forest floor and harvesting residues, which concomitantly affect tree growth (Zabowski et al., 1994). Growth responses to organic matter removal are variable depending on species type and site conditions. Several studies have reported that organic matter removal reduced the growth of trees such as Sitka spruce (*Picea sitchensis*), eucalypt (*Eucalyptus globules)*, aspen (*Populus tremuloides* Michx.), and white spruce possibly due to the reduced nutrient availability and modified soil

environment (Proe and Dutch, 1994; Stone and Elioff, 1998; Nzila et al., 2002; Kabzems and Haeussler, 2005) or have no effect on growth of trees such as radiata pine, Douglas-fir, and lodgepole pine (Smethurst and Nambiar, 1990; Zabowski et al., 2000). Mendham et al. (2003) found that retaining residues increased eucalypt seedling growth only on a poor site. Egnell and Valinger (2003) found that Scots pine (*Pinus sylvestris* L.) diameter and height growth, and basal area did not become apparent after whole tree harvesting until Age 12, 24, and 15, respectively. Interpreting early, short-term growth data has to be done carefully and continuous monitoring of tree growth is required to determine if the short-term responses will continue to be expressed in long-term stand development.

3. Summary

This thesis is organized into six chapters. Following this introductory and literature review chapter, the next chapter discusses the effects of soil compaction and organic matter removal on soil microbial properties and net N mineralization rates in a boreal aspen forest soil. Chapter 3 presents the results of the effects of soil compaction and organic matter removal on soil enzyme activities in a boreal aspen forest soil. Chapter 4 presents and discusses the effects of soil compaction and forest litter addition on soil microbial properties, C and N mineralization rates in a boreal lodgepole pine forest soil under laboratory

controlled conditions. Chapter 5 is focused on the impact of soil compaction and organic matter removal on understory vegetation community structure, aspen and white spruce growth and their foliar $\delta^{13}C$ and $\delta^{15}N$. The last chapter summarizes the thesis findings and discusses management implications.

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Fig. I -1. Long-term soil productivity network in North America (Courtesy of Robert F. Powers)

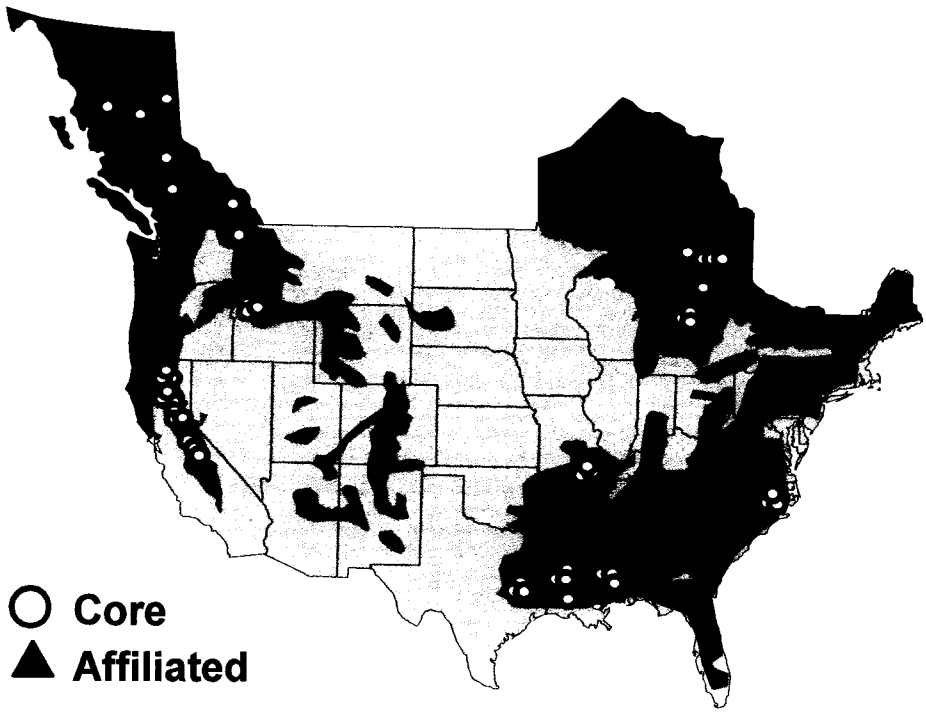
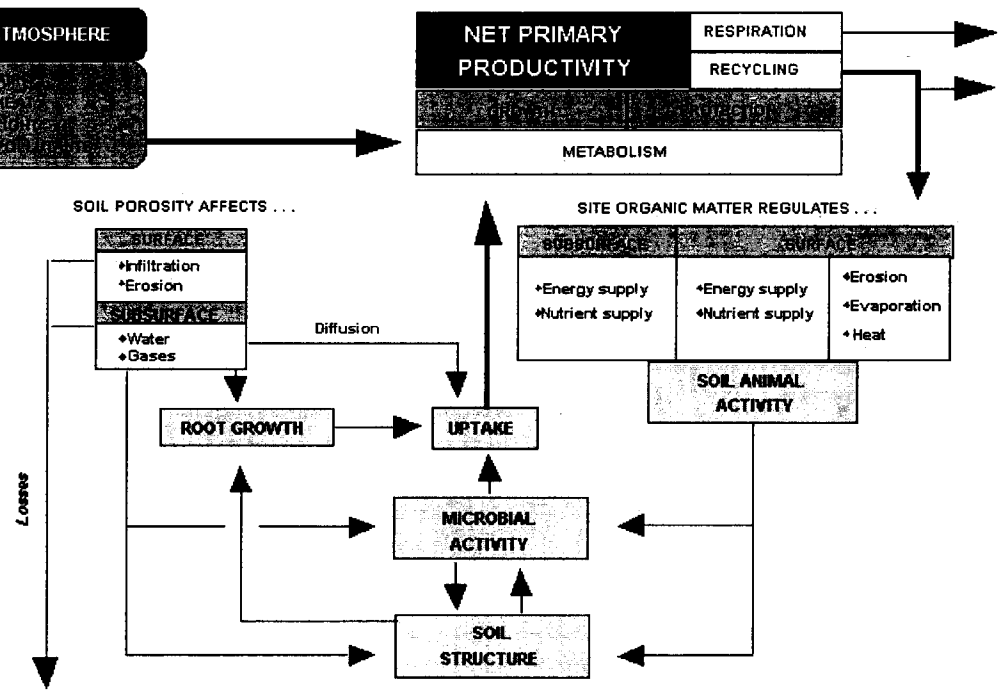


Figure I-2. Conceptual model on the influence of soil porosity and site organic matter on soil fundamental processes that regulate primary productivity within climatic constraints (Powers et al., 1990)



[1]Chapter 2. Effects of soil compaction and forest floor removal on soil microbial properties and N transformations in a boreal forest long-term soil productivity study

1. Introduction

Forest management practices such as timber harvesting and mechanical site preparation have the potential to cause detrimental levels of soil and site disturbances, particularly soil compaction and organic matter removal (Greacen and Sands, 1980; Corns, 1988; Jurgensen et al., 1997; Kozlowski, 1999). Concerns over the effects of management activities on forest productivity led to the initiation of the long-term soil productivity (LTSP) study in 1989 on national forest lands in the United States by the USDA Forest Service (Powers et al., 1990). Today, a coordinated research network of more than 100 LTSP and affiliated sites have been established across North America. The LTSP study hypothesized that soil macroporosity and site organic matter content are two principal factors directly affected by forest management practices that could change long-term soil productivity (Powers et al., 1990). Although soil compaction tends to be more random, less frequent, and less uniform in forest soils as compared with agricultural soils (Greacen and Sands, 1980), the effects

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of soil compaction can persist in a forest soil for several decades depending on soil texture, machine activity, soil water content, and other soil conditions at the time of harvesting (Corns, 1988; Kozlowski, 1999), thus affecting forest productivity in the long term.

Many studies have investigated the impact of compaction on soil physical properties and tree growth (Conlin and van den Driessche, 1996; Huang et al., 1996; Gomez et al., 2002); however, relatively few studies have focused on the effects of compaction on microbial properties and processes in forest soils (Piatek and Allen, 1999; Li et al., 2003 and 2004). Microbial biomass is one of the most labile fractions of soil organic matter and plays a pivotal role in mediating C and N cycling in the soil (Jenkinson and Rayner, 1977) and can be a sensitive indicator of changes caused by forest management practices (Sparling, 1992; Bosatta and Agren, 1993). By changing the proportions of macro- and microporosity, soil compaction could cause oxygen deficiency and protect organic material and microbial biomass against degradation by microorganisms and microfauna, and could concomitantly inhibit microbial activities and reduce N mineralization rates (Kaiser et al., 1991; Breland and Hansen, 1996). However, following harvesting soil microbes may become adapted to poor soil aeration and increase anaerobic decomposition under increased soil wetness and reduced air-filled porosity in boreal forest soils (Startsev et al., 1998). Much uncertainty

remains on the effects of soil compaction on biological properties and processes in boreal forest soils.

Management of organic matter in boreal forests entails two divergent considerations: 1) to maintain the organic matter and nutrient capitals on the site to promote long-term site productivity; and 2) to manipulate the organic matter to increase rates of decomposition and nutrient mineralization and reduce competing vegetation to enhance short-term productivity such as seedling growth (Prescott et al., 2000). Aspen ecosystems in north-eastern British Columbia commonly contain forest floor profiles that exhibit a layer dominated by soil faunal activity over one dominated by fungi (Fons et al., 1998). This is in contrast to the thick, mor humus form, with comparatively slow turnover rates and low nutrient availability commonly found in boreal forest ecosystems (Prescott et al., 2000). Forest floor removal may stimulate mineralization by improving environmental conditions for microbial activities (Hendrickson et al., 1985). However, Zabowski et al. (1994) suggested that forest floor removal could dramatically intensify nutrient export. Morris et al. (1983) reported that 300 kg N ha^{-1} was displaced during site preparation in a flatwoods forest in the southeastern United States. Retention of harvesting residue may be a preferred option for nutrient conservation and N mineralization, thereby meeting the long-term N requirement of crop trees (Piatek and Allen, 1999; O'Connell et al., 2004). Organic material retention can significantly increase microbial biomass due to

increased carbon availability for microbial metabolism (Mendham et al., 2002); however, the interaction between organic matter removal and soil compaction on microbial properties and processes is poorly studied in boreal forest soils.

In boreal forests of British Columbia, Canada, mechanical site preparation such as removal of harvesting residue and scalping are often employed to facilitate tree planting and to improve microclimatic conditions for tree growth (McMinn and Hedin, 1990). My study was undertaken at a boreal forest LTSP site near Dawson Creek, British Columbia to determine the effects of soil compaction and organic matter removal on soil physical and chemical properties, microbial biomass C (MBC) and N (MBN), and net N mineralization and nitrification rates. I hypothesized that MBC and MBN, and N transformation rates would be significantly lower in plots that were compacted and/or had organic matter removed than in plots that were non-compacted or had the forest floor intact.

2. Materials and methods

2.1. Study site and experimental design

The study site is located near Dawson Creek (55° 58' N, 120° 28' W), in north-eastern British Columbia. The study site is representative of mesic aspen

ecosystems in the moist and warm subzone of the Boreal White and Black Spruce biogeoclimatic zone (BWBSmw) (DeLong et al., 1991). Elevation is approximately 720 m and the average slope is 4%, with a south aspect. The area has a mean annual temperature of 1.6 °C with the highest (15.2 °C) and lowest (-14.7 °C) mean monthly temperature found in July and January, respectively. Mean annual precipitation is 482 mm, approximately half of which occurs as snow, and about 70% of rainfall occurs in the growing season between May and August (Environment Canada, 2002). Prior to harvest, the forest stand was dominated by aspen (*Populus tremuloides* Michx.), with minor amounts of white spruce (*Picea glauca* [Moench] Voss), lodgepole pine (*Pinus contorta*) and balsam poplar (*Populus balsamifera*) (Holcomb, 1996). Soils on the study site were developed on a silt loam veneer, 20 to 30 cm thick, laid over a clay loam. The soil is classified as Orthic Luvic Gleysols (Soil Classification Working Group, 1998). The pretreatment forest floor thickness averaged 7 cm. Details of soil properties before harvesting are listed in Table II-1 (Kabzems, 1996).

The study used a 3 x 3 completely randomized factorial experimental design with three replications implemented over a 4-year period. The experimental design followed what was proposed for the LTSP study by the USDA Forest Service (Powers et al., 1990). Treatment plots measuring 40 x 70 m were delineated prior to logging and randomly assigned to one of nine combinations of soil compaction and organic matter removal treatments. Plots

were harvested between January and February 1995 on frozen ground to ensure that no soil disturbance occurred during the harvesting phase. Following logging the treatment plots were established in 1995 (9 plots), 1998 (9 plots) and 1999 (9 plots). None of the treatment years included a complete set of all nine treatments; thus plot establishment date could not be used as a blocking factor.

In this study, I investigated the extreme treatment levels within each factor to form a factorial combination of two compaction (C0: no soil compaction, the undisturbed plots did not receive any post-harvest compaction and C2: severe soil compaction, the mineral soil was depressed by 4 to 5 cm using a vibrating pad mounted on an excavator) and two organic matter removal levels (OM1: stem-only harvesting, the trees were delimbed in the forest. Tree tops, limbs and all non merchantable woody materials were left on the forest floor and OM3: whole tree harvesting plus forest floor removal, all woody and nonwoody material was removed from the plot and the forest floor was stripped to expose the mineral soil using an excavator) with 3 replications for a total of 12 plots. It should be noted that all 12 plots were not established in the same year. The matrix for the plot installation was as follows:

OM1C0: 1995 (rep 1 & 2), 1999 (rep 3)

OM1C2: 1995 (rep 1 & 2), 1999 (rep 3)

OM3C0: 1995 (rep 1), 1999 (rep 2 & 3)

OM1C0: 1995 (rep 1), 1999 (rep 2 & 3)

A limitation common to many LTSP installations mainly was caused by the complex logistics of setting up experiments of this size and the availability of funds and suitable sites, resulting in plots established in different years (Axelrood et al., 2002) or having the study done on pseudoreplicated samples (Gomez et al., 2002). In the statistical analysis described below, I treated the year since plot establishment as a covariable to remove the effect of year since plot establishment on the measured soil microbiological parameters.

2.2. Soil sampling and analyses

Soil samples from the forest floor (LFH) and mineral soil layer to a depth of 10 cm were collected on July 14, September 14, and October 27, 2002, and May 20 and July 23, 2003. Three soil cores (6.3 cm in diameter) were collected in each plot from randomly selected locations and bulked to form a composite sample for each layer. Soil samples were immediately placed on ice and shipped to the laboratory in a cooler. Soil samples were sieved (2 mm) and stored at 4 °C until further analysis. All extractions were done within one week of sample collection.

The initial moisture content in the sieved forest floor and mineral soil samples was measured gravimetrically after drying in an oven at 70 and 105 °C, respectively (Kalra and Maynard, 1991). Soil aeration porosity was calculated as

$AP = (1-D_b/2.65) - \theta_m * D_b$, where AP is the aeration porosity, D_b is the soil bulk density, and θ_m is the water content on a mass basis (Hillel, 1982). Soil bulk density was calculated based on the volume of the soil core and oven-dry soil mass. Soil texture was determined based on particle size analysis using the Bouyoucos hydrometer method (Kalra and Maynard, 1991). Thermistors to monitor soil temperature were installed at 1 and 10 cm depth below the ground surface where the forest floor was retained and 5 cm below the mineral soil surface where the forest floor was removed. Temperature was recorded on Campbell Scientific CR10 or CR10X dataloggers (Campbell Scientific, Logan, UT). Because the average depth of forest floor was 5 cm in my study plots, I could compare soil temperature at the 10 cm depth (from ground surface) in the forest floor retained to the 5 cm depth in the forest floor removal treatments.

Soil MBC and MBN were measured by the chloroform fumigation-extraction method (Brookes et al., 1985). Twenty-gram field-moist mineral soil (5 g forest floor) was fumigated with alcohol-free chloroform for 24-h in an evacuated desiccator. Fumigated and control (unfumigated) samples were extracted with 80 ml 0.5 M K_2SO_4 and shaken for 1 h on a flatbed shaker. Extracts were filtered using Whatman No. 42 filter papers and frozen at -18 °C until further analysis. Extractable C and N were analyzed using a TOC-V total organic carbon analyzer (Shimadzu Corporation, Kyoto, Japan). Soil MBC was calculated as the difference in extractable C contents between fumigated and

control samples divided by a K_{EC} factor of 0.38 (Vance et al., 1987). The K_{EC} factor was used to account for the efficiency of extraction for MBC. Soil MBN was calculated as the difference in extractable N contents between the fumigated and unfumigated samples divided by a K_{EN} factor of 0.45 (Jenkinson, 1988). Similarly, the K_{EN} factor was used to account for the efficiency of extraction for MBN.

Net N mineralization and nitrification rates were quantified by in-situ incubation of intact cores using the buried bag method (Hart and Firestone, 1989). In each plot, 3 soil cores (6.3 cm in diameter) were randomly collected from locations close to where the samples for initial mineral N measurement were collected. Each soil core was separated into forest floor and 0-10 cm mineral soil and placed into individual plastic bags and incubated at their respective depth. Sample incubation commenced on July 14, September 14 and October 27 in 2002, and May 20 and July 23 in 2003. Samples were retrieved after 30-60 days of incubation (except for the winter incubation period) with the last set of incubated soil samples retrieved on August 22, 2003. Ten-gram field-moist mineral soil (3 g forest floor) was extracted with 50 ml 0.5 M K_2SO_4 to determine NH_4-N and NO_3-N concentrations in both pre- and post-incubation samples. After shaken for 1 h on a flatbed shaker, the extracts were filtered using Whatman No. 42 filter papers and analyzed colorimetrically by the indophenol blue method for NH_4-N (Mulvaney, 1996) and by the vanadium oxidation method for NO_3-N (Doane and

Horwath, 2003). Net N mineralization and nitrification rates were calculated by subtracting pre-incubation extractable N ($NH_4 + NO_3$) from post-incubation extractable N concentrations (Raison et al., 1987).

Total soil C and N contents were determined by the combustion method using the solid sample module SSM-5000A analyzer linked to a TOC-V total organic C analyzer (Shimadzu Corporation, Kyoto, Japan). Soluble organic C and total extractable N contents were measured on 0.5 M K_2SO4 extracts of non-fumigated samples using the TOC-V total organic C analyzer (Shimadzu Corporation, Kyoto, Japan). Soluble organic N was calculated as the difference between the total extractable N and inorganic N in the same extract. Soil pH was measured with a pH meter using 1:10 and 1:2.5 (w/v) ratios of sample to deionized water for the forest floor and mineral soil, respectively.

2.3. Statistical analyses

The SAS package was used to perform all analyses (SAS Institute Inc., 1999). Assumptions of normally distributed errors and homogeneity of variances were tested. Violating data sets were log (moisture content in the forest floor) or square root (both MBC and rate of net N mineralization in the mineral soil) transformed. Means presented in this paper were based on original data. A GLM

procedure for the mixed model was used to test the effects of soil compaction and forest floor removal on aeration porosity, soil moisture content, MBC, MBN, microbial C:N ratio, and net N mineralization and nitrification rates for each depth. The effect of forest floor removal treatment can not be detected for LFH layers. The Proc Mixed procedure was used to analyze unbalanced repeated measures data or to handle missing observations in repeated measures data. Because treatments were applied in different years, year since installation was used as a covariable to test if it affected the dependent variables. No significance of the year since installation was found for any dependent variable. Correlation analysis was used to evaluate the relationship between MBC and soluble organic carbon, and between MBN and soluble organic nitrogen. Statistical significance was accepted at $\alpha = 0.05$ for all statistical analyses.

3. Results

3.1. Soil physical and chemical properties

Compaction increased average soil bulk density by 0.26-0.30 Mg m^{-3} in the mineral soil ($P < 0.001$, ANOVA data not shown), with bulk density around 1.15 Mg m^{-3} in the non-compacted treatment (Table II-2). Aeration porosity in the mineral soil was reduced by as much as 50% by soil compaction (Fig. II-1

and Table II-3, $P < 0.001$), with aeration porosity generally maintained around 30% throughout the year in the non-compacted plots (Fig. II-1). Between September 2002 and May 2003, aeration porosity in the mineral soil fell below 15% in the compacted soil. In the forest floor, moisture content was not significantly affected by soil compaction, but showed strong seasonal variations with the highest (423%) and lowest mean values (96%) occurring in May 2003 and July 2002, respectively (Fig. II-2a and Table II-3). In the mineral soil, the interaction between soil compaction and forest floor removal on soil moisture content was significant, showing that soil compaction reduced water content by 11% after forest floor removal, but did not affect soil water content with the presence of intact forest floor (Fig. II-2b and Table II-3). Water content in the mineral soil had the same seasonal pattern as that in the forest floor with the highest (27%) and lowest mean values (14%) occurred in May 2003 and July 2002, respectively (Fig. II-2b).

In the forest floor, compaction reduced mean soil temperature by 2.2 °C between July and September 2002 and 2.8 °C between June and September 2003 (Fig. II-3a). In the mineral soil, compaction also reduced the mean soil temperature by 0.7 °C throughout the growing season (May to September) (Fig. II-3b). Forest floor removal increased the mean temperature in the mineral soil

by 4.4 °C during the growing season while decreasing the mean temperature by 0.6 °C in the winter (Fig. II-3b).

Compaction did not affect total C and N contents, C:N ratio, and pH in the forest floor (Table II-2), but increased total C and N contents, and C:N ratio in the mineral soil by 55.1%, 28.1%, and 26.7% (Table II-2; $P < 0.05$, ANOVA data not shown), respectively. Forest floor removal did not affect total soil C and N contents, C:N ratio, and pH in the mineral soil (Table II-2; $P > 0.05$, ANOVA data not shown).

3.2. Soil MBC, MBN, and microbial C:N ratio

Soil MBC, MBN and microbial C:N ratio in the forest floor were not affected by soil compaction, but MBC and MBN showed strong seasonal variations (Fig. II-4a, 4b, 4c and Table II-3). Soil MBC and MBN peaked in September 2002 with mean values (across the treatments) of 17,408 and 3,307 mg kg^{-1}, respectively, with the lowest in July 2002 with mean values of 9,141 and 1,586 mg kg^{-1}, respectively (Fig. II-4a and 4b).

In the mineral soil, soil compaction did not affect MBC (Fig. II-4d) but decreased MBN (Fig. II-4e and Table II-3; $P = 0.052$) and increased microbial

C:N ratio (Fig. II-4f and Table II-3). Forest floor removal tended to decrease MBC except in July 2002 (Fig. II-4d and Table II-3; $P = 0.089$), and decreased MBN by 11.7% (Fig. II-4e and Table II-3; $P = 0.050$). MBN did not show strong seasonal variations while microbial C:N ratio varied with sampling dates where the highest (10.5) and lowest mean values (7.4) occurred in July 2003 and September 2002, respectively (Fig. II-4f).

3.3. Net N mineralization and nitrification rates

In the forest floor, nitrogen was immobilized during the growing season in July 2002 and 2003 instead of being mineralized. Net N mineralization rates were not affected by soil compaction but showed strong seasonal variations with the highest mean value (1.48 mg N kg d^{-1}) occurring in May 2003 (Fig. II-5a and Table II-3). In the mineral soil, compaction did not affect net N mineralization rates either. The interaction between forest floor removal and sampling date on net N mineralization rates was significant, showing that forest floor removal increased net N mineralization rates in July 2002 and reduced N immobilization rates in May 2003, but did not affect net mineralization rates in the mineral soil in other sampling dates (Fig. II-5b and Table II-3).

For net nitrification rates in the forest floor, the interaction between soil compaction and sampling date was significant, with the rates reduced by compaction in May 2003, but not affected in any other sampling dates (Fig. II-5c and Table II-3). In the mineral soil, the interactions between soil compaction and sampling date, and forest floor removal and sampling date were significant. Soil compaction reduced nitrification rates while forest floor removal increased nitrification rates in July 2003, however, neither soil compaction nor forest floor removal affected nitrification in any other sampling dates (Fig. II-5d and Table II-3).

4. Discussion

4.1. Soil physical and chemical properties

Bulk density between 1.40 and 1.55 Mg m^{-3} is considered as the critical level at which plant roots can not penetrate soils with light and medium texture (Daddow and Warrington, 1983; Kozlowski, 1999). In compacted plots, bulk density exceeded the critical value of 1.40 Mg m^{-3} (Table II-2). Such high bulk densities may adversely affect soil biological properties and processes, thereby affecting soil productivity. Compacted soils had less than 15% aeration porosity

in the winter of 2002 and early growing season of 2003. When air-filled porosity falls below 10% of the total soil volume, microbial activity and plant growth can be severely limited in most soils (Brady and Weil, 2002). Soil compaction and forest floor removal reduced the water content of mineral soil by 11% after forest floor removal, probably as a consequence of reduced water infiltration rate and greater runoff of water (Greacen and Sands, 1980). When harvesting slash and forest floor were retained, no effect of soil compaction on soil water content was expected due to the high water holding capacity of the organic material and the effect of logging slash on minimizing the impact of rain drops on the soil and on increasing infiltration rates. This is consistent with findings from another LTSP site in British Columbia (Kamaluddin et al., 2005). In other studies, soil compaction has been shown to increase soil water content (Gomez et al., 2002; Li et al., 2003) when compaction increases the relative proportion of micropores, thereby increasing unsaturated hydraulic conductivity (Sands et al., 1979). The slightly lower soil temperatures I found in the compacted soil during the two growing seasons disagreed with the results of Kranabetter and Chapman (1999) and Li et al. (2003). They attributed increased soil temperatures to the higher thermal conductivity of the denser soil. In my study, forest floor removal increased soil temperature during the growing season, consistent with the findings of O'Connell et al. (2004) who reported increased soil temperatures when residues were removed following harvesting.

The increased mineral soil total C and N contents, and C:N ratio after compaction could be attributed to the physical protection of organic material from degradation by microorganisms (Breland and Hansen, 1996). There was also a potential confounding effect from soil compaction as soil compaction would have caused a greater soil thickness to be collected relative to the non-compacted soil. However, since soil C and N contents are generally lower in the deeper soil layers than in the surface under natural conditions, the greater soil C and N content after compaction may be explained by changed soil C and N cycling processes but cannot be explained by the greater soil thickness collected in the compaction treatment. The nonsignificant effects of forest floor removal on total mineral soil C and N contents, and C:N ratios in the mineral soil were consistent with the findings of Piatek and Allen (1999). Total soil organic matter generally changes very slowly in such a treatment and the changes can be difficult to detect in the short term (Mendham et al., 2002); however, soil microbial properties may be a more sensitive indicator to changes in soil properties in response to disturbances such as forest floor removal and soil compaction.

4.2. Soil MBC, MBN, and microbial C:N ratio

Soil compaction can decrease microbial biomass due to oxygen deficiency in the compacted soil (Kaiser et al., 1991). However, Breland and

Hansen (1996) found increased microbial biomass in a compacted soil owing to the increased physical protection of organic material and microbes against predation by microorganisms and microfauna. In my study, soil compaction did not affect MBC in both the forest floor and mineral soil, consistent with Jensen et al. (1996a and 1996b), Jordan et al. (2003), and Li et al. (2004). For example, Li et al. (2004) found that soil type had a greater effect on soil microbial biomass than soil treatments. I found that MBN was more affected by soil compaction as compared to MBC. In my study, soil compaction increased microbial C:N ratio in the mineral soil, indicating a potential change in microbial community composition, because the C:N ratio of fungi is typically higher than that of bacteria (Marumoto et al., 1982). Contrary to my results, Li et al. (2003) found that soil compaction consistently reduced microbial C:N ratios. They indicated that compaction resulted in changes in microbial community composition with fewer fungi and reduced carbohydrates because of decreased fine root production. Further research into the effects of compaction on soil microbial biomass and microbial composition is needed.

In this study, forest floor removal decreased MBN. Li et al. (2004) also found that whole tree harvesting plus forest floor removal reduced MBN six years after the treatments were applied. Residue retention was shown to cause significant increases in MBC and MBN one and five years after plantation establishment (Mendham et al., 2002). I did not find any relationship between

MBN and soil moisture content ($R^2 = 0.02$; $P = 0.593$, data not shown), or soil temperature ($R^2 = 0.01$; $P = 0.995$, data not shown). The higher microbial biomass levels in the mineral soil may be related to higher availability of C, measured as soluble organic carbon ($R^2 = 0.14$; $P = 0.011$, data not shown), and soluble organic N ($R^2 = 0.30$; $P = 0.001$, data not shown).

Seasonal changes in soil microbial population sizes have been found to be directly related to the turnover of organic matter and the cycling of nutrients in soil, thereby affecting nutrient availability (McGill et al., 1986). Seasonal changes in microbial biomass are driven by changes in soil C availability and environmental factors. Seasonal dynamics of microbial biomass can vary from stable to fluctuating amounts in the growing season (Smith and Paul, 1994; Chang et al., 1995; Chen et al., 2003). I found significant relationships between soil MBC and temperature ($R^2 = 0.25$; $P = 0.051$, data not shown), and moisture content ($R^2 = 0.34$; $P = 0.017$, data not shown). My data set indicates that MBC was more sensitive to the seasonal changes in environmental conditions and more dynamic than MBN. Chen et al. (2003) found, however, that MBN was more sensitive to seasonal changes; therefore, one could not expect any uniform and general relationship in very diverse ecosystems.

4.3. Soil net N mineralization and nitrification rates

Little information is available in the literature on the effects of soil compaction and forest floor removal on microbially driven soil processes such as N mineralization and nitrification in boreal forest ecosystems. Soil compaction can reduce nutrient availability by modifying rates of mineralization (Whalley et al., 1995). Lower N mineralization rates have been attributed to the poor aeration and restricted microbial access to the organic N (Li et al., 2003). On the other hand, the possibility of microbial adaptation to poor aeration has been poorly studied and its relationship to soil N cycling processes is poorly understood. It is possible that soil compaction improves the physical protection of organic material against the attack of microorganisms and therefore causes lower N mineralization rates (Breland and Hansen, 1996). This hypothesis is consistent with my observation of increases in organic C and N in the compacted soils (Table II-2). Soil compaction appeared to inhibit the activities of aerobic bacteria such as nitrifiers (activities strictly restricted to aerobic conditions) because nitrification was significantly reduced by soil compaction. De Neve and Hofman (2000) found that soil compaction reduced nitrification rates but did not affect N mineralization rates, similar to what I found in my experiment. The influence of soil compaction on nitrification rates should be considered in conjunction with any effects on N mineralization. Due to lower net N mineralization rates, soil compaction significantly reduced available N in both the forest floor and mineral soil with a greater reduction in NO_3-N levels ($P < 0.05$, data not shown). Li et al. (2003) reported that soil compaction reduced

available N by 28% with the greater reduction in NO_3 in year two; however, five years after harvesting, the compaction effect disappeared in their study.

O'Connell et al. (2004) reported that annual N mineralization rates in the surface soil (0-10 cm) were significantly higher in residue-retained treatments as compared to low residue treatments 4 years after the application of treatments, indicating that N mineralized from the retained residue contributed to the increased N availability. Piatek and Allen (1999) found that in a mid-rotation loblolly pine stand, N mineralization rates were 11 kg N ha^{-1} greater in the stem-only than in the whole-tree harvest treatments. In my study I found that forest floor removal increased N mineralization and nitrification rates in parts of the growing season in the mineral soil (Fig. II-5). I found a strong positive relationship between net N mineralization rates and soil temperature ($R^2 = 0.76$, $P = 0.006$, data not shown). Therefore, the hypothesis that forest floor removal would result in lower net N mineralization rates was not supported. In the short term, organic matter displacement or removal may stimulate mineralization in the mineral soil due to elevated soil temperature. Although N mineralization and nitrification rates were higher after forest floor removal, available N contents were unexpectedly lower. Forge et al. (2001) found that clearcutting reduced the capacity of microbial immobilization of ammonium and nitrate and therefore increased the potential of N losses through leaching and denitrification in Interior Cedar (*Thuja plicata* Donn ex D. Don) -Hemlock (*Tsuga heterophylla* (Raf.)

Sarg.) (ICH) forests in the southern interior of British Columbia. Hope et al. (2000) also found a greater potential for N loss through nitrate leaching and denitrification. Plant uptake of N may be minimal because of the limited development of root systems of young trees and mineral N may have been lost through denitrification and/or nitrate leaching (Vitousek and Matson, 1984). The exact mechanism for the lower N availability in the mineral soils in the forest floor removal treatment that had higher N mineralization and nitrification rates is unclear and deserves further study. N deficiency has been found to be widespread throughout the interior of British Columbia and to limit tree growth for species such as white spruce and lodgepole pine (Brockley and Simpson, 2004). Harvesting residue or forest floor removal also exports nutrients from the ecosystem, as much as 650 kg N ha^{-1} can be removed from a single disturbance (Tew et al., 1986). On my study site, as much as 1,167 kg N ha^{-1} (Table II-1) was lost after the forest floor was completely removed. In the long term, forest floor removal may pose a threat on forest productivity (Vitousek et al., 1992).

5. Conclusions

In the Boreal White and Black Spruce long-term soil productivity experiment established near Dawson Creek, British Columbia, compaction changed soil biophysical conditions, such as reduced soil aeration porosity, and lowered growing season soil temperature and moisture content. Soil compaction

decreased MBN but increased microbial C:N ratio in the mineral soil, and reduced nitrification rates in both the forest floor and mineral soils. Forest floor removal tended to decrease microbial biomass, most likely as a result of reduced substrate availability for microbial metabolism. Forest floor removal increased net N mineralization and nitrification rates in the mineral soil in certain sampling dates possibly as a result of the increased soil temperature. The hypothesis that forest floor removal would result in lower net N mineralization and nitrification rates was not supported, suggesting that forest floor removal did not have a negative effect on N transformation rates in the short-term; however, N export in the removed organic matter was relatively high. Continued monitoring of the research plots will help elucidate the long-term effects of both soil compaction and organic matter removal on N cycling processes and stand productivity.

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Table II-1. Pretreatment soil physical and chemical properties (Kabzems, 1996)

Soil depth	Bulk density ($Mg\ m^{-3}$)	Aeration porosity (%)	Texture	Total C ($g\ m^{-2}$)	Total N ($g\ m^{-2}$)	Available N ($g\ m^{-2}$)	pH
Forest floor (7-0 cm)	0.08	NA*	NA	2,464	117	7.33	5.7
Mineral soil (0-10 cm)	1.14	23.9	Loam-silt loam	908	86	2.98	6.2

*NA: not applicable

Table II-2. Physical and chemical properties of the forest floor (LFH) and mineral soil (0-10 cm) layers measured in July 2002.

Values are means with standard errors given in parentheses. (n=3)

Treatment*	Bulk density ($Mg\ m^{-3}$)	Total C ($g\ kg^{-1}$)	Total N ($g\ kg^{-1}$)	Soil C:N ratio	Available N ($mg\ kg^{-1}$)	pH (in H_2O)
			Forest floor			
OM1C0	0.11	372.1	13.90	24	45.21	5.61
	(0.01)	(12.2)	(2.88)	(3.9)	(2.59)	(0.06)
OM1C2	0.13	405.6	15.20	28	35.71	5.59
	(0.01)	(26.5)	(2.73)	(6.0)	(2.39)	(0.13)
			Mineral soil			
OM1C0	1.15	9.8	0.64	16	1.34	6.04
	(0.04)	(1.9)	(0.04)	(3.2)	(0.01)	(0.05)
OM1C2	1.41	15.5	0.80	20	0.93	6.02
	(0.06)	(1.1)	(0.01)	(2.4)	(0.04)	(0.13)
OM3C0	1.16	9.7	0.63	14	1.32	6.00
	(0.04)	(1.6)	(0.26)	(2.8)	(0.15)	(0.17)
OM3C2	1.46	14.9	0.83	18	0.97	6.05
	(0.16)	(4.5)	(0.14)	(4.1)	(0.10)	(0.06)

* Treatment codes: OM1C0, stem-only harvesting without compaction; OM1C2, stem-only harvesting with severe compaction; OM3C0, whole tree harvesting plus forest floor removal without compaction; OM3C2, whole tree harvesting plus forest floor removal with severe compaction.

Table II-3. Analysis of variance (*P* values) of the effects of soil compaction, forest floor removal, and sampling date on aeration porosity, soil moisture content, soil microbial properties and processes measured between July 2002 and 2003. *P* values less than 0.05 are highlighted in the table, NA-not applicable.

Source of variance	d.f.	Aeration porosity	Moisture content	Microbial biomass C	Microbial biomass N	Microbial C:N ratio	Net N mineralization	Net nitrification
				Forest floor				
Compaction (C)	1	NA	0.149	0.123	0.142	0.775	0.666	**0.027**
Time (T)	3	NA	**<0.001**	**<0.001**	**<0.001**	0.057	**<0.001**	**<0.001**
C*T	3	NA	0.684	0.318	0.265	0.558	0.814	**0.004**
				Mineral soil				
C	1	**<0.001**	0.770	0.708	0.052	**0.008**	0.669	**0.020**
Forest floor removal (OM)	1	0.719	0.093	0.089	0.050	0.426	0.140	0.212
C*OM	1	0.111	**0.010**	0.679	0.502	0.094	0.175	0.742
T	3	**<0.001**	**<0.001**	**0.028**	0.305	**<0.001**	**<0.001**	**<0.001**
C*T	3	0.686	0.713	0.919	0.398	0.538	0.160	**0.004**
OM*T	3	0.292	0.600	0.129	0.242	0.118	**0.001**	**0.037**
C*OM*T	3	0.248	0.193	0.430	0.941	0.364	0.394	0.951

Figure II-1. Effects of soil compaction and forest floor removal on mineral soil aeration porosity. Vertical bars are standard errors. (n=3)

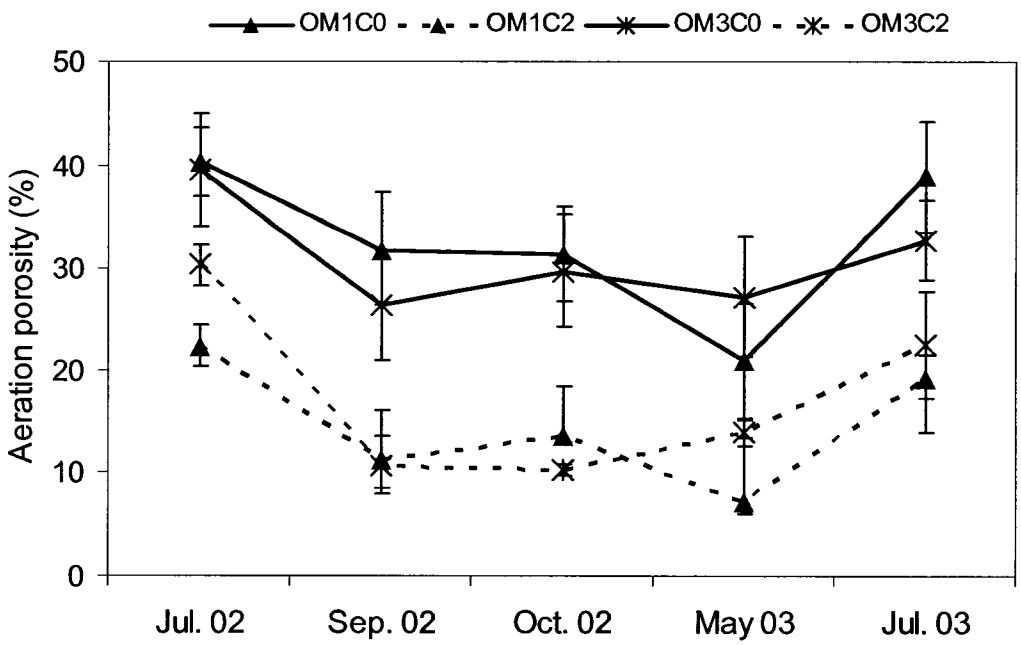


Figure II-2. Effects of soil compaction and forest floor removal on moisture content in a) the forest floor and b) the 0-10 cm mineral soil. Vertical bars are standard errors. (n=3)

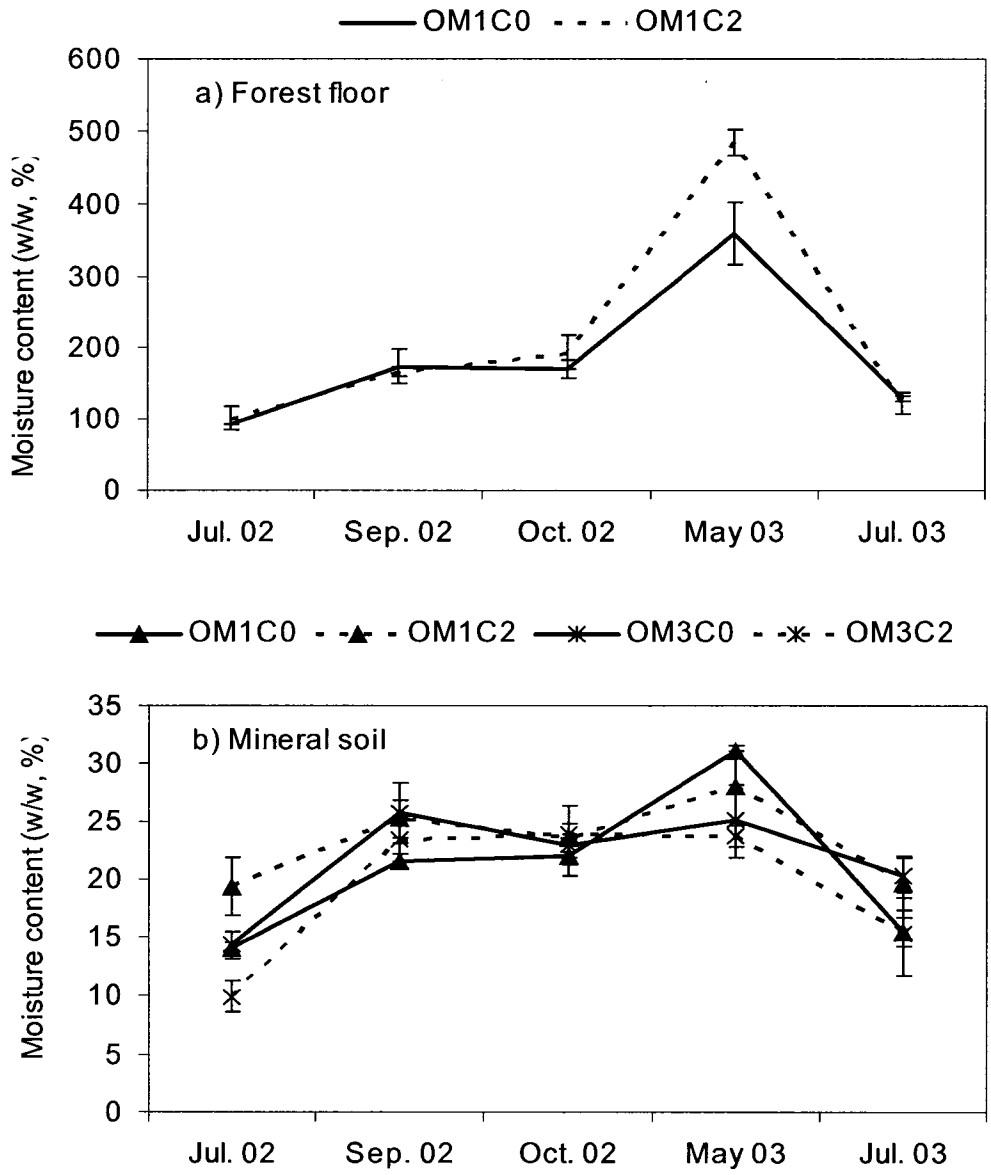


Figure II-3. Effects of soil compaction and forest floor removal on temperature a) in the forest floor and b) at 5 cm below the mineral soil surface. Vertical bars are standard errors. (n=3)

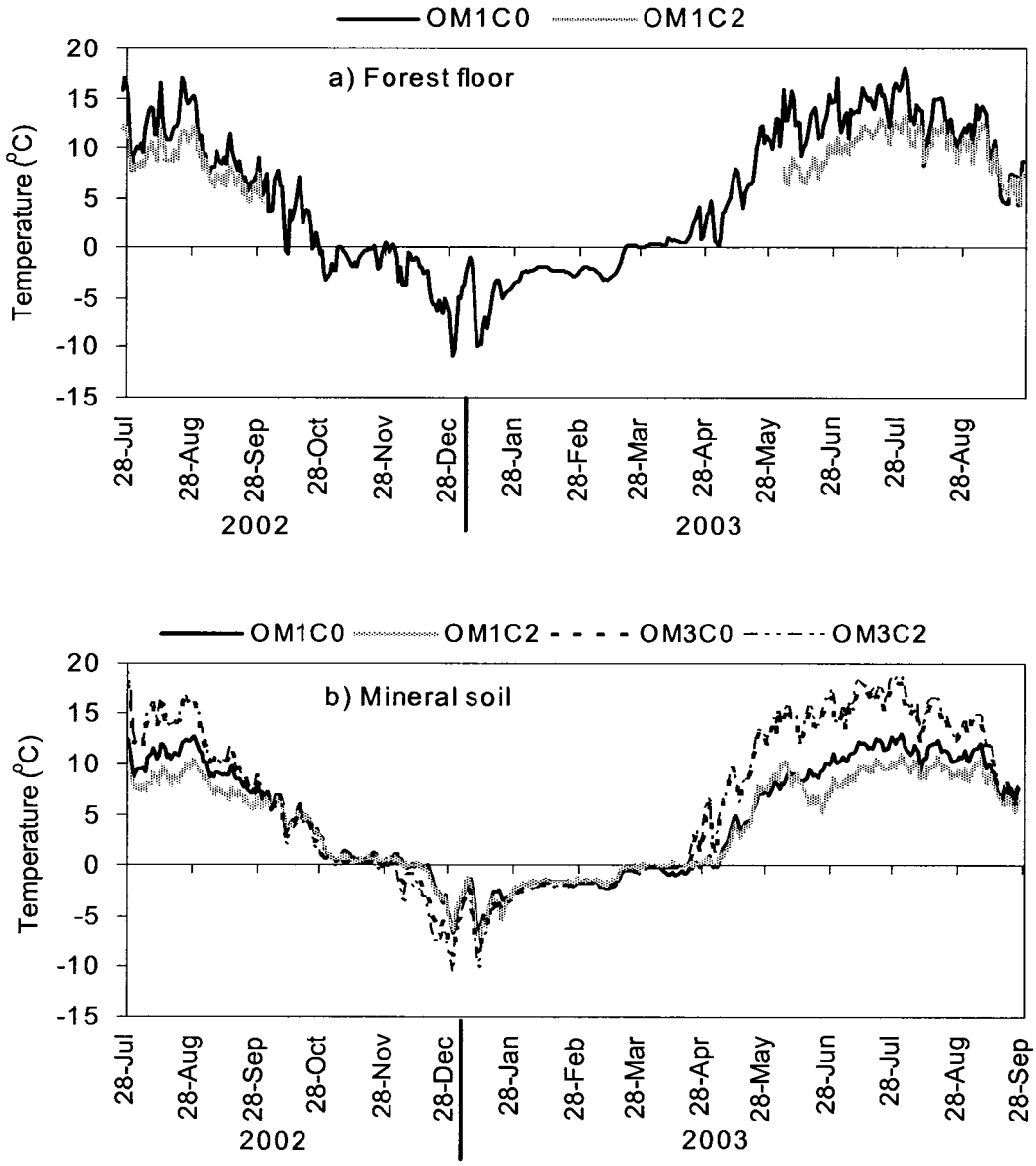


Figure II -4. Effects of soil compaction and forest floor removal on a) MBC in the forest floor; b) MBC in the 0-10 cm mineral soil; c) MBN in the forest floor; d) MBN in the 0-10 cm mineral soil; e) microbial C:N in the forest floor; and f) microbial C:N in the 0-10 cm mineral soil. Vertical bars are standard errors. (n=3)

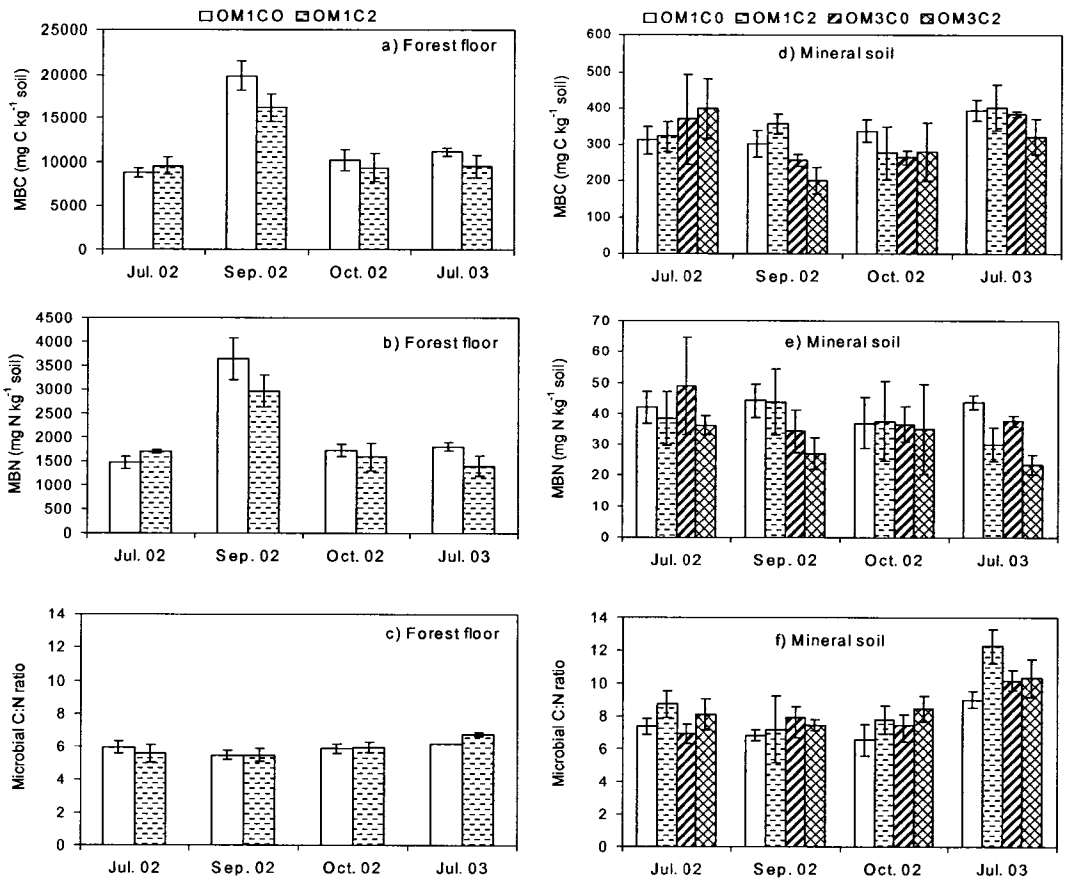
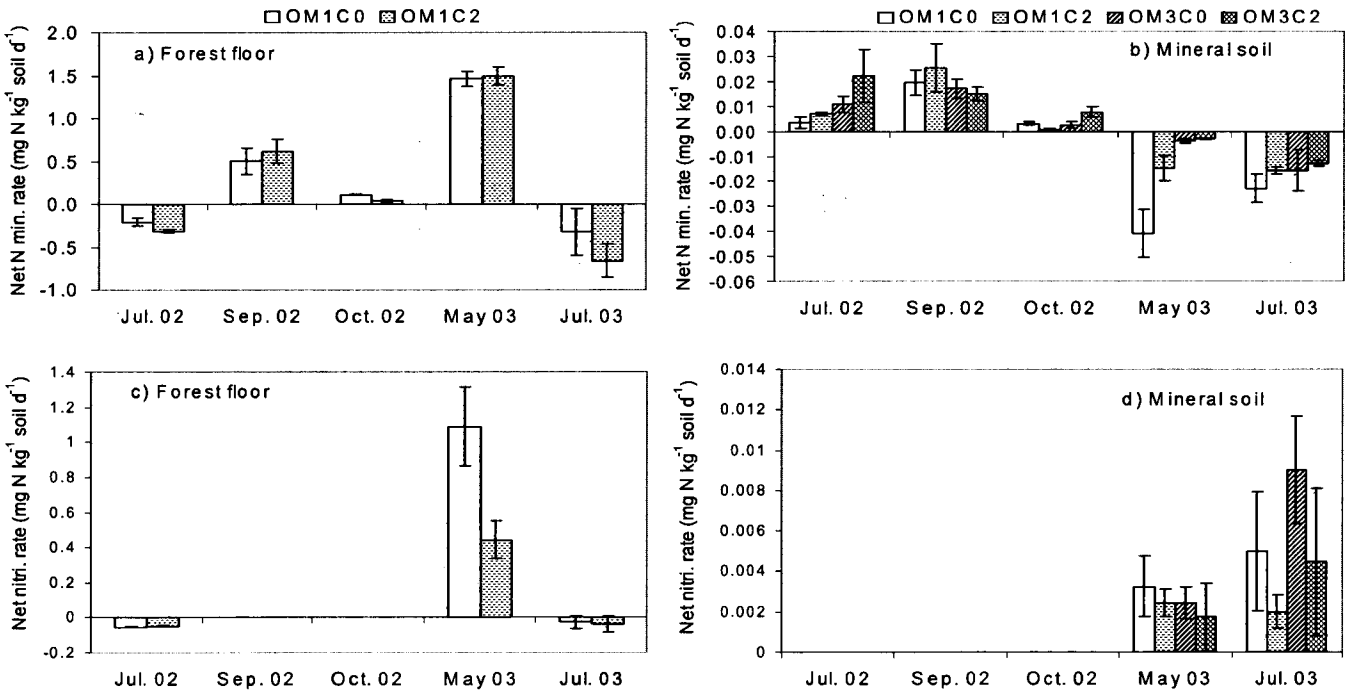


Figure II-5. Effects of soil compaction and forest floor removal on a) net mineralization rates in the forest floor; b) net mineralization rates in the 0-10 cm mineral soil; c) net nitrification rates in the forest floor; and d) net nitrification rates in the 0-10 cm mineral soil. Vertical bars are standard errors. (n=3)



Chapter 3. Effects of soil compaction and forest floor removal on microbial biomass and enzyme activities in a boreal aspen forest long-term soil productivity study

1. Introduction

Soil enzymes, proteins with catalytic properties, are produced mainly by soil micro-organisms because of their large biomass and high metabolic activities and to some extent by plant roots and soil animals (Ladd, 1978; Tabatabai and Dick, 1994). Enzymes are known to be involved in nutrient cycling and as such their activities can be used as potential indicators of nutrient cycling processes. In addition, soil enzymes are specific for the types of chemical reactions in which they participate. For example, dehydrogenase is an intracellular enzyme involved in microbial respiratory processes (Dick, 1994). In contrast, protease and phosphatase are extracellular enzymes. Protease is involved in breaking down proteins, resulting in the release of NH_4-N (Ladd and Butler, 1972). Phosphatase plays a critical role in the production of inorganic P through its catalysis on the breakdown of organic P esters to release inorganic P (Speir and Ross, 1982). Soil enzymes are very sensitive to both natural and human-induced disturbances and may show a quick response to changes induced by such disturbances (Dick et al., 1988).

Soil compaction and forest floor removal are two examples of disturbances caused by forest harvesting practices and mechanical site preparation in boreal forests (Corns, 1988; McMinn and Hedin, 1990). Many studies have found that soil physical and chemical properties such as soil porosity, aeration, water content, temperature, and substrate availability are affected by soil compaction and forest floor removal (Tew et al., 1986; Zabowski et al., 1994; Gomez et al., 2002; Tan et al., 2005). By changing the percentage of macro- and microporosity, soil compaction may cause oxygen deficiency by reducing oxygen diffusion rates that then affect the activities of enzymes such as catalase and phosphatase (Glinski et al., 1986; Pagliai and De Nobili, 1993). Soil compaction has been found to reduce the activities of enzymes such as phosphatase, amidase, and dehydrogenase (Dick et al., 1988; Jordan et al., 2003); however, higher phosphatase activity has been found in compacted soil, suggesting that microbial communities may be tolerant and resilient to soil compaction (Buck et al., 2000; Shestak and Busse, 2005). Postharvest forest management practices have been found to reduce the activities of extracellular enzymes (e.g., glucosidase, cellobiohydrolase, and phenol oxidase) involved in litter decomposition (Waldrop et al., 2003; Hassett and Zak, 2005). Quilchano and Marañón (2000) found that site factors (soil pH, available nutrients, and soil texture) and sampling season had greater influence on variation in enzyme activities than management factors (shrub-cleared and thinned forest). Changes in soil enzyme activities after soil compaction and forest floor removal are

complicated and may depend on enzyme type, site and soil types under different climatic regimes (Dick et al., 1988; Li et al., 2002).

Enzyme activities may correlate with microbial population size and they have been used to understand the complex organic matter decomposition process. In an earlier study, I found that soil compaction reduced microbial biomass N in the mineral soil and forest floor removal tended to reduce microbial biomass C and N (Tan et al., 2005). I would expect that soil compaction and forest floor removal will also reduce soil enzyme activities at this study site. The objectives of this study were to determine the effects of soil compaction and forest floor removal on the activities of soil enzymes (dehydrogenase, protease, acid and alkaline phosphatase), and to relate enzyme activities to soil physical and chemical properties and microbial biomass in a boreal aspen (*Populus tremuloides* Michx.) forest long-term soil productivity (LTSP) site near Dawson Creek in British Columbia, Canada.

2. Materials and Methods

2.1. Study site and experimental design

The study site is located near Dawson Creek (55° 58' N, 120° 28' W), in north-eastern British Columbia. The research site is representative of mesic aspen

ecosystems in the moist and warm subzone of the Boreal White and Black Spruce biogeoclimatic zone (BWBSmw) (DeLong et al., 1991). Elevation is approximately 720 m and the average slope is 4%, with a south aspect. The area has a mean annual temperature of 1.6 °C and mean annual precipitation of 482 mm, with approximately half of which fall as snow, and about 70% of rainfall occurs in the growing season between May and August (Environment Canada, 2006). Soils on the study site were developed on a silt loam veneer, 20 to 30 cm thick, laid over a clay loam. The soil is classified as Orthic Luvic Gleysols (Soil Classification Working Group, 1998). Details of soil properties before harvesting and post-treatment can be found in Tan et al. (2005).

The LTSP study uses a 3 x 3 completely randomized factorial experimental design with three replications implemented over a 4-year period. Treatment plots measured 40 x 70 m were delineated prior to logging and were randomly assigned to one of nine combinations of soil compaction and organic matter removal treatments. Plots were harvested between January and February 1995 on frozen ground to ensure that no soil disturbance occurred during the harvesting phase. In this study, I investigated the extreme treatment levels within each factor to form a factorial combination of two compaction (C0: no soil compaction, the undisturbed plots did not receive any post-harvest compaction and C2: severe soil compaction, the mineral soil was depressed by 4 to 5 cm using a vibrating pad mounted on an excavator) and two organic matter removal

levels (OM1: stem-only harvesting, the trees were delimbed in the forest, with tree tops, limbs and all non merchantable woody materials left on the forest floor, and OM3: whole-tree harvesting plus forest floor removal (referred to as FFR hereafter). In the OM3 treatment, all the woody and nonwoody material was removed from the plot and the forest floor was stripped to expose the mineral soil using an excavator. The treatments were replicated three times. As was indicated in Tan et al. (2005), all 12 plots were not established in the same year. In the statistical analysis described below, I treated the year since plot establishment as a covariable to remove the effect of year since plot establishment on the measured soil biological parameters.

2.2. Soil sampling

Forest floor and 0-10 cm mineral soil samples were collected on June 20 and August 20 of 2005. Three soil cores (6.3 cm in diameter) were collected in each plot from randomly selected locations and bulked to form a composite sample for each layer. Soil samples were immediately placed on ice and shipped to the laboratory in a cooler. Half of each fresh soil sample was sieved (4 mm) and samples were stored at 4 °C until further analysis on enzyme activities and microbial biomass. Another half was promptly air-dried, ground and sieved (< 0.25 mm) for soil chemical analyses.

2.3. Physical and chemical analyses

The initial moisture content in the sieved forest floor and mineral soil samples was measured gravimetrically after drying in an oven at 70 and 105 °C, respectively (Kalra and Maynard, 1991). Soil pH was measured with a pH meter using 1:10 and 1:2.5 (w/v) ratios of sample to deionized water for the forest floor and mineral soil, respectively (Kalra and Maynard, 1991). Total soil C was determined by the wet digestion method (Walkley-Black procedure). Total soil N was measured using a TOC-V total organic C analyzer attached with a TN module (Shimadzu Corporation, Kyoto, Japan) after kjeldahl digestion with sulfuric acid. Total soil P was determined by the ammonium molybdate ascorbic acid method after digestion with sulfuric acid-hydrogen peroxide (Kalra and Maynard, 1991; Kuo, 1996). Available N was analyzed colorimetrically by the indophenol blue method for NH_4-N (Mulvaney, 1996) and by the vanadium oxidation method for NO_3-N (Doane and Horwath, 2003). Available P was determined by the ammonium molybdate ascorbic acid method as described by Karla and Maynard (1991).

2.4. Microbial biomass C, N, and P measurement

Soil microbial biomass C (MBC), N (MBN), and P (MBP) were measured using the chloroform fumigation-extraction method (Brookes et al.,

1982; Brookes et al., 1985; Vance et al., 1987). All extractions were done within one week of sample collection. Twenty grams of moist soil samples from each treatment were fumigated with alcohol-free chloroform for 24 hours in an evacuated desiccator. Fumigated and control (unfumigated) samples were extracted with 80 mL 0.5 M K_2SO_4 for MBC and MBN, 80 mL 0.5 M $NaHCO_3$ for MBP and shaken for one hour on a reciprocating shaker. Extracts were filtered using Whatman No. 42 filter papers and kept frozen at -18 °C until further analysis. Extractable C and N were analyzed using the TOC-V analyzer (Shimadzu Corporation, Kyoto, Japan) connected with a TN module. To determine total extractable P in the fumigated and unfumigated soils, 10 mL extracts were digested for about 1 hour after adding 0.5 mL saturated $MgCl_2$ and 2 mL $HClO_4$ (70%, v/v) (Brookes et al., 1982). After digestion, the residue was boiled for 2 to 3 min with 10 mL 0.6 M HCl, cooled down to room temperature, and then diluted to 50 mL before colorimetric analysis. Inorganic P was analyzed by the ammonium molybdate ascorbic acid method as described by Karla and Maynard (1991). Soil MBC, MBN, and MBP was calculated as the difference in extractable C, N, and P contents between the fumigated and control samples divided by a K_{EC} factor of 0.38 for MBC (Vance et al., 1987), a K_{EN} factor of 0.45 (Jenkinson, 1988) for MBN, and a K_{EP} factor of 0.40 for MBP (Brookes et al., 1982), respectively. The K_{EC}, K_{EN}, and K_{EP} factors were used to account for the efficiency of extraction for MBC, MBN, and MBP, respectively.

2.5. Enzyme assays

Fresh soil was used for all enzyme assays. Dehydrogenase activity was determined using the reduction of 2,3,5- triphenyltetrazolium chloride (TTC) method as described by Tabatabai (1994). A sample of 20 g of moist mineral soil (< 4 mm) (1 g for forest floor) and 0.2 g $CaCO_3$ were mixed thoroughly and then 6 g of this mixture (0.3 g for forest floor) was dispensed in each of three test tubes. To each tube 1 mL 3% aqueous TCC solution and 2.5 mL distilled water were added. This amount of liquid should saturate the soil so that a small amount of free liquid appears at the surface of the soil after mixing. The content of each tube was mixed using a glass rod and the tube was corked and incubated at 37°C in an incubator. After 24 hours, the trephenylformanzan was extracted by adding 10 mL methanol and shaken for 1 min. The filtrate was collected in a 100 mL volumetric flask with a funnel plugged with absorbent cotton. The tube was washed with additional methanol until the red color disappeared from the cotton plug. The filtrate was then diluted with additional methanol to a final volume of 100 mL. The color intensity was determined by using a spectrometer at a wavelength of 485 nm with methanol as a blank.

Protease activity was measured following a modified method of Ladd and Butler (1972). One gram fresh soil (0.1 g for forest floor) was mixed with 2.5 mL sodium caseinate (10 g mL^{-1}) in 0.1 M Tris-sodium borate buffer at pH = 8.1.

This mixture was incubated at 37°C for 1 hour. Enzyme activities were stopped by adding 2 mL 17.5% tricloracetic acid. After centrifugation, 2 mL of the supernatant was mixed with 3 mL of 1.4 M Na_2CO_3 and 1 mL Folin reagent. Absorbance was measured at 700 nm (blue color) as compared to the similarly treated tyrosine standards. Controls either without soil or without substrate were used.

Phosphomonoesterases (acid and alkaline phosphatase) were measured based on the colorimetric estimation of the *p*-nitrophenol release from *p*-nitrophenyl phosphate (PNP) (Tabatabai, 1994). One gram of fresh mineral soil (0.1 g for forest floor) was placed in a 50 mL Erlenmeyer flask, and then 0.2 mL toluene, 4 mL of tris-hydroxymethyl aminomethane (THAM, with maleic acid, citric, and boric acid) buffer (pH 6.5 for acid phosphatase assay or pH 11 for alkaline phosphatase assay), 1 mL *p*-nitrophenyl phosphate solution made in the same buffer was added, and then the flask was swirled for a few seconds to mix the content. After stoppering the flask, I placed the flask in an incubator at 37 °C for 1 hour. Then I removed the stopper, added 1 mL 0.5 M $CaCl_2$ and 4 mL 0.5 M NaOH, swirled for a few seconds, and then filtered the soil suspension through Whatman No. 2 filter papers. The yellow color intensity was measured with a spectrometer at a wavelength of 420 nm. Controls were performed with each soil analyzed to account for the color not derived from *p*-nitrophenol released by phosphatase activity. To perform the controls, I followed the procedure described

for the assay of the phosphatase activity, but made the addition of 1 mL PNP solution immediately after the additions of 1 mL 0.5 M $CaCl_2$ and 4 mL 0.5 M NaOH.

2.6. Statistical analysis

The SAS package was used to perform all statistical analyses (SAS Institute Inc., 1999). Assumptions of normally distributed errors and homogeneity of variances were tested. A GLM procedure for the mixed model was used to test the effects of soil compaction and FFR on soil moisture content, soil chemical properties, microbial biomass, and enzyme activities for each depth. Because treatment plots were established in different years, year since installation was used as a covariable to test if it affected the dependent variables. No significance of the year since installation was found for any dependent variable. Correlation analysis was used to evaluate the relationship between soil physical and chemical properties, microbial biomass, and enzyme activities. Statistical significance was accepted at $\alpha = 0.05$ for all statistical analyses.

3. Results

3.1. Soil physical and chemical properties

In the forest floor, soil moisture content, soil pH, total C, N, and P concentrations, and available N and P concentrations were not affected by soil compaction or sampling date, with the exception of available N being significantly higher in August than in June (Table Ⅲ-1). In the mineral soil, soil compaction did not affect any soil properties other than reducing available N by 53% when the forest floor was intact. Forest floor removal did not affect soil pH or total P, but did significantly reduce soil moisture content, total C, total N, and available P by 16, 34, 25, and 38%, respectively. Available N was reduced by 52% by FFR in the noncompacted soil, but was not affected by FFR in the compacted soil. Only available P in the mineral soil increased from June to August.

3.2. Soil microbial biomass C, N, and P

In the forest floor, MBC, MBN, and MBP were not affected by soil compaction or sampling date (Table Ⅲ-2 & 3). In the mineral soil, soil compaction reduced MBP by 47% when forest floor was intact but did not affect MBC or MBN regardless of FFR (Table III-2 & 3). Forest floor removal reduced MBC and MBN in the mineral soil by 46 and 49%, respectively, regardless of soil compaction, and MBP by 50% in the noncompacted soil, but did not affect MBP in the compacted soil. Soil MBC, MBN, and MBP were not different between the two sampling dates.

3.3. Soil enzyme activities

In the forest floor, soil compaction did not affect the activities of dehydrogenase, protease, or acid and alkaline phosphatase (Fig. Ⅲ-1a, 2a, 3a, and 3b; Table Ⅲ-3). Dehydrogenase and Protease activities were greater in August than in June. In the mineral soil, soil compaction did not affect dehydrogenase activities (Fig. Ⅲ-1b and Table Ⅲ-3), but reduced protease and alkaline phosphatase activities by 28 and 27%, respectively, regardless of FFR, and acid phosphatase activities by 48% when forest floor was intact, but did not affect acid phosphatase when forest floor was removed (Fig. Ⅲ-2b, 3c, and 3d; Table Ⅲ-3). Forest floor removal did not affect dehydrogenase activities, but reduced protease activities by 25% regardless of soil compaction, and acid phosphatase by 39% in the noncompacted soil but did not affect acid phosphatase in the compacted soil (Fig. Ⅲ-1b, 2b, and 3c; Table Ⅲ-3). The interaction between FFR and sampling date on alkaline phosphatase activities was significant, showing that alkaline phosphatase activities were reduced from the FFR by 45% in August but not were affected by FFR in June (Fig. Ⅲ-3d; Table Ⅲ-3).

3.4. Correlation between soil physical, chemical, and biological properties

Many positive correlations were observed among soil physical, chemical, and biological properties (Table Ⅲ-4). For example, soil moisture content had significant positive correlations with total C and N, and microbial biomass C, N and P. Both available N and P were positively correlated with microbial biomass and activities of most enzymes. Strong correlations were observed between microbial biomass and enzyme activities.

4. Discussion

Soil compaction reduced protease and phosphatase activities, most likely due to the reduced aeration porosity (Tan et al., 2005). Soil enzyme activities have been found to be positively correlated with the volume of soil occupied by pores ranging from 30 to 200 μm, which are considered the most important pores responsible for soil aeration (Pagliai and De Nobili, 1993). Dick et al. (1988) attributed lower MBC and activities of all the enzymes they assayed (dehydrogenase, phosphatase, arysulfatase, and amidase) in the compacted mineral soil to changes in soil physical properties (e.g., decreased total porosity, water infiltration rate, aeration porosity, etc.) and reduced root growth. In a loblolly pine forest grown on sandy loam soil, increased bulk density (from 1.3 to 1.6 g cm^{-3}) reduced protease activities, and tended to reduce acid and alkaline phosphatase activities (Li et al., 2002). Contrary to the findings above, in a laboratory experiment, Buck et al. (2000) found higher acid phosphatase activity

in the compacted soil, possibly due to favorable conditions for colonization with decomposer microflora on the basis of closer contact between the mineral soil and mulch material. Acid phosphatase may be more sensitive to soil compaction than alkaline phosphatase in forest soils. In a greenhouse study, Jordan et al. (2003) also found that severe soil compaction (bulk density at 1.8 g cm^{-3}) reduced the activities of acid phosphatase, but did not affect that of alkaline phosphatase in a loamy soil. In my study, reduced microbial biomass, and protease and phosphatase activities (those involved in N and P transformations) most likely led to reductions in nutrient availabilities. Reduced trembling aspen and white spruce (*Picea glauca* [Moench] Voss) growth caused by soil compaction previously reported (Tan et al., 2006) may be directly related to reductions in microbial biomass and enzyme activities. Further research is needed to quantify the relationship between enzymatic activities associated with nutrient cycling and long-term soil productivity in boreal forest ecosystems.

Forest floor removal resulted in negative effects on microbial biomass, and protease and phosphatase activities in the mineral soil. Reductions in enzyme activities and microbial biomass caused by FFR may have limited the decomposition of organic residues thereby reducing available N and P concentrations in the mineral soil. My results are consistent with the literature. For example, Hassett and Zak (2005) reported 10-30% reductions in extracellular enzyme activities caused by intensive aspen harvesting (merchantable bole

harvest, whole tree harvest, and whole tree harvest plus forest floor removal) as compared with no harvesting, attributing those effects to reduced litter input and changes in soil climate following clear-cut harvest. In another similar study, Waldrop et al. (2003) found that the activities of extracellular enzymes (e.g., phosphatase, peroxidase, a-glucosidase, etc.) in the forest floor were reduced by postharvest management (slash, mechanical chipping and piling, and broadcast burning), resulting from changes in water potential and litter quality. In my study, reduced microbial biomass and enzyme activities after FFR were related to the reduced soil moisture content (Table Ⅲ-4), or nutrient loss (Tan et al., 2005) as changes in environmental conditions and nutrient availability may affect soil microbial populations and enzyme activities. Contrary to the above results, Jordan et al. (2003) found that placing forest litter (oak leaves) on the mineral soil surface reduced alkaline phosphatase activity in the mineral soil. The mechanism for such an effect was not clear. No differences of the activities of arylsulfatase and phosphatase between whole tree harvesting and whole tree harvesting plus scarification treatments were found in a jack pine (*Pinus Banksiana* Lamb.) ecosystem (Staddon et al., 1998). Forest soil types, regional climate, composition of microorganisms, and specificity of enzymes to catalyze certain reactions make the predictions on the response of enzyme activities to FFR difficult.

Soil enzyme activities integrate information about microbial status and soil physical and chemical properties and reflect soil fertility (Sinsabaugh et al., 1993). Many studies found that soil enzyme activities were positively correlated with microbial biomass (Dick et al., 1988; Li et al., 2002; Waldrop et al., 2003; Hassett and Zak, 2005). For example, Dick et al. (1988) found significantly positive correlations between MBC and the activities of dehydrogenase and phosphatase. The strong correlation between MBC and dehydrogenase activities reflects the fact that both MBC and dehydrogenase are associated with viable cells. Reductions in microbial biomass in this study may be directly related to declines in protease and acid phosphatase activities after soil compaction and FFR treatments were applied, similar to what was reported by Hassett and Zak (2005), who found that reduced enzyme activities were related to the reduced microbial biomass after forest harvesting. Reduction in available N was related to decreases in MBN and protease activities after soil compaction and FFR, indicating that MBN and protease activities play important roles in N cycling by generating NH_4-N, making N available for plant uptake. Similarly, soil available P was positively correlated with MBP and phosphatase activities, indicating the role of MBP and phosphatase in P cycling and thus, P availability. Measurement of biological parameters such as microbial biomass and enzyme activities could help forest managers identify the impact of management practices on soil fertility, long before such benefits could be measured by tree growth and long-term soil productivity (Dick, 1994).

This study suggests that microbial biomass and certain enzyme activities were sensitive to and negatively affected by soil compaction and FFR in this boreal forest soil. Reductions in microbial biomass and enzyme activities may affect N and P transformations, thereby reducing N and P availabilities. My findings are consistent with most other studies on soil compaction and FFR within the LTSP network in North America. My study indicates that if microbial biomass and enzyme activities do not recover after stands establish, reductions in N and P availability could potentially limit the long-term productivity in boreal forest ecosystems.

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Table III-1. Effects of soil compaction and forest floor removal on soil physical and chemical properties in June and August 2005. Values are means with standard errors given in parentheses (n=3).

Treatment *	Moisture content ($g\ kg^{-1}$)		Soil pH (in H_2O)		Total C ($g\ kg^{-1}$)		Total N ($g\ kg^{-1}$)		Total P ($g\ kg^{-1}$)		Available N ($mg\ N\ kg^{-1}$)		Available P ($mg\ P\ kg^{-1}$)	
	Jun.	Aug.	Jun.	Aug.	Jun.	Aug.	Jun.	Aug.	Jun.	Aug.	Jun.	Aug.	Jun.	Aug.
Forest floor														
OM1C0	1953 (143)	2307 (320)	5.26 (0.10)	5.39 (0.04)	371.5 (11.0)	367.1 (8.1)	14.58 (1.18)	17.69 (0.44)	1.50 (0.04)	1.45 (0.08)	49.5 (4.3)	73.6 (15.9)	219.4 (15.9)	228.5 (14.3)
OM1C2	2430 (310)	2746 (234)	5.41 (0.17)	5.29 (0.05)	398.7 (8.1)	397.5 (1.1)	17.49 (0.37)	18.09 (0.79)	1.72 (0.13)	1.77 (0.14)	37.8 (3.2)	67.7 (19.0)	208.4 (28.5)	203.9 (20.2)
Mineral soil														
OM1C0	293 (13)	326 (20)	6.11 (0.05)	6.09 (0.03)	14.7 (1.0)	14.4 (2.1)	0.94 (0.02)	0.88 (0.13)	0.55 (0.02)	0.55 (0.06)	1.8 (0.4)	2.0 (0.4)	11.0 (1.7)	15.2 (1.6)
OM1C2	283 (14)	309 (24)	6.03 (0.04)	6.12 (0.04)	14.0 (1.5)	12.1 (2.0)	0.96 (0.08)	0.77 (0.12)	0.55 (0.08)	0.53 (0.06)	0.7 (0.1)	1.0 (0.5)	10.0 (1.8)	14.5 (1.2)
OM3C0	268 (34)	278 (17)	6.26 (0.04)	6.10 (0.05)	9.4 (0.7)	8.8 (0.2)	0.68 (0.08)	0.60 (0.02)	0.50 (0.02)	0.48 (0.03)	0.7 (0.1)	1.0 (0.4)	5.5 (1.4)	10.8 (1.5)
OM3C2	214 (28)	260 (12)	6.14 (0.10)	6.05 (0.05)	9.5 (1.5)	8.8 (1.7)	0.71 (0.10)	0.68 (0.14)	0.54 (0.11)	0.49 (0.13)	0.7 (0.1)	0.9 (0.1)	5.7 (1.7)	10.2 (0.7)

*Treatment codes: OM1C0, stem-only harvest with no compaction; OM1C2, stem-only harvest with severe compaction; OM3C0, forest floor removal with no compaction; OM3C2, forest floor removal with severe compaction.

Table III-2. Effects of soil compaction and forest floor removal on microbial biomass C, N, and P, and microbial C:N and C:P ratios in June and August 2005. Values are means with standard errors given in parentheses (n=3).

Treatment*	Microbial biomass C (mg C kg^{-1})		Microbial biomass N (mg N kg^{-1})		Microbial C:N ratio		Microbial biomass P (mg P kg^{-1})		Microbial C:P ratio	
	Jun.	Aug.	Jun.	Aug.	Jun.	Aug.	Jun.	Aug.	Jun.	Aug.
					Forest floor					
OM1C0	13995 (1136)	13016 (1161)	1949 (313)	1747 (145)	6.1 (0.1)	6.6 (0.4)	631 (19)	643 (83)	22.0 (3.8)	18.1 (1.3)
OM1C2	13140 (341)	12535 (732)	1938 (143)	1781 (76)	6.9 (0.7)	7.0 (0.3)	600 (59)	695 (44)	21.7 (4.2)	18.1 (0.1)
					Mineral soil					
OM1C0	532 (169)	549 (123)	67 (4)	73 (17)	8.1 (0.2)	7.5 (0.2)	39 (3)	34 (5)	13.2 (1.0)	15.8 (1.4)
OM1C2	41 (12)	477 (44)	48 (1)	54 (6)	8.7 (0.1)	8.9 (0.3)	20 (1)	19 (2)	22.2 (1.5)	21.9 (2.0)
OM3C0	387 (11)	252 (23)	37 (2)	30 (1)	8.0 (0.9)	8.4 (0.9)	20 (1)	17 (1)	14.5 (0.7)	15.1 (0.2)
OM3C2	239 (12)	196 (15)	33 (4)	24 (3)	7.3 (0.7)	7.4 (0.3)	17 (3)	17 (1)	14.1 (1.4)	10.8 (1.3)

* Treatment codes are described in the footnote of Table III-1

Table III-3. Analysis of variance (*P* values) of the effects of soil compaction, forest floor removal, and sampling date on microbial biomass C, N, and P, and activities of dehydrogenase, protease, acid and alkaline phosphatase measured in June and August 2005. *P* values less than 0.05 are highlighted in the table.

Source of variance	d.f.	Microbial biomass C	Microbial biomass N	Microbial biomass P	Dehydrog-enase	Protease	Acid phosphatse	Alkaline phosphatase
				Forest floor				
Compaction (C)	1	0.552	0.789	0.664	0.434	0.418	0.776	0.423
Time (T)	1	0.346	0.645	0.758	**0.023**	*0.037*	0.996	0.779
C*T	1	0.653	0.699	0.818	0.365	0.423	0.878	0.652
				Mineral soil				
C	1	0.535	0.185	**0.037**	0.072	**0.022**	**0.002**	0.055
Forest floor removal (OM)	1	0.048	**0.003**	**0.017**	0.060	**0.039**	**0.008**	**0.025**
C*OM	1	0.835	0.477	**0.048**	0.502	0.812	**0.016**	0.125
T	1	0.283	0.624	0.067	0.305	0.117	0.113	0.326
C*T	1	0.698	0.710	0.089	0.398	0.420	0.160	0.213
OM*T	1	0.296	0.696	0.196	0.242	0.108	0.253	**0.047**
C*OM*T	1	0.885	0.988	0.326	0.941	0.654	0.394	0.874

Table III-4. Correlation coefficient (r value) among soil moisture content (MC), pH, total C (TC), total N (TN), total P (TP), available N (AN), available P (AP), microbial biomass C (MBC), N (MBN), and P (MBP), and activities of dehydrogenase (DHG), protease (PRT), acid phosphatase (ACP) and alkaline phosphatases (AKP) in the mineral soil (n = 12). Highlighted correlation coefficients were significant at $\alpha = 0.05$.

Variable	MC	pH	TC	TN	TP	AN	AP	MBC	MBN	MBP	DHG	PRT	ACP
pH	0.34												
TC	**0.84**	0.02											
TN	**0.75**	-0.17	**0.94**										
TP	0.43	-0.39	**0.69**	**0.84**									
AN	0.53	-0.38	0.47	0.47	0.46								
AP	0.49	-0.17	**0.60**	0.47	**0.63**	0.50							
MBC	**0.72**	0.19	**0.70**	0.53	0.27	**0.62**	**0.81**						
MBN	**0.69**	0.14	**0.74**	**0.57**	0.30	**0.69**	**0.82**	**0.98**					
MBP	**0.67**	-0.04	**0.75**	**0.61**	0.25	**0.65**	**0.71**	**0.76**	**0.82**				
DHG	0.35	0.09	0.33	0.27	0.43	**0.68**	0.44	**0.60**	**0.58**	0.26			
PRT	0.54	-0.05	**0.66**	0.54	0.43	**0.83**	**0.67**	**0.73**	**0.82**	**0.84**	**0.60**		
ACP	0.36	-0.01	0.42	0.31	0.14	**0.59**	**0.58**	**0.69**	**0.75**	**0.70**	0.48	**0.67**	
ALP	0.56	-0.16	**0.73**	**0.59**	**0.61**	0.47	0.78	**0.83**	**0.82**	**0.76**	0.35	**0.72**	**0.61**

Figure Ⅲ-1. Effects of soil compaction and forest floor removal on soil dehydrogenase activity in a) forest floor and b) 0-10 cm mineral soil in June and August 2005. Treatment codes are the same as in Table Ⅲ-1. TPF stands for trephenylformanzan (n=3)

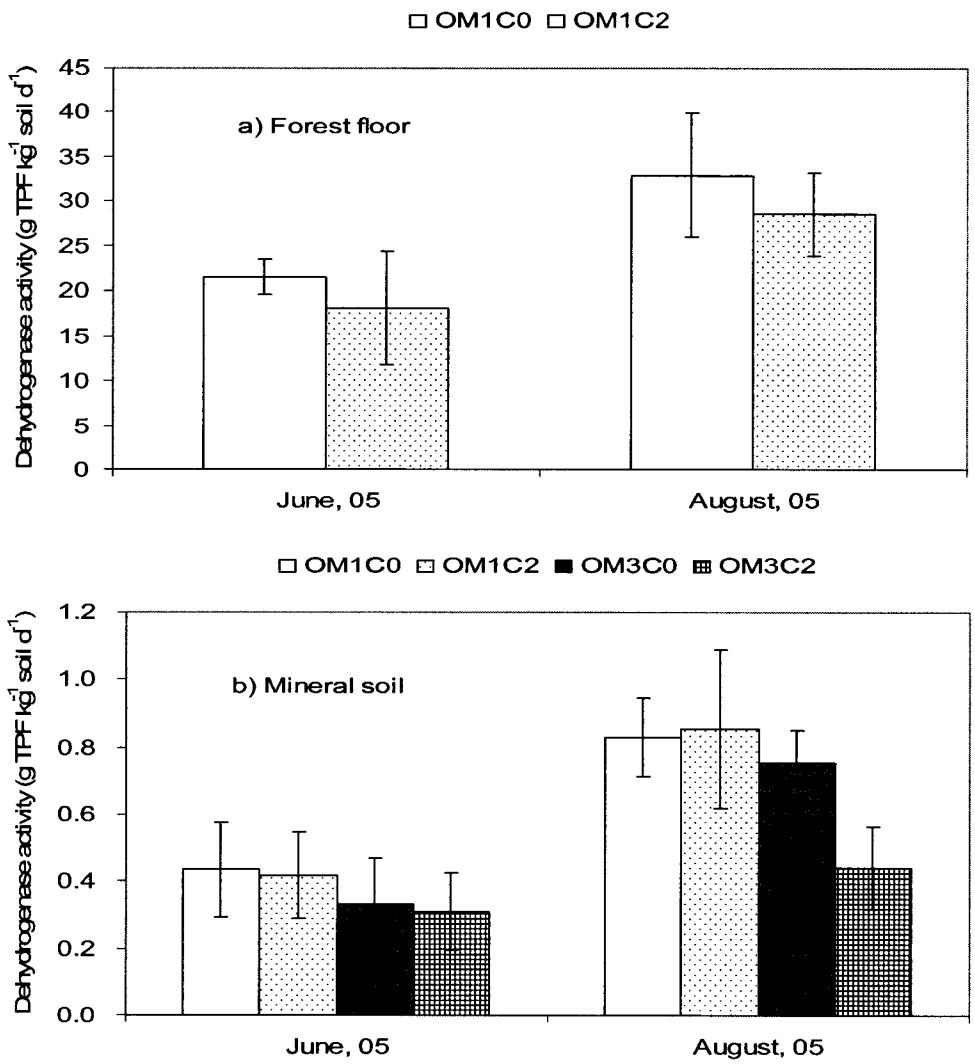


Figure Ⅲ-2. Effects of soil compaction and forest floor removal on soil protease activity in a) forest floor and b) 0-10 cm mineral soil in June and August 2005. Treatment codes are the same as in Table Ⅲ-1. (n=3)

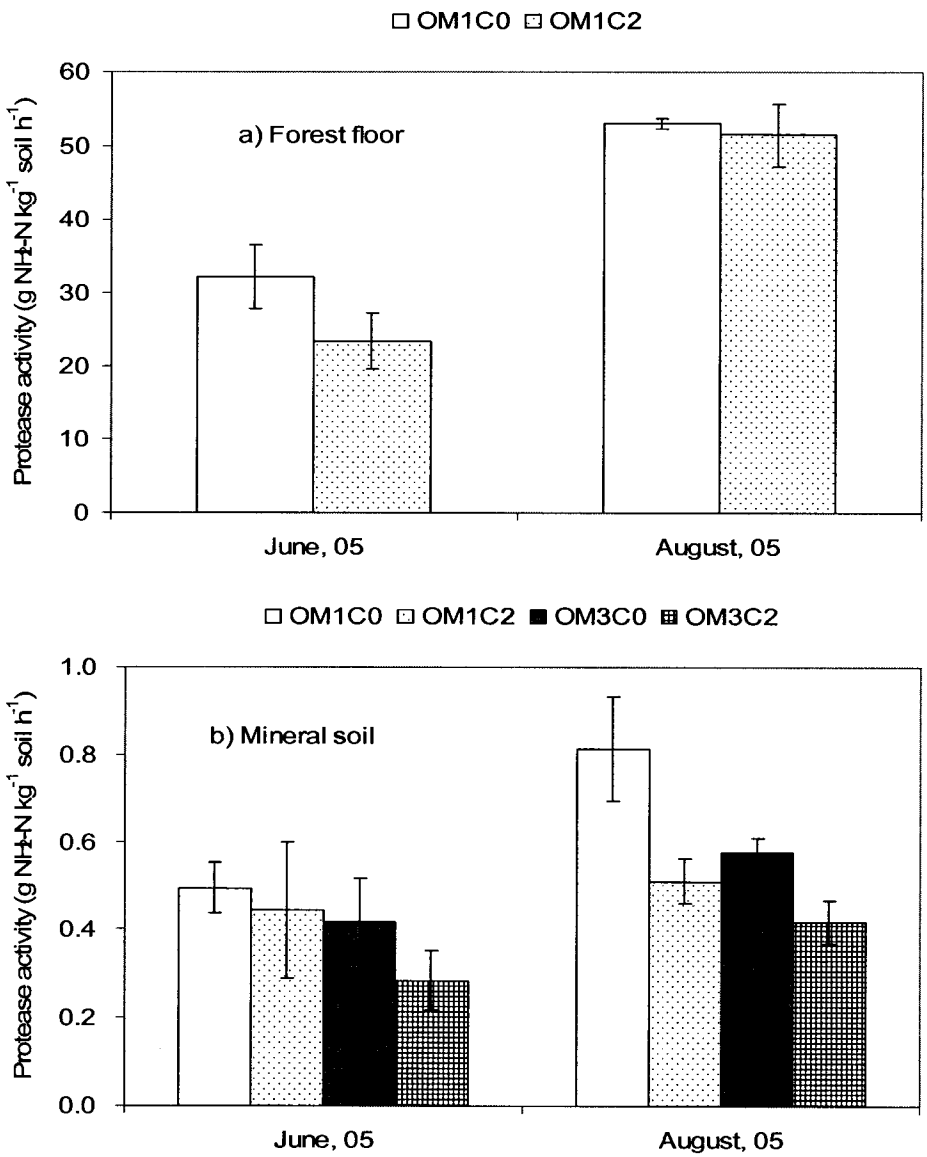
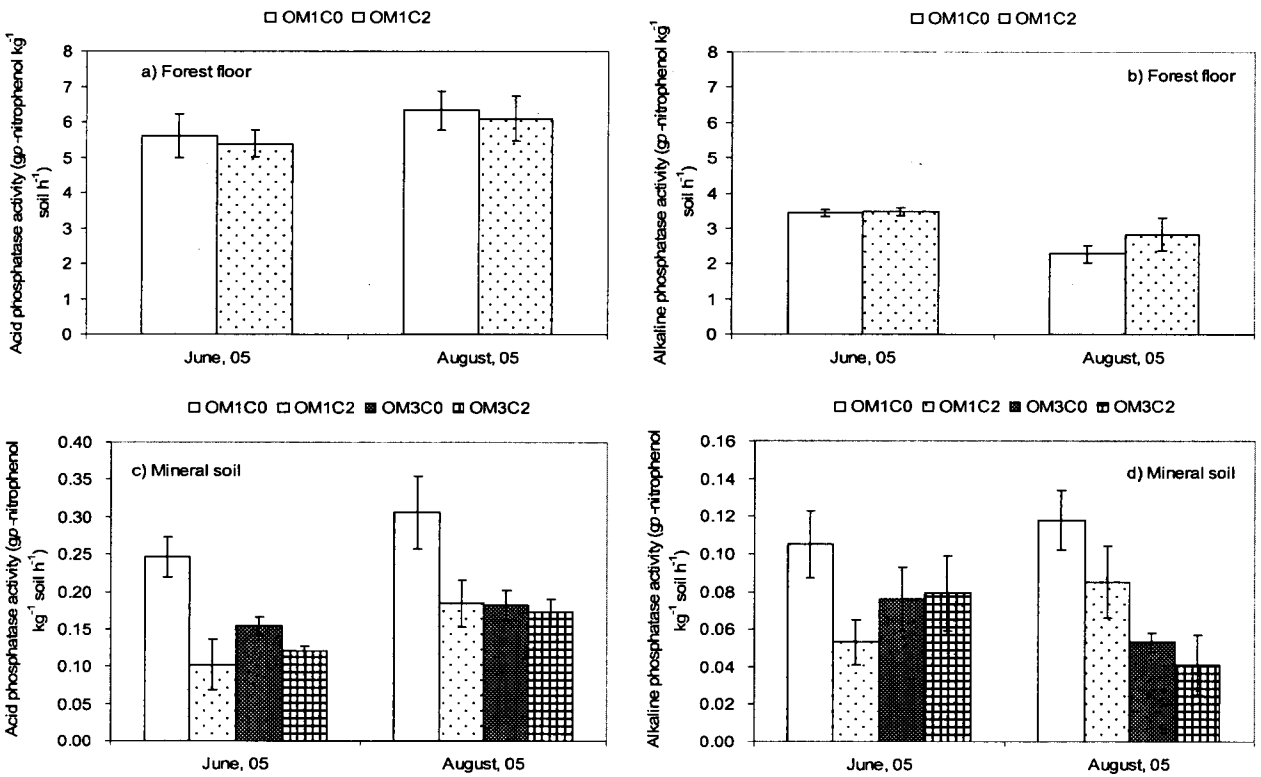


Figure III-3. Effects of soil compaction and forest floor removal on soil acid phosphatase activity in a) forest floor and b) 0-10 cm mineral soil, and on alkaline phosphatase activity in c) forest floor and d) 0-10 cm mineral soil in June and August 2005. Treatment codes are the same as in Table III-1. (n=3)



[2]Chapter 4. Soil compaction and forest litter amendment affect carbon and net nitrogen mineralization in a boreal forest soil

1. Introduction

In boreal forest ecosystems where low soil temperature and low litter quality prevail, forest management practices are often challenged by the surface accumulation of litter and slow rates of decomposition (Messier et al., 1995). To enhance stand productivity, mechanical site preparation after harvesting has been extensively applied to improve environmental conditions for tree growth, control weed competition, and stimulate organic matter decomposition and nutrient release (Salonius, 1983; McKinnon et al., 2002). Such practices may incorporate forest litter into the mineral soil through the use of plows, disc trenchers, choppers, and crushers (McMinn and Hedin, 1990), and may at the same time result in soil compaction from the use of heavy forestry equipment (Greacen and Sands, 1980; Kozlowski, 1999).

Soil compaction has been reported to change soil physical properties such as increase soil bulk density, and decrease soil porosity and water infiltration

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(Greacen and Sands, 1980; Huang et al., 1996). Changes in soil physical, chemical, and biological properties are correlated; for example, soil compaction can shift soil conditions towards an anaerobic state that is associated with reduced aerobic microbial activities, increased denitrification rates, and reduced uptake of nutrients as a prelude to reducing plant growth (Greacen and Sands, 1980; Kozlowski, 1999). In an earlier field-based study, I found that soil compaction reduced microbial N immobilization and net nitrification rates in a representative mesic aspen ecosystem in a Boreal White and Black Spruce long-term soil productivity site (Tan et al., 2005). Dick et al. (1988) also found that soil compaction reduced microbial activities, but they indicated that various soil types might respond to soil compaction differently in various climatic regimes with regard to alterations in biological properties. Some boreal forests are frequently subjected to water-logging, and under such conditions soil compaction after clear-cut harvesting may not affect microbial activities, owing to the resident anaerobes being adapted to increased soil wetness (Startsev et al., 1998). In general, the effects of soil compaction on microbial properties and processes in boreal forest soils are poorly understood.

Organic materials have different decomposition rates and form a continuum from labile to recalcitrant fractions. Addition of labile C substrates into the soil may increase microbial immobilization of N (Vitousek et al., 1992) and cause lower net N mineralization rates shortly after the incorporation of

organic matter (Frey et al., 2003). Messier et al. (1995) found that adding and mixing the forest floor with the mineral soil had negative effects on nutrient availability on low productivity sites but had negligible effects on high productivity sites when measured two and five years after the treatments were applied. Such mixing may control competing vegetation rather than stimulating decomposition rates (Messier et al., 1995). Although it has been hypothesized that adding and mixing forest litter with mineral soil increases rates of organic matter decomposition, there is no clear evidence that this is the case in boreal ecosystems. Understanding N dynamics in forest soils into which organic material has been added is important for improving the management of boreal forest soils.

Certain aspects of the relationship between forest litter manipulation and soil compaction have been the focus of recent studies. For example, forest litter addition to the soil has been recommended as a means to prevent soil compaction and as a source of nutrients and for increasing soil cation exchange capacity, as well as for adequate water retention to rehabilitate badly degraded sandy soils (Greacen and Sands, 1980; Soane, 1990; Kozlowski, 1999). However, I have not found any work that focuses on the effects of compaction on biological properties and processes in boreal forest soils, where forest litter is incorporated into the soil. Due to complexities such as spatial variability, and interactions between soil compaction and temperature and other climatic conditions in the

field (Greacen and Sands, 1980), laboratory experiments have advantages in testing the effects of soil compaction and forest litter amendment on soil biological properties and processes.

The objective of this study was to examine, through a 9-month laboratory incubation experiment (under controlled temperature and soil moisture conditions), the effects of soil compaction and forest litter amendment and mixing (referred to as forest litter amendment thereafter) on soil microbial biomass C (MBC) and N (MBN) contents, soluble organic C and N contents, as well as C and net N mineralization rates. I hypothesized that microbial biomass, soluble organic C and N, and C and net N mineralization rates would be significantly lower in soils that are compacted and/or do not have forest litter amended than in soils that are noncompacted or have forest litter amended.

2. Materials and methods

2.1. Soil and forest litter

The soil collected for this laboratory study is an Eluviated Eutric Brunisol (Soil Classification Working Group, 1998) that is a common forest soil in the boreal forest region. The soil was collected from the surface 10 cm mineral soil in a lodgepole pine (*Pinus contorta* Dougl. var. *latifolia*) stand (53°17′ N,

116°19′ W) about 35 kilometers south of Edson, in western Alberta. The site is located in the Lower Foothills Natural Subregion (Beckingham et al., 1996) and has a rolling topography, with a slope gradient of about 3-5%. The lodgepole pine stand regenerated naturally on this site after a wildfire in 1956. The area has a mean annual temperature of 2.0 °C and precipitation of 562.4 mm (Environment Canada, 2002). Parent material is lacustrine with underlying till material.

After collection, soil samples were placed on ice in a cooler and transported back to the laboratory. Visible coarse fragments and roots were removed and the soil was sieved through a 4 mm sieve before storage in a cool room at 4 °C. The soil has a silt loam texture, having 21% sand, 67% silt, 12% clay, 1.40% total organic C, 0.10% total N, and a pH_{H2O} of 4.05. The forest litter used in this experiment was primarily comprised of leaf litter of coniferous needles and deciduous foliage, along with partially decomposed leaf litter from the forest floor, having 37.70% organic C, 1.20% total N, a C:N ratio of 31, and a mean bulk density of 0.17 Mg m^{-3}.

2.2. Treatments and incubation procedures

Two soil compaction levels, no compaction (control, bulk density at 1.1 Mg m^{-3}, as observed in the field) and severe compaction (bulk density at 1.5 Mg

m^{-3} as the upper limit of bulk density at which roots do not penetrate wet soils very well, e.g., Kozlowski, 1999), were applied to the soil with or without forest litter amended. Thus, there were a total of four treatment combinations: forest litter unamended and noncompacted (OM0C0), forest litter unamended and compacted (OM0C1), forest litter amended and noncompacted (OM1C0), and forest litter amended and compacted (OM1C1).

For incubation, 3 g of forest litter was mixed with the moist soil (the weight of soil varied according to the bulk density of the treatment) and packed into a plastic vial, 4.4 cm in diameter and 3.3 cm deep, following the method developed by De Neve and Hofman (2000). The forest litter amendment rate was equivalent to 20 t ha^{-1} of forest litter being added. The 0.1 MPa pressure plate (Soil Moisture Equipment Co., Santa Barbara, California) was used to determine the water holding capacity of the soil or the soil and forest litter mixture at -15 kPa, for both the compacted and noncompacted treatments. To do this, three duplicate soil samples for each treatment were placed into labeled rubber rings on the plate and then saturated overnight. The desired pressure (15 kPa) was applied to the saturated soil to extract the excess water for 24 hours. Then, soil moisture content was determined by oven-drying a portion of the moist soil at 105 °C for 24 hours. Using a metal cylinder with diameter equal to the inner diameter of the vial, the soil-forest litter mixture was uniaxially compacted to the desired bulk density for a volume of 50 cm^3, following the method of De Neve

and Hofman (2000). For both bulk densities of compacted and noncompacted soils, cores with forest litter unamended were also prepared. All the samples were incubated at a room temperature of 20 °C, and their moisture content was adjusted to 75% of water holding capacity. Soil moisture content was maintained at 75% of water holding capacity in order to reduce gaseous N losses by denitrification (De Neve and Hofman, 2000). Four replicate samples were collected from each treatment at Day 7, 37, 68, 160, and 280.

To determine C mineralization rates, soils were incubated in sealed 1 L Mason jars with 10 mL of 1 M NaOH contained in a 50 mL beaker included as a CO_2 trap (De Neve and Hofman, 2000). During the 9-month incubation, the NaOH traps were removed monthly and the retrieved beakers with NaOH were titrated with 1 M HCl, after adding 5 mL of 1 M $BaCl_2$, to determine the quantity of CO_2 absorbed. After the CO_2 traps were removed, the glass jars were flushed with compressed air to allow the replenishment of O_2 and a uniform starting condition in air composition for the next incubation period. At the same time, adjustments were made to reestablish proper soil moisture content in the plastic vials. Beakers containing fresh NaOH were then added. The highest rate of oxygen consumption was 4 mmol 30 d^{-1} throughout the incubation period while a 1 L Mason jar holds about 9 mmol oxygen calculated by the Ideal Gas Law, $PV = nRT$, where P is the pressure of the oxygen, V is the volume the oxygen occupied, n is the number of moles of oxygen present, R is the universal gas

constant, and T is temperature in Kelvin (Lide, 2003). Thus, an aerobic condition ought to have been maintained for each of the monthly incubation periods.

2.3. Chemical analyses and calculations

Soil MBC and MBN were measured using the chloroform fumigation-extraction method (Brookes et al., 1985; Vance et al., 1987). Twenty grams of moist soil samples from each treatment were fumigated with alcohol-free chloroform for 24 hours in an evacuated desiccator. Fumigated and control (unfumigated) samples were extracted with 80 mL 0.5 M K_2SO_4 and shaken for one hour on a reciprocating shaker. Extracts were filtered using Whatman No. 42 filter papers and kept frozen at -18 °C until further analysis. Extractable C and N were analyzed using a TOC-V total organic C analyzer (Shimadzu Corporation, Kyoto, Japan). Soil MBC was calculated as the difference in extractable C contents between the fumigated and control samples divided by a K_{EC} factor of 0.38 (Vance et al., 1987). The K_{EC} factor was used to account for the efficiency of extraction for MBC. Soil MBN was calculated as the difference in extractable N contents between the fumigated and control samples divided by a K_{EN} factor of 0.45 (Jenkinson, 1988). Similarly, the K_{EN} factor was used to account for the efficiency of extraction for MBN.

Extracts of the unfumigated soils were also analyzed for NH_4-N concentrations colorimetrically using the indophenol blue method (Mulvaney, 1996) and for NO_3^--N concentrations using the vanadium oxidation method (Doane and Horwath, 2003). Soil soluble organic C was measured as the extractable C contents in the unfumigated samples, as there was no inorganic C in the extracts based on the soil pH of 4.05 and experimental test in the laboratory. Soil soluble organic N was calculated by subtracting the inorganic N ($NH_4^+ + NO_3^-$) contents from the total extractable N contents in the unfumigated samples. Net N mineralization rates were estimated by subtracting the NH_4^+ and NO_3^- contents measured initially from those of the current month. Net nitrification rates were calculated in the same way as for the net N mineralization rates but based on changes in NO_3^- contents.

2.4. Statistical analysis

The SAS package (SAS Institute Inc., 1999) was used to perform all statistical analyses. Some dependent variables were log (soluble organic C and N, and C mineralization rate) or square root transformed (net N mineralization and nitrification rates) in order to meet the assumptions of normality and homogeneity. Other dependent variables were not transformed as their distribution was normal and error variance was homogeneous. Means presented in this paper were based on original data. Analysis of variance was performed to

test the effects of soil compaction and forest litter amendment on soil MBC, MBN, soluble organic C and N, C and net N mineralization rates, and net nitrification rates. The Proc Mixed procedure was used to analyze unbalanced repeated measures data. Linear regression analysis was performed to evaluate the relationships between soil soluble organic C and MBC, soluble organic C and MBN, MBN and soluble organic N using the general linear model (GLM) procedure. The Proc Model procedure was used to fit the measured data to the zero- and first-order kinetics for forest litter unamended and amended soils, respectively. In all comparisons, $\alpha = 0.05$ was used as the significance level.

3. Results

3.1. Soil MBC and MBN contents

In the forest litter unamended soil, compaction significantly reduced MBC content by 19% on Day 7 and MBN content by 24% at the end of the 9-month incubation (Fig. Ⅳ-1a and 1b; Table Ⅳ-1). In the forest litter amended soil, compaction significantly reduced MBC content by an average of 26% from day 37 to 160; and MBN content by 24% in the first 5-month incubation period (Fig. Ⅳ-1a and 1b; Table Ⅳ-1). When there was no compaction, forest litter amendment significantly increased MBC and MBN contents during the first 160 days of the incubation, but reduced MBC and MBN contents in the last sampling

date (Fig. Ⅳ-1a and 1b; Table Ⅳ-1). When there was compaction, forest litter amendment increased MBC content only initially, then had no effect on either MBC or MBN content for most of the other sampling dates, but reduced MBC and MBN contents on the last two sampling dates (Fig. Ⅳ-1a and 1b; Table Ⅳ-1). In most cases, MBC and MBN peaked at Day 68 and thereafter decreased with the incubation time.

3.2. Soil soluble organic C and N contents

Soil compaction significantly reduced soluble organic C contents in the forest litter unamended soil and soluble organic N contents in the forest litter amended soil in the last sampling date (Fig. Ⅳ-2a and 2b; Table Ⅳ-1). Forest litter amendment significantly increased soluble organic C and N contents on every sampling date but the initial one, regardless of the level of soil compaction (Fig. Ⅳ-2a and 2b; Table Ⅳ-1). Throughout the incubation time, soil soluble organic C decreased in the first 37 days and then increased untill the end of the incubation time while soluble organic N increased at different rates in all the treatments. Soil soluble organic C content was negatively related to both MBC ($R^2 = 0.36$, $P = 0.005$, ANOVA data not shown) and MBN ($R^2 = 0.29$, $P = 0.015$, ANOVA data not shown) contents, while no relationship was found between soluble organic N and MBN ($R^2 = 0.13$, $P > 0.05$, ANOVA data not shown).

3.3. Carbon mineralization rates

Carbon mineralization in the forest litter unamended soil followed zero-order kinetics, and the rates were significantly lower in the compacted than in the noncompatced soil (Fig. Ⅳ-3; Table Ⅳ-2). In the forest litter amended soil, C mineralization followed first-order kinetics. Soil compaction significantly reduced C mineralization rates and the amounts of readily mineralizable C (C_0) (Fig. Ⅳ-3; Table Ⅳ-2). Towards the end of the 9-month incubation period, cumulative amounts of CO_2-C evolved were significantly greater in the noncompacted soil with forest litter amended than in the other treatments, with 1.82, 1.57, 2.61, and 1.70 mg C g^{-1} soil mineralized from OM0C0, OM0C1, OM1C0, and OM1C1, respectively (Fig. Ⅳ-3).

3.4. Net N mineralization and nitrification rates

The general pattern of net N mineralization was linear in the forest litter unamended soil. Soil compaction did not affect net N mineralization rates (Fig. Ⅳ-4a; Table Ⅳ-2). In the forest litter amended soil, net N mineralization followed first-order kinetics. There were no differences of net N mineralization rates and readily mineralizable nitrogen (N_0) between compacted and noncompacted soils (Fig. Ⅳ-4a; Table Ⅳ-2). Net N mineralization was generally more rapid in the forest litter amended than in the unamended soils

throughout the incubation (Fig. Ⅳ-4a). After 9-months, the total amount of N mineralized from OM0C0, OM0C1, OM1C0, and OM1C1 was 40.4, 38.7, 61.2, and 58.6 mg kg^{-1} soil, respectively (Fig. Ⅳ-4a).

Soil compaction significantly reduced net nitrification rates in the forest litter unamended treatment from Day 68 till the end of the incubation, and reduced total NO_3^--N production by 50% at the end of the incubation time (Fig. Ⅳ-4b). In the forest litter amended soil, soil compaction significantly reduced net nitrification rates from Day 68 to 160 of the incubation, but did not affect total NO_3^--N production (Fig. Ⅳ-4b). Forest litter amendment significantly increased net nitrification rates over every sampling period, regardless of the level of soil compaction, and increased the amount of NO_3^--N produced by 177% and 429% at the end of the incubation time in the noncompacted and compacted treatments, respectively (Fig. Ⅳ-4b).

4. Discussion

4.1. Soil MBC, MBN, soluble organic C and N

Microbial organisms are considered the most important agent in the soil ecosystem for litter decomposition and nutrient cycling (Wardle, 1992).

Microbial biomass was reported to be an early indicator of changes caused by disturbances that result from forest management practices (Chang et al., 1995). Under controlled laboratory conditions in this study, I found that soil compaction often reduced microbial biomass, particularly when forest litter was amended, likely due to poor aeration because compaction reduced aeration porosity from 35.5% to 12.5% (data not shown), in agreement with van der Linden et al. (1989). However, Jensen et al. (1996) in their laboratory experiment did not detect any direct effect of compaction on microbial biomass within air-filled pores between 0.01 and 0.53 m^3 m^{-3}; they nevertheless indicated that soil microbial activity was likely more sensitive to soil compaction than microbial biomass. When forest litter was amended, the greater negative effect of soil compaction on microbial biomass was possibly due to the aggravated effects of forest litter amendment on reducing soil aeration in the compacted soil, as the initially high C mineralization rates (Fig. Ⅳ-3) can quickly deplete oxygen concentrations in the compacted soil.

By adding forest litter to the soil, microbial biomass in the noncompacted treatment markedly increased in the early stage of incubation as compared with the other treatments, likely because the newly added forest litter provided readily available C substrates that stimulated microbial growth. After the 5-month incubation, however, microbial biomass in the forest litter amended treatments declined markedly and microbial population turnover produced soluble organic C

and N (Fig. Ⅳ-1 and 2). The mineral N that was not leached and had accumulated in the soil of the forest litter amended treatment may have inhibited microbial growth. Application of inorganic fertilizer N has been reported to decrease microbial biomass (McAndrew and Malhi, 1992; Thirukkumaran and Parkinson, 2000).

Information on the effects of soil compaction and forest litter amendment on soluble organic C and N dynamics in forest soils is rather limited. Soluble organic C is often used as a measure of available C for microbial growth or as an indicator of microbial turnover (McDowell and Likens, 1988; Kalbitz et al., 2000). In my study, soil compaction only reduced soluble organic C and N contents in the last sampling date. Comparing the temporal changes of MBC, MBN, and soluble organic C and N, it is apparent that MBC and MBN responded to the treatments much faster than soluble organic C and N. The C:N ratio of soluble organic matter (between 2.4 and 7.7, data not shown) did not differ much from the microbial C:N ratio. I also found that soluble organic C was negatively related to both MBC and MBN, indicating that the turnover of microbial populations will increase soluble organic C content in the soil. Forest litter amendment increased soluble organic C and N contents because the added organic material was a source for soluble organic C and N (Cronan et al., 1992).

4.2. C mineralization rates

De Neve and Hofman (2000) found that mineralization of fresh residues added to soil was depressed under severe compaction (bulk densities at 1.5 and 1.6 Mg m^{-3}) in a loamy sand soil, but was not affected when fresh residues were not added or soil compaction was less severe. The dramatic reduction in C mineralization rates caused by soil compaction in this study supports field measurements where total soil C content was found to increase after soil compaction (Powers et al., 2005; Tan et al., 2005). In contrast, Kaiser et al. (1991) found that soil compaction increased ^{14}C-CO_2 release from a silt loam soil with ^{14}C-labeled wheat straw added, owing to the higher energy demand for C assimilation under anaerobic conditions that were created by soil compaction. In a field study, Startsev et al. (1998) found that poor aeration did not inhibit the decomposition of forest litter in a boreal forest soil and speculated that some anaerobic microbes might have proliferated under such conditions.

In the forest litter amended treatment, the decomposition rate constant I calculated was close to the lignin decay constant of 0.006 (Paul and Clark, 1996), and only 3.9% and 4.9% of total organic C was mineralized during the first 10 days, in the noncompacted and compacted soils, respectively. These values were dramatically lower than what was reported in De Neve and Hofman (2000), who found that 25% of total crop residue C was mineralized within the first 10 days. In boreal forest ecosystems, most of the forest litter added into the soil after timber harvesting would be forest floor material that has a lower C availability

and rates of mineralization than fresh leaf litter (Korsaeth et al., 2002), therefore the lower residue decomposition rate is expected.

4.3. Net N mineralization and nitrification rates

The lack of soil compaction effects on net N mineralization rates in the forest litter unamended soil was consistent with other studies (De Neve and Hofman, 2000; Li et al., 2003; Tan et al., 2005). In one case, the absence of a significant influence of soil compaction on net N mineralization rates was attributed to the light soil texture (De Neve and Hofman, 2000). In a laboratory experiment, lower N mineralization rates after compaction were attributed to N losses through denitrification that arise under high water content or low porosity conditions (Jensen et al., 1996). At the end of my incubation period, a significantly greater amount of NO_3^--N was produced in the noncompacted soil (Fig. Ⅳ-4b), indicating that compaction limited the activities of nitrifiers due to O_2 deficiency, because nitrification only occurs under aerobic conditions, assuming that denitrification rates were low at 75% of water holding capacity (De Neve and Hofman, 2000). Adding forest litter to the soil did not change the effect of soil compaction on net N mineralization rates (Fig. Ⅳ-4a). This rejects my hypothesis that net N mineralization rates would be lower in the compacted than in the noncompacted soils with forest litter amended. However, a few studies have found that soil compaction significantly reduced net N

mineralization rates in organic matter amended treatments (van der Linden, 1989; Breland and Hansen, 1996; De Neve and Hofman, 2000). For example, Breland and Hansen (1996) reported that soil compaction reduced the mineralization rates of ^{15}N-labeled clover by 18%, owing to the increased physical protection of organic material and microbial biomass against nematode attack.

When forest litter is added to soils, net N mineralization rates can be affected in both directions. Frey et al. (2003) found that when forest floor material was added to the upper 2-3 cm of mineral soil, it did not increase NH_4^+ or NO_3^- availability; rather, it resulted in lower net N mineralization rates, possibly due to increased N immobilization. Messier et al. (1995) reported that forest litter and mineral soil mixing did not affect or diminish decomposition and mineralization rates in a western hemlock (*Tsuga heterophylla*) stand in British Columbia. They suggested that, rather than increasing nutrient availability, mixing may contribute to the control of competing vegetation, and thus promote tree growth through reduced competition for soil nutrients. In general, adding fresh residue (particularly organic material such as straw that has high C:N ratios) to the soil will increase N immobilization (Paul and Clark, 1996). However, the organic material used in this study has a C:N ratio of 31, therefore increased net N mineralization after forest litter amendment was expected. Remineralization of recently immobilized N in dead microbes is considered to contribute to net N mineralization rates in forest soils (Chang et al., 1997; Chang

and Preston, 1998). In a laboratory experiment involving the incubation of soils in which harvesting residue was added, Pluth et al. (1995) found that the remineralization rates of freshly immobilized N were seven times greater than those of native forest litter. Therefore, a model appropriate for gauging the residual N mineralization of boreal forest soils needs to be considered to better understand the dynamics of N in boreal forest soils.

5. Conclusions

This 9-month laboratory incubation experiment demonstrated that soil compaction had a negative effect on microbial biomass, soluble organic C and N, C mineralization and net nitrification rates. Prevention and amelioration of soil compaction need to be considered by forest managers. Forest litter amendment increased microbial biomass in the early stage of the incubation and soluble organic C and N contents on every sampling date except the initial one. A positive effect on C and net N mineralization and nitrification rates was found in the forest litter amended treatment. Under field conditions, forest litter addition and mixing through mechanical site preparation may control weed competition by destroying the roots of the non-crop vegetation; however, by stimulating microbial growth and increasing nutrient availability in the early stage, forest litter addition and mixing may increase the competition of understory vegetation for nutrients with the crop trees. Further studies are needed to verify the

relationships found in this laboratory experiment and their applications in field conditions.

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Table IV-1. Analysis of variance (*P* values) of the effects of soil compaction and forest litter (OM) amendment on microbial biomass C (MBC), microbial biomass N (MBN), soluble organic C and N in a 9-month laboratory incubation experiment.

Source of variance	Microbial biomass C	Microbial biomass N	Soluble organic C	Soluble organic N
Compaction (C)	<0.001	<0.001	0.001	0.264
OM amendment (OM)	0.795	0.410	<0.001	<0.001
C*OM	0.024	0.024	0.582	0.999
Time (T)	<0.001	<0.001	< 0.001	< 0.001
C*T	<0.595	0.982	0.695	0.663
OM*T	<0.001	<0.001	<0.001	<0.001
C*OM*T	<0.001	0.001	0.007	0.010

Table IV-2. Carbon and net N mineralization rates in the forest litter unamended treatments followed zero-order kinetics ($C_{(t)}=k*t$ for C mineralization, where $C_{(t)}$ is cumulative C mineralized, k is rate constant, t is time; $N_{(t)}=k*t$ for N mineralization, where $N_{(t)}$ is the cumulative N mineralized) and in the forest litter amended treatments followed first-order kinetics ($C_{(t)}=C_0(1-e^{-kt})$ for C mineralization, where C_0 is the potentially mineralizable C; $N(t)=N_0(1-e^{-kt})$ for N mineralization, where N_0 is the potentially mineralizable N). R^2 is the coefficient of determination.

Soil compaction	Forest litter unamended				Forest litter amended					
	C mineralization		Net N mineralization		C mineralization			Net N mineralization		
	k		k		k	C_0		k	N_0	
	($mg\ C\ kg^{-1}\ d^{-1}$)	R^2	($mg\ N\ kg^{-1}\ d^{-1}$)	R^2	(day^{-1})	($mg\ C\ kg^{-1}$)	R^2	(day^{-1})	($mg\ N\ kg^{-1}$)	R^2
No compaction	6.76	0.99	0.147	0.97	0.005	3920	0.99	0.007	74.59	0.97
Compaction	5.90	0.93	0.140	0.99	0.004	2150	0.99	0.006	76.51	0.97

Figure Ⅳ-1. Effects of soil compaction and forest litter amendment on a) soil microbial biomass C and b) microbial biomass N during a 9-month laboratory incubation experiment. Vertical bars are standard errors (n = 4).

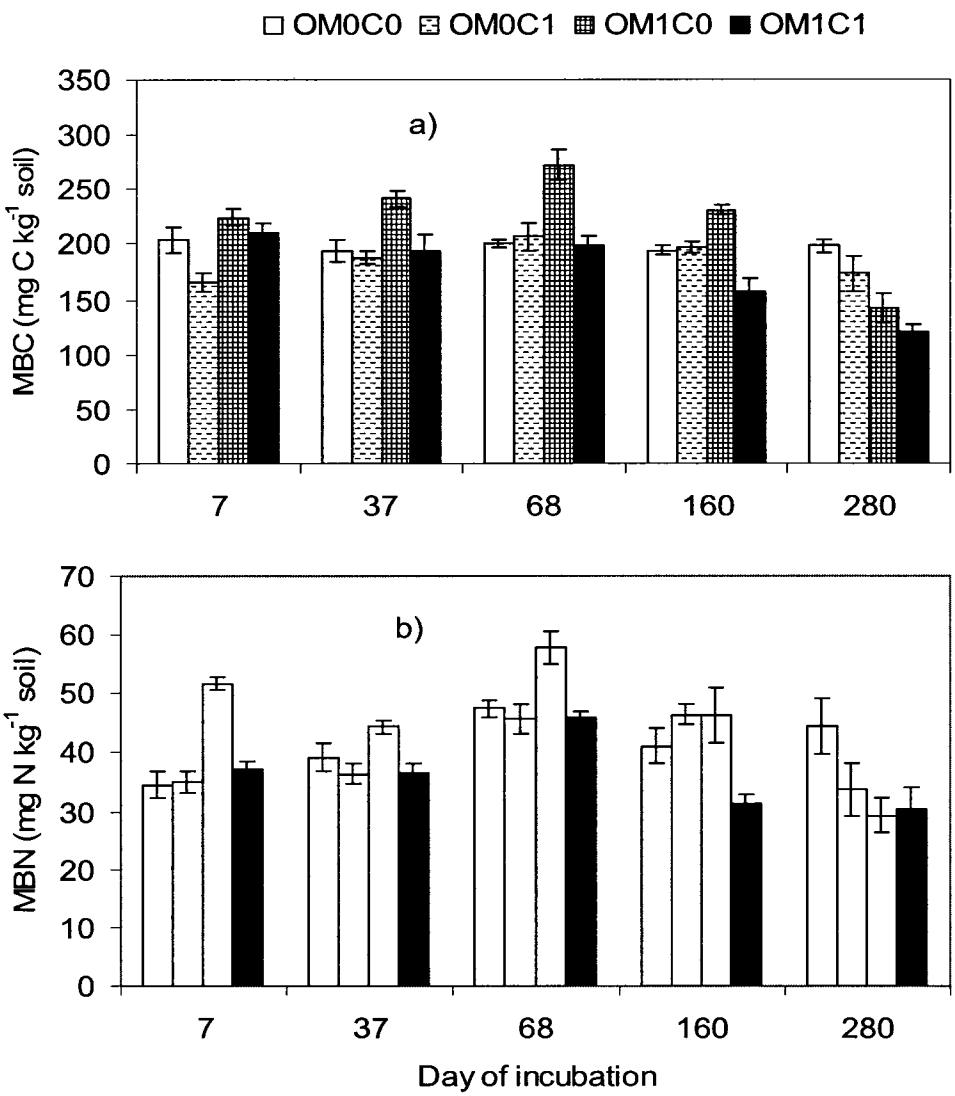


Figure Ⅳ-2. Effects of soil compaction and forest litter amendment on the effects of a) soluble organic C and b) soluble organic N during a 9-month laboratory incubation experiment. Vertical bars are standard errors (n = 4).

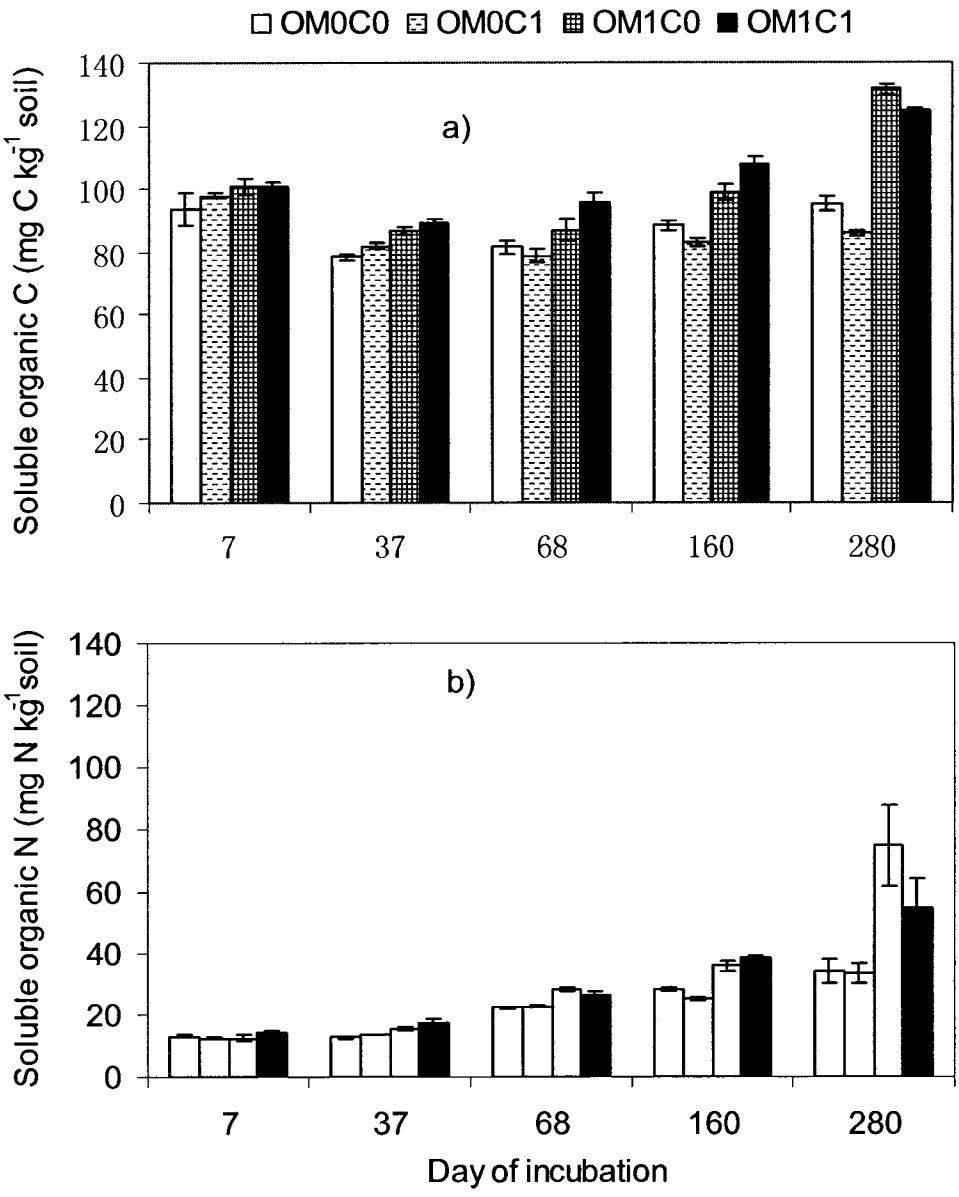


Figure IV-3. Measured (symbols, n = 4) and simulated (lines) C mineralization rates during a 9-month laboratory incubation experiment after soil compaction and forest litter amendment treatments were applied.

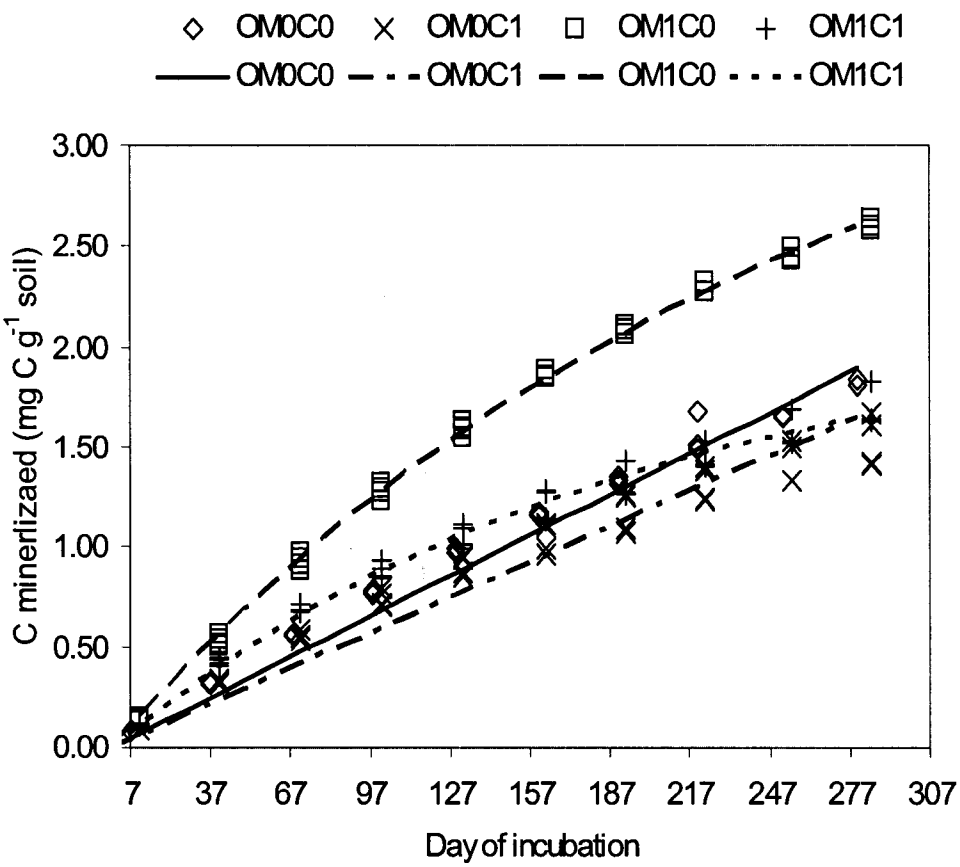
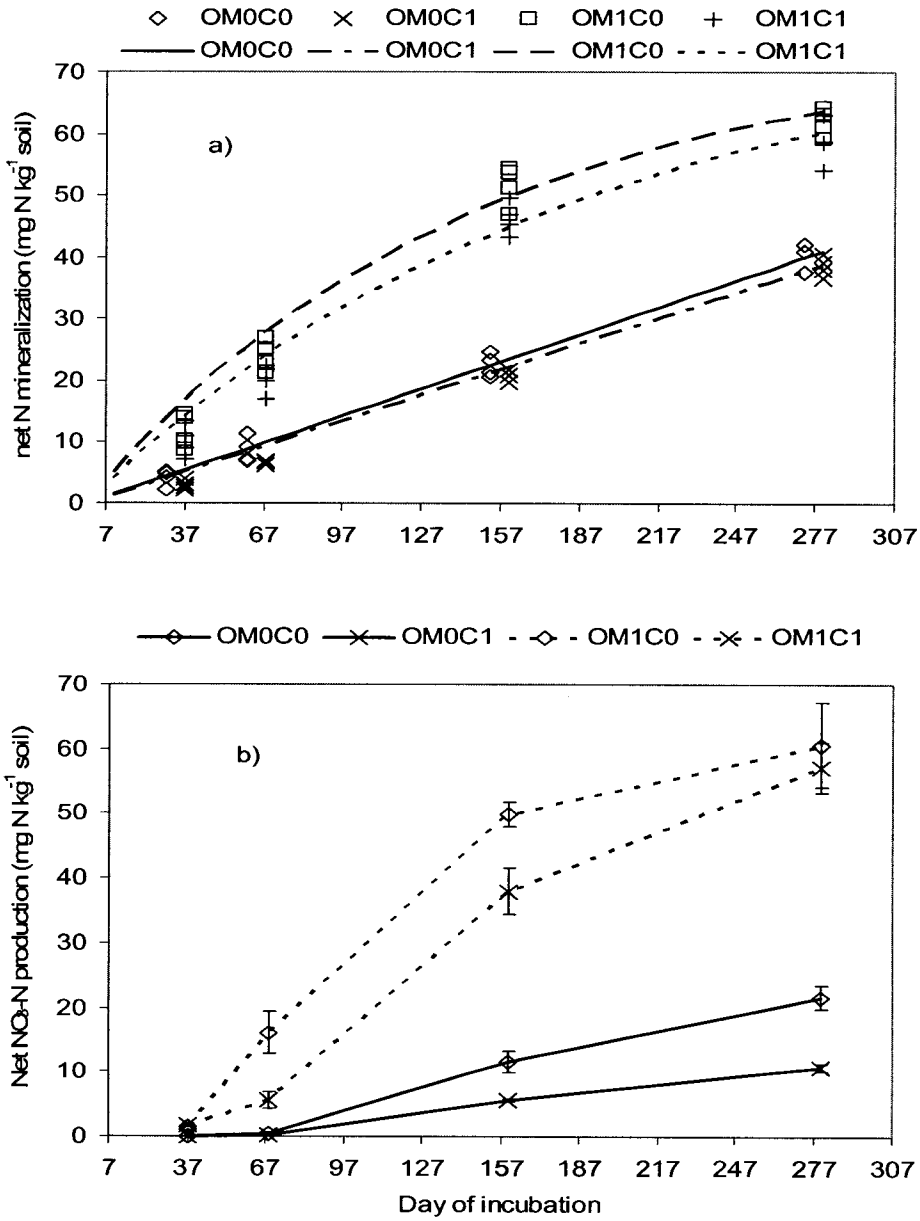


Figure Ⅳ-4. a) Measured (symbols, n = 4) and simulated (lines) net N mineralization rates after soil compaction and forest litter amendment treatments were applied and b) the effects of the soil compaction and forest litter amendment on net nitrification rates. Vertical bars in Fig. Ⅳ-4b are standard errors (n=4).



[3]Chapter 5. Response of forest vegetation and foliar $\delta^{13}C$ and $\delta^{15}N$ to soil compaction and forest floor removal in a boreal aspen forest

1. Introduction

Trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* [Moench] Voss) are two of the most widely distributed commercial tree species in boreal mixedwood forests (Nienstaedt and Zasada, 1990; Peterson and Peterson, 1992; Coates et al., 1994). Accelerated harvesting of boreal mixedwood forests (particularly in more northern latitudes) has increased the potential to cause detrimental levels of soil and site disturbances, particularly soil compaction and forest floor displacement (Corns, 1988; Kozlowski, 1999). Such disturbances can affect soil microclimatic conditions and nutrient availability and therefore alter the growth of both overstory and understory species and alter long-term production. After harvesting, and especially when there is extensive soil disturbance, early successional understory species may respond to the increased light and nutrient availability and quickly colonize the site (Matsushima, 2005). The understory may compete with crop trees for light or other resource, thereby

[3] A version of this chapter has been published. Xiao Tan, Richard Kabzems, and Scott Chang 2006. Forest Ecology and Management. 222: 450-458.

reducing tree survival and growth in the early successional stage of a rotation (Coates et al., 1994; Matsushima, 2005).

Soil compaction can lead to physiological dysfunctions in plants through altering water and mineral nutrient availabilities as a prelude to reducing plant growth (Kozlowski, 1999). The effects of soil compaction on the growth of economically significant tree species such as ponderosa pine (*Pinus ponderosa* var. *ponderosa* Dougl. ex Laws) (Gomez et al., 2002a and b), Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) (Dykstra and Curran, 2000), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) (Conlin and van den Driessche, 1996; Dykstra and Curran, 2000), radiata pine (*Pinus radiata* D. Don) (Sands and Bowen, 1978; Nambiar and Sands, 1992), and loblolly pine (*Pinus taeda* L.) (Kormanik et al., 1998; Tuttle et al., 1988) have been reported. Forest floor removal may also affect tree growth by affecting soil environmental conditions such as moisture content and temperature, and nutrient availability (Van Cleve et al., 1983; Zabowski et al., 1994). However, only a few studies have focused on the effects of soil compaction and forest floor removal on the growth of aspen and white spruce in boreal mixedwood forests (Corns, 1988; Stone and Elioff, 1998; Brais, 2001). Soil compaction has been reported to reduce aspen sucker density and height growth, while forest floor removal was found to increase aspen sucker density by disturbing aspen root systems and increasing soil temperature (Stone and Elioff, 1998). White spruce may differ from aspen in their

response to disturbances, as tree response to soil compaction is species specific (Kozlowski, 1999). Soil compaction has been reported to reduce white spruce seedling growth in the Foothills of Alberta (Corns, 1988) and to increase white spruce mortality on a fine-textured soil in Quebec (Brais, 2001).

Whether water availability (if it is altered by soil compaction and forest floor removal) affected plant growth may be inferred from foliar carbon isotopic composition ($\delta^{13}C$) as limited water availability will decrease the discrimination against ^{13}C during photosynthesis (Gomez et al., 2002c; Choi et al., 2005a). White spruce may be an ideal species for testing the $\delta^{13}C$ technique because guard cells begin to close at xylem water potentials of -1.6 MPa, thus reducing C isotope discrimination in the photosynthesis process (Coates et al., 1994), but as far as I know the application of the $\delta^{13}C$ method in aspen or white spruce has not been reported. Little information is available on the effects of soil compaction and forest floor removal on aspen and white spruce nutrient status or their relationship with tree growth. Soil compaction may affect plant nutrient uptake by influencing nutrient movement in the soil through mass flow and diffusion processes (Greacen and Sands, 1980); while forest floor removal offsite may dramatically export nutrients out of a site (Tew et al., 1986), thereby affecting forest productivity in the long-term. Because nitrogen isotope abundance ($\delta^{15}N$) is an integrator of nitrogen isotopic composition of external N sources and isotopic fractionations during N transformation, assimilation, loss, and internal

translocation (Högberg, 1997), $\delta^{15}N$ of tree tissues may provide insight into the effects of compaction and forest floor removal on soil N dynamics.

This study was undertaken at a boreal aspen forest LTSP site near Dawson Creek in north-eastern British Columbia. The objectives of this study were to investigate the changes in understory community structure and species richness, and aspen and white spruce growth, unit leaf area (the surface area of 100 needles) and weight, to study tree species foliar $\delta^{13}C$ and $\delta^{15}N$, and to relate $\delta^{13}C$ and $\delta^{15}N$ results to potential treatment effects on plant water use efficiency, soil N dynamics and plant nutrient acquisition under an extreme level of soil compaction and whole tree harvesting plus forest floor removal (as compared with stem-only harvesting).

2. Materials and Methods

2.1. *Study site and experimental design*

The study site is located near Dawson Creek (55° 58' N, 120° 28' W), in north-eastern British Columbia, that lies within the moist, warm subzone of the Boreal White and Black Spruce (BWBSmw) biogeoclimatic zone (DeLong et al., 1991). The site has an elevation of approximately 720 m, an average slope of 4%, and a southerly aspect. The area has a mean annual temperature of 1.6 °C and

mean annual precipitation of 482 mm with about 50% of which come down as snow (Environment Canada, 2002). Soils on the study site were developed on a silt loam veneer, 20 to 30 cm thick, laid over a clay loam. The soil is classified as Orthic Luvic Gleysols (Soil Classification Working Group, 1998). Prior to harvest, stands were dominated by aspen with an average density of 600 stems per hectare, with white spruce, lodgepole pine and balsam poplar (*Populus balsamifera*) present as minor species (Holcmb, 1996). Common shrub species were prickly rose (*Rosa acicularis*), soopolallie (*Shepherdia canadensis*), and high-bush cranberry (*Viburnum edule*) (Kabzems, 2000). A varied herb layer was also present. Moss cover was very limited, being restricted to the bases of trees and the surface of woody debris on the forest floor (Kabzems, 2000).

A 3 × 3 completely randomized factorial experiment with three replications was implemented over a 4-year period. The experimental design followed what was proposed for the LTSP study by the USDA Forest Service (Powers et al., 1990). Details of the experimental design are presented in Tan et al. (2005).

In this study, I investigated the extreme treatment levels within each factor to form a factorial combination of two levels of compaction (C0: no soil compaction, the undisturbed plots did not receive any post-harvest compaction and C2: severe soil compaction, the mineral soil was depressed by 4 to 5 cm using

a vibrating pad mounted on an excavator) and two levels of organic matter removal (OM1: stem-only harvesting, the trees were delimbed in the forest, and tops, limbs, and all woody debris were left on the forest floor and OM3: whole tree harvesting plus forest floor removal, all woody and nonwoody material was removed from the plot and the forest floor was stripped to expose the mineral soil using an excavator. OM3 will be referred to as the forest floor removal treatment) with 3 replicates for a total of 12 plots (Kabzems, 1996). In other words, only a subset of the original 3 x 3 experiment was used in this study. Therefore, there were four treatment combinations: stem-only harvesting without soil compaction (OM1C0), stem-only harvesting with severe soil compaction (OM1C2), forest floor removal without soil compaction (OM3C0), and forest floor removal with severe soil compaction (OM3C2).

It should be noted that all 12 plots were not established in the same year, a limitation common to many LTSP installations mainly caused by the complex logistics of setting up experiments of this size and the availability of funding and suitable sites, resulting in plots being established in different years (Axelrood et al., 2002) or having the study done on pseudoreplicated samples (Gomez et al., 2002a). In the statistical analysis described below, I further treated the year since plot establishment as a covariable to remove the effect of year since plot establishment on some of the measured parameters.

After the treatments were applied, one half of each plot was randomly selected to allow aspen regeneration naturally (the aspen plot), and the other half left for planting white spruce seedlings (the spruce plot). Within each of the aspen plots, nine measurement subplots (3.99 m radius, 0.005 ha) were randomly located to assess aspen regeneration and height growth. From the nine aspen subplots, three were randomly selected for annual assessments of aspen regeneration. The mean of those nine or three measurement subplots for each plot was used for statistical analysis. In the centre of each white spruce plot, 100 white spruce seedlings were tagged for the measurement of tree diameter and height. Those white spruce seedlings received a manual brushing treatment in a 1.25 m radius around the seedling annually to minimize the effect of the competing vegetation on tree growth. The measured white spruce seedlings were at least five meters from plot boundaries to minimize potential edge effect.

2.2. Vegetation measurements

In 2001, within each treatment plot, two randomly located vegetation description sub-subplots with a 3.99 m radius were established in each of the aspen and white spruce plots. In this study, I selected two measurement subplots from the aspen plots to estimate understory cover and species richness. Total cover (percent) was estimated by strata (shrubs, herbs, and mosses) and species. Species richness (the total number of understory species present per subplot) was

measured by determining species present in each subplot for each understory stratum.

2.3. Tree growth measurements

Within each aspen plot, the total number of aspen suckers was recorded in three measurement subplots randomly selected from the nine subplots that were set up to estimate stand density in 2002. Aspen maximum height was recorded as the height of the tallest aspen stem in each quarter of the nine measurement subplots. Visual estimates of aspen average height were recorded where the aspen maximum height was measured.

By 2002, all 12 plots had grown at least four growing seasons post-treatment. White spruce ground level (root collar) diameter and height were measured for all tagged trees every year after planting. Root collar diameter was measured using a digital caliper with a resolution to 0.01 mm and height was measured with a metric ruler (up to one meter) or metric tape measure (where trees were taller than one meter) held against the tree stem. When aspen grew taller than 3 meters, a fiberglass height pole was used to measure height. Dead or damaged trees were recorded but not used to calculate mean diameter or height.

2.4. Foliar and soil sampling and analyses

Fifteen trees were randomly selected from each treatment plot and sampled from the upper 1/3 portion of the crown in August and October 2004 from the aspen and white spruce plots, respectively. After collection, foliar samples were immediately placed on ice in a cooler and shipped to the laboratory. Fifty aspen leaves and 150 white spruce needles were randomly selected for measuring leaf area using a flatbed scanner (ScanJet 4c/T) with the SigmaScan Pro5 software (SYSTAT Software Inc., 1999), and then they were oven dried at 60 °C for 48 hours to measure leaf weight. Foliar samples were then milled to fine powder and analyzed for C and N concentrations, and ^{13}C and ^{15}N compositions using a continuous flow elemental combustion analyzer (Costech EC4010, Milano, Italy) linked to a Thermo Finnigan Malt Delta Plus Advantage Mass Spectrometer (Thermo Electron Corporation, Germany).

From July 2002 to 2003, net N mineralization and nitrification rates in the forest floor and 0-10 cm mineral soil were quantified by in-situ incubation of intact cores using the buried bag method (Hart and Firestone, 1989). The details of the method were provided in Tan et al. (2005). Total net N mineralization ($NH_4^+ + NO_3^-$) and nitrification rates were calculated as the sum of mineralized N ($NH_4^+ + NO_3^-$) and NO_3-N contents in the measured field incubation periods between July 2002 and 2003.

2.5. Statistical analyses

The SAS package (SAS Institute Inc., 1999) was used to perform all statistical analyses. Assumptions of homogeneity of variances and normality of error distribution were tested. No heterogeneity was detected in the data set and distributions were normal except percent of moss cover which was log transformed. The GLM procedure was used to test the effects of soil compaction and forest floor removal on understory cover and species richness, aspen density, maximum and average height, white spruce diameter and height increment, aspen and white spruce unit leaf area and unit leaf weight, specific leaf area, foliar C and N concentrations, and foliar $\delta^{13}C$ and $\delta^{15}N$. Because treatments were applied in different years for the three replications, year since installation was used as a covariable to test if it affected any of the dependent variables, other than white spruce diameter and height increment per year because these variables were all measured after four growing seasons. No significance of the year since installation was found for any of those dependent variables. When an interaction term was significant, multiple comparisons were made for one treatment with the level of the other treatments fixed. Tukey's HSD test was used for all multiple comparisons. Correlation analysis was used to evaluate the relationships between aspen and white spruce foliar $\delta^{15}N$ and net N mineralization and nitrification rates in both the forest floor and 0-10 cm mineral soil, between aspen foliar $\delta^{15}N$ and aspen maximum height, and between average height and foliar N concentration. Statistical significance was set at $\alpha = 0.05$ for all analyses.

3. Results and discussion

3.1. Understory cover and species richness

When the forest floor was removed, soil compaction increased understory total cover by 38% but did not affect species richness; when the forest floor was intact, soil compaction had no effect on understory total cover, but reduced species richness resulting in the highest total understory cover and species richness in the compacted soil with forest floor removal (Fig. V-1a and 1b; Table V-1). The increase in total cover and species richness by soil compaction and forest floor removal treatments was caused by increases in moss and shrub cover, and moss species richness, respectively (Fig. V-1a and 1b; Table V-1). Fire moss (*Ceratodon purpureus*), a common pioneer species, had colonized the disturbed sites and its cover increased by 46% after soil compaction and 36% after forest floor removal (data not shown). Moss species such as juniper moss (*Polytrichum juniperinum*) and glow moss (*Aulacomnium* spp.) appeared after forest floor removal. Kranabetter (1999) found that soil compaction stimulated the germination of bronze sedge (*Carex aenea*), bentgrass and willowherb (*Epilobium* spp.) seeds stored in the forest floor the second year after compaction. He suggested that zonal plant communities may re-colonize the sites and become adapted to the new conditions within a few years after disturbance.

In my study, moss cover prior to harvest was very limited and restricted to the bases of trees and surfaces of woody debris on the forest floor (Kabzems, 2000). The quick establishment of moss species on disturbed soils may cause strong competition between moss and crop trees for nutrients and water and the moss layer and the accumulated organic matter can be an effective insulator that reduces temperature in the rooting zone (Nienstaedt and Zasada, 1990), which can offset the increase in soil temperature when forest floor was removed. Soil compaction combined with forest floor removal reduced bluejoint cover (data not shown), possibly because bluejoint rhizomes were located primarily in the forest floor horizon and were removed with surface organic material, thereby reducing bluejoint competition with aspen for water and nutrients. However, the total cover of the herbaceous layer was not reduced, probably because soil compaction and forest floor removal stimulated the germination of dormant seeds of species such as Alsike clover (*Trifolium pretense*) and bentgrass (*Agrostis scabra*) that can quickly colonize the disturbed sites, offsetting the decline in the density of other herbaceous species such as bluejoint grass.

3.2. Aspen and white spruce growth

Soil compaction or forest floor removal did not affect aspen stand density, unit leaf weight, and specific leaf area (Table V −2). Forest floor removal reduced aspen unit leaf area by 18% (Table V −2). Leaf area re-development following

disturbance is critical to maintaining the root system and the subsequent growth of aspen clones (Fraser et al., 2004), suggesting that the reduction in aspen leaf area after soil compaction or forest floor removal could negatively impact the future growth and productivity of regenerating aspen stands at the long-term soil productivity site.

Soil compaction reduced aspen maximum height by 35% with the forest floor intact, but did not contribute to further height reduction beyond that achieved by forest floor removal (Fig. V-2a; Table V-1). Forest floor removal reduced aspen maximum height by 52 and 66% in the noncompacted and compacted treatments, respectively (Fig. V-2a; Table V-1). Aspen average height was reduced by soil compaction and forest floor removal by 20 and 60%, respectively (Fig. V-2a; Table V-1). These results are consistent with those of Stone and Elioff (1998), who found that five years after harvesting, heavily trafficked areas (soil compacted) with forest floor removal reduced aspen basal diameter and height, and aspen biomass by two-thirds. In my study, I found that the understory total cover was negatively related to aspen maximum height (R^2 = 0.38, P = 0.048, ANOVA data not shown). By stimulating understory vegetation growth, forest floor removal may cause severe competition for light, water, and nutrients between aspen and understory vegetation (Landhäusser and Lieffers, 1998), thereby reducing aspen stand productivity.

White spruce unit leaf area and unit leaf weight were reduced by soil compaction by 29 and 33%, respectively, with forest floor intact, but were not affected when the forest floor was removed (Table V-2). Unit leaf area and unit leaf weight were reduced by forest floor removal by 29 and 32%, respectively, in the non-compaction treatment, but were not affected by forest floor removal in the compaction treatment (Table 2). Soil compaction and forest floor removal tended to reduce white spruce diameter increment (Fig. V-2b; Table V-1). Soil compaction reduced height increment by 58% when the forest floor was intact, but had no additional effect on height increment after forest floor removal (Fig. V-2b; Table V-1). Forest floor removal reduced white spruce height increment by 35% in the non-compaction treatment, but did not affect height increment in the compaction treatment (Fig. V-2b; Table V-1). These results are similar to a greenhouse experiment of Corns (1988), in which white spruce seedling growth was reduced by soil compaction on four soils developed on different parent materials in the foothills of west-central Alberta. However, Brais (2001) found that soil compaction increased white spruce height as much as 25% five years after plantation establishment, and she attributed this to the reduced competition in the compacted soil; in my study, competing vegetation was controlled around spruce seedlings on all treatments, therefore this factor was not applicable.

My results show that the effects of soil compaction on aspen and white spruce growth were dependent on the presence or absence of the forest floor,

consistent with results from other similar studies, which indicate that soil compaction and forest floor removal often interact to influence soil processes and tree growth (Stone and Elioff, 1998; Gomez et al., 2002b; Choi et al. 2005b; Kamaluddin et al. 2005; Tan et al., 2005). The most vigorous aspen and white spruce grew on the least disturbed sites, consistent with Stone and Elioff (1998), who also found that soil compaction and forest floor removal reduced aspen foliar and stem biomass. Gomez et al. (2002b) found that noncompaction + forest floor intact was beneficial to ponderosa pine growth in loam and clay soils, while in a sandy loam soil, compaction + forest floor intact showed the best tree growth. They indicated that tree responses to soil compaction and forest floor removal are not universal for soils with different textures.

3.3. Aspen and white spruce foliar $\delta^{13}C$ and $\delta^{15}N$

Soil compaction or forest floor removal did not affect aspen or white spruce foliar $\delta^{13}C$, indicating that in 2004 soil water availability was not affected by either compaction or forest floor removal, in disagreement with Gomez et al. (2002c), who found that variation in leaf $\delta^{13}C$ provided an integrative index of ponderosa pine plant water status in soils disturbed by compaction. Gomez et al. (2002c) attributed the success of the leaf $\delta^{13}C$ technique to differentiate treatment effects and plant water status to the fact that their study area was located in a xeric environment. My study area was located in a mesic environment and 2004 was a

relatively wet year (660.8 mm precipitation vs 30-year mean annual precipitation of 482.0 mm) which could partially explain the absence of the leaf $\delta^{13}C$ signature in both aspen and white spruce trees. Stable isotope response of trees to treatments may vary depending on site characteristics such as precipitation and tree species (Choi et al., 2005b); therefore, site- and species-specific foliar $\delta^{13}C$ ranges need to be established for evaluating the effects of soil disturbances.

Forest floor removal reduced foliar N concentrations of aspen by 9% but did not affect that of white spruce (Table V-2). Foliar N concentrations of 2.5-4.0% and 2.0-2.5% were documented for aspen growing in fertile and infertile soils, respectively (Hemming and Lindroth, 1995; Lindroth and Hwang, 1996). The reduced foliar %N by forest floor removal led foliar %N to fall below the critical value of 2.5%, possibly due to N losses (as much as 1167 kg ha^{-1}) when the forest floor was completely removed (Tan et al., 2005). I found that understory cover was negatively related to aspen foliar N concentration ($R^2 = 0.33$, $P = 0.05$, ANOVA data not shown), indicating that by stimulating the growth of understory vegetation, forest floor removal may affect nutrient availability for crop trees, thereby reducing tree growth.

Values of foliar $\delta^{15}N$ were within the range of values (-6.0 to 3.0 ‰) normally observed in forest ecosystems (Garten, 1993). Soil compaction reduced aspen foliar $\delta^{15}N$ without forest floor removal, but did not affect foliar $\delta^{15}N$ when

forest floor was removed (Fig. V-3b; Table V-1). Forest floor removal increased aspen foliar $\delta^{15}N$ regardless of the compaction treatment (Fig. V-3b). Those results indicate that most likely there was a change in isotopic ratio of the plant available N pools as foliar $\delta^{15}N$ values integrate the ^{15}N abundance in the available N pools and ^{15}N fractionation during N transformations (Choi et al., 2005b). The highest foliar $\delta^{15}N$ in the compacted soil with forest floor removed may be related to the high N loss potential (such as through denitrification and nitrate leaching losses as discussed below) in this treatment because such N loss processes cause ^{15}N abundance in the substrate to increase or to a shift in mycorrhizal association in tree species and mycorrhizal discrimination in N uptake (Chang and Handley, 2000; Hobbie et al., 1999). Soil compaction or forest floor removal may alter soil N transformation patterns by changing soil water content and temperature (Zabowski et al., 1994), thereby affecting foliar $\delta^{15}N$. Högbom et al. (2002) suggested that N losses (NO_3^- loss) after clearcutting may increase plant $\delta^{15}N$. Choi et al. (2005b) found that forest floor removal increased foliar $\delta^{15}N$, while soil compaction had no effect on foliar $\delta^{15}N$ in both lodgepole pine and Douglas-fir stands on a calcareous soil LTSP site near Nelson, in interior B.C. They attributed the higher foliar $\delta^{15}N$ after forest floor removal to the altered isotope composition of N available for plant uptake because of the different $\delta^{15}N$ signatures of the available N in the forest floor and mineral soil.

In my study, increased N losses occurred possibly via leaching or denitrification of NO_3-N due to the increased nitrification rate with forest floor removal (Tan et al., 2005). No correlation was found between aspen foliar $\delta^{15}N$ and net N ($NH_4^+ + NO_3^-$) mineralization in the forest floor ($R^2 = 0.23$, $P = 0.332$; Fig. V-4a), while a strong correlation between aspen foliar $\delta^{15}N$ and net nitrification in the forest floor ($R^2 = 0.87$, $P = 0.007$; Fig. V-4b) was found. Aspen foliar $\delta^{15}N$ was also positively correlated with net N mineralization ($R^2 = 0.42$, $P = 0.022$; Fig. V-4c) and net nitrification ($R^2 = 0.32$, $P = 0.045$; Fig. V-4d) in the mineral soil. These relationships indicate that aspen foliar $\delta^{15}N$ patterns reflect N cycling processes in the soil. Nitrification has been suggested as a strongly discriminating process that leads to $\delta^{15}N$ enrichment of the remaining NH_4^+ pool in a soil (Högberg, 1997). Garten (1993) and Garten and Van Miegroet (1994) found that plant $\delta^{15}N$ was positively correlated with nitrification rates in the mineral soil (0-10 cm). Strong correlations were found between aspen foliar $\delta^{15}N$ and aspen maximum height ($R^2 = 0.48$, $P = 0.013$; Fig. V-5a), average height ($R^2 = 0.58$, $P = 0.004$; Fig. V-5b), and foliar N concentration ($R^2 = 0.54$, $P = 0.047$; Fig. V-5c). The reduced foliar N concentration of aspen in the forest floor removal treatment further indicated the lower N availability in the soil, which was consistent with the higher foliar $\delta^{15}N$ (Fig. V-5c). Aspen foliar $\delta^{15}N$ values were lower in the compaction treatment related to lower potential N losses;

nitrification rates were reduced in the compacted soil due to poor soil aeration (Tan et al., 2005).

Neither soil compaction nor forest floor removal affected white spruce foliar $\delta^{15}N$ (Fig. V-3a and 3b; Table V-1). No correlations were found between white spruce foliar $\delta^{15}N$ and net N mineralization or nitrification in both the forest floor and mineral soil (Fig. V-4a, 4b, 4c, 4d). White spruce and aspen foliar $\delta^{15}N$ responded to soil compaction and forest floor removal differently, probably due to their different physiological and biochemical traits. Aspen has a higher water and nutrient demand for its rapid growth than white spruce in early stand development (Nienstaedt and Zasada, 1990; Perala, 1990). White spruce can tolerate a wide range of fertility levels and may not be as sensitive as aspen to the reduced nutrient availability with forest floor removal. However, the exact mechanism is not clear as to why white spruce foliar $\delta^{15}N$ values were not closely related to N cycling processes.

4. Conclusions

This study shows that soil compaction and forest floor removal increased total understory cover and species richness, which may increase competition between understory vegetation and crop trees, thereby potentially reducing stand productivity. Soil compaction and forest floor removal have negative effects on

the growth of aspen (maximum and average height, and unit leaf area) and white spruce (unit leaf area, unit leaf weight, and height increment) during early stand development. Forest floor removal reduced aspen foliar N concentrations and altered soil N cycling processes as was reflected in the changes in foliar $\delta^{15}N$. In the relatively wet year of 2004, foliar $\delta^{13}C$ patterns indicated that soil compaction or forest floor removal treatments did not change water availability for the growth of aspen and white spruce or change the water use efficiency of the two species. My results suggest that it is important to minimize the extent of soil compaction and forest floor displacement in forest management operations in boreal aspen forest ecosystems in order to minimize the negative effects on the early establishment and growth of tree species and soil N dynamics.

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Table V-1. Analysis of variance (*P* values) of the effects of soil compaction and forest floor removal on understory cover and species richness by strata (shrub, herb, and moss layers) measured in 2001, aspen maximum and average height measured in 2002, white spruce root collar diameter and height increment measured four growing seasons after the treatments were applied, and aspen and white spruce foliar $\delta^{13}C$ and $\delta^{15}N$ in 2004. The *P* values less than 0.05 are highlighted in the table.

Source of variation	Plant cover				Species richness			
	Total	Shrub	Herb	Moss	Total	Shrub	Herb	Moss
C†	**0.036**	0.099	0.545	**0.034**	0.450	0.767	0.092	0.999
OM‡	0.083	0.982	0.407	**<0.001**	0.160	**0.010**	0.494	**0.005**
C × OM	**0.010**	0.102	0.079	0.282	**0.032**	0.292	0.052	0.999
	Aspen				Spruce			
	Maximum height	Average height	Foliar $\delta^{13}C$	Foliar $\delta^{15}N$	Diameter increment	Height increment	Foliar $\delta^{13}C$	Foliar $\delta^{15}N$
C	**0.006**	**0.035**	0.422	**0.004**	0.077	**0.016**	0.269	0.715
OM	**<0.001**	**<0.001**	0.738	**<0.001**	0.053	**0.004**	0.616	0.113
C × OM	**0.013**	0.091	0.703	**0.009**	0.073	**0.049**	0.695	0.801

†: C-soil compaction; ‡: OM-forest floor removal

Table V-2. Effects of soil compaction and forest floor removal on aspen and white spruce tree growth and foliar C and N concentrations in 2004. Standard errors of the means are in parentheses. Values with the same letter are not statistically different between treatments in a column ($P > 0.05$). NA: not applicable as spruce was planted.

Treatment*	Stand density (stems ha^{-1})		Unit leaf area (cm^2 100 $leaves^{-1}$)		Unit leaf weight (g 100 $leaves^{-1}$)		Specific leaf area (m^2 kg^{-1})		Total N (g kg^{-1})	
	Aspen	Spruce	Aspen	Spruce	Aspen	Spruce	Aspen	Spruce	Aspen	Spruce
OM1C0*	28,933 a		1533 a	8.57 a	14.02 a	0.29 a	11.1 a	3.0 a	26.0 a	12.3 a
	(6,889)	NA	(181.6)	(0.54)	(2.38)	(0.03)	(0.6)	(0.1)	(0.31)	(2.05)
OM1C2	30,733 a		1322 a	6.09 b	10.66 a	0.20 b	12.4 a	3.1 a	24.5 a	14.6 a
	(8,578)	NA	(220.0)	(0.20)	(1.88)	(0.00)	(0.2)	(0.1)	(0.39)	(2.12)
OM3C0	41,600 a		1160 b	6.12 b	9.94 a	0.20 b	11.7 a	3.1 a	23.5 b	16.0 a
	(4,756)	NA	(34.0)	(0.13)	(0.14)	(0.01)	(0.3)	(0.1)	(0.49)	(0.30)
OM3C2	43,056 a		1167 b	5.99 b	10.32 a	0.19 b	11.3 a	3.1 a	22.8 b	15.0 a
	(6,023)	NA	(75.9)	(0.44)	(0.44)	(0.02)	(0.3)	(0.1)	(0.53)	(0.62)

*Treatment codes: OM1C0, stem-only harvesting without compaction; OM1C2, stem-only harvesting with severe compaction; OM3C0, whole tree harvesting plus forest floor removal without compaction; OM3C2, whole tree harvesting plus forest floor removal with severe compaction.

Figure V-1. Effects of soil compaction and forest floor removal on a) understory cover and b) species richness by strata (shrub, herbs, and moss layers) measured in 2001 (n = 3).

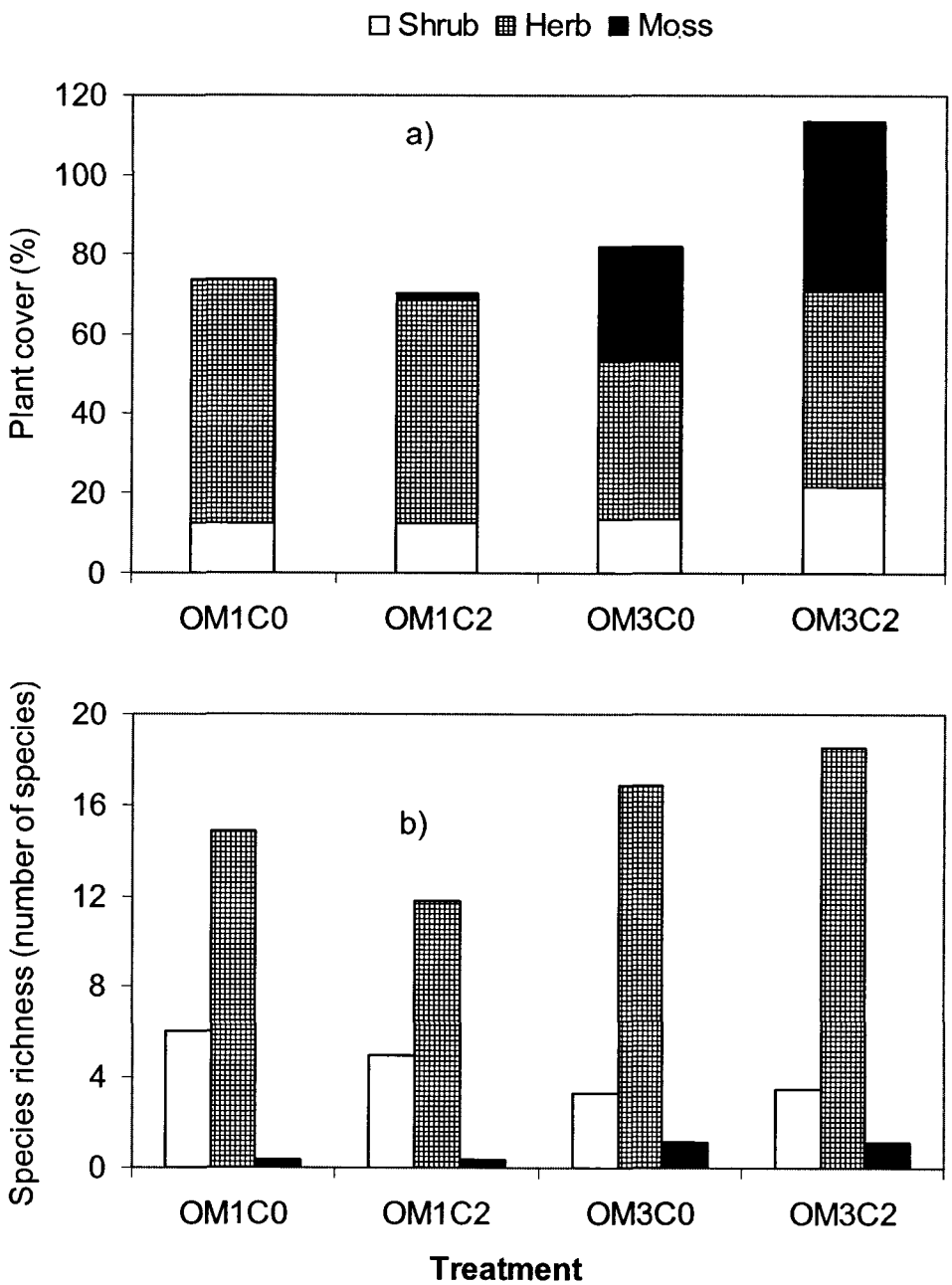


Figure V-2. Effects of soil compaction and forest floor removal on a) aspen maximum and average height measured in 2002 and b) white spruce root collar diameter and height increment measured four growing seasons after the treatments were applied (n = 3).

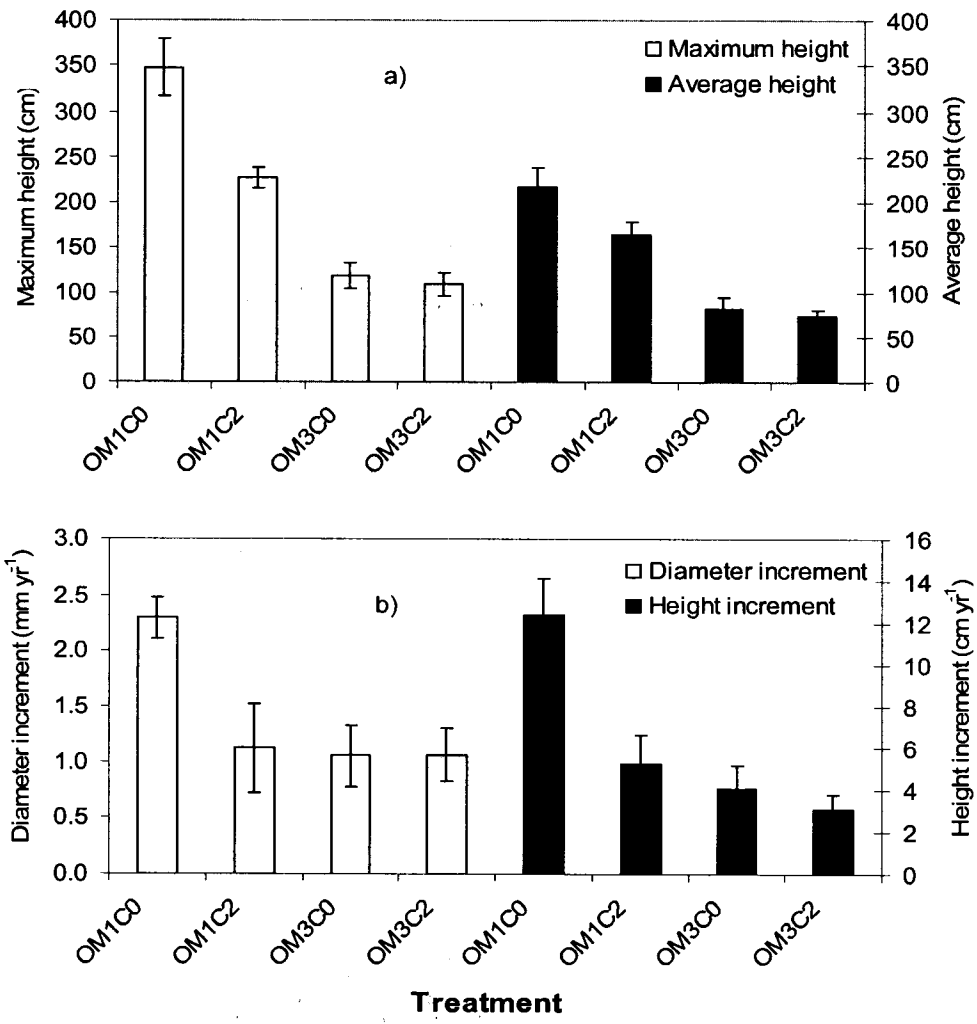


Figure V -3. Effects of soil compaction and forest floor removal on a) aspen and white spruce foliar $\delta^{13}C$ and b) aspen and white spruce foliar $\delta^{15}N$ measured in 2004 (n = 3).

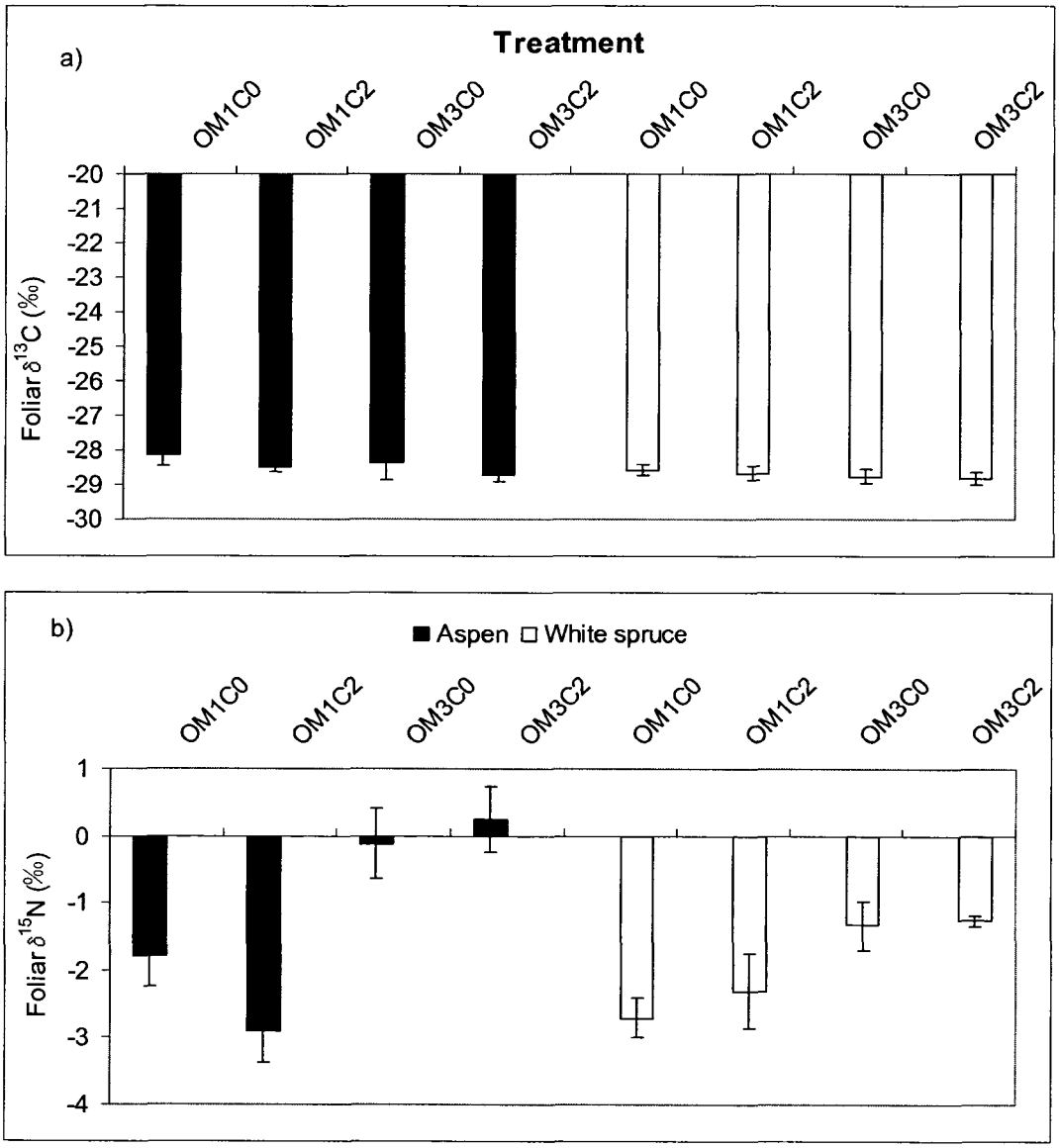


Figure V-4. Regression of aspen (♦) and white spruce (×) foliar $\delta^{15}N$ with a) net N ($NH_4^+ + NO_3^-$) mineralization in the forest floor (n = 6), b) net nitrification in the forest floor (n = 6); c) net N mineralization in the 0-10 cm mineral soil (n = 12), and d) net nitrification in the 0-10 cm mineral soil (n = 12). The solid line is the regression line for aspen.

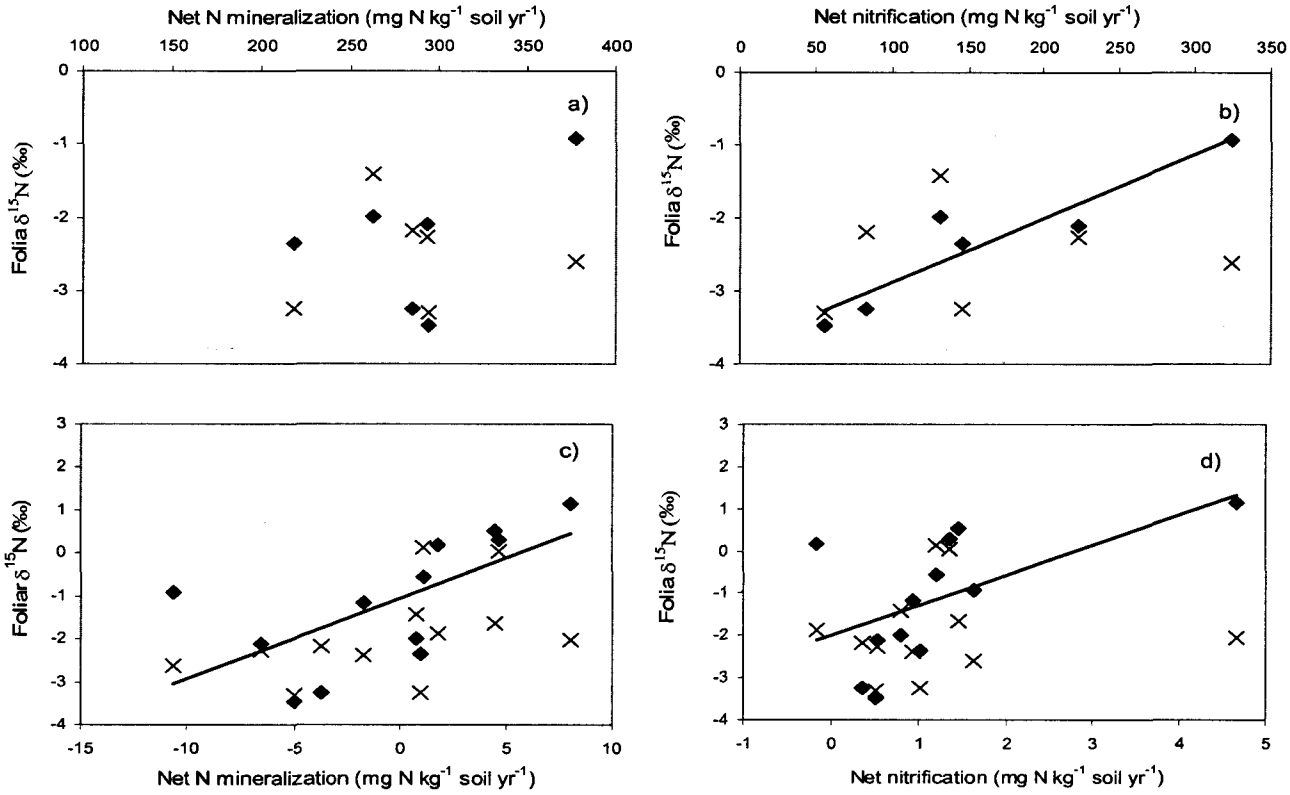
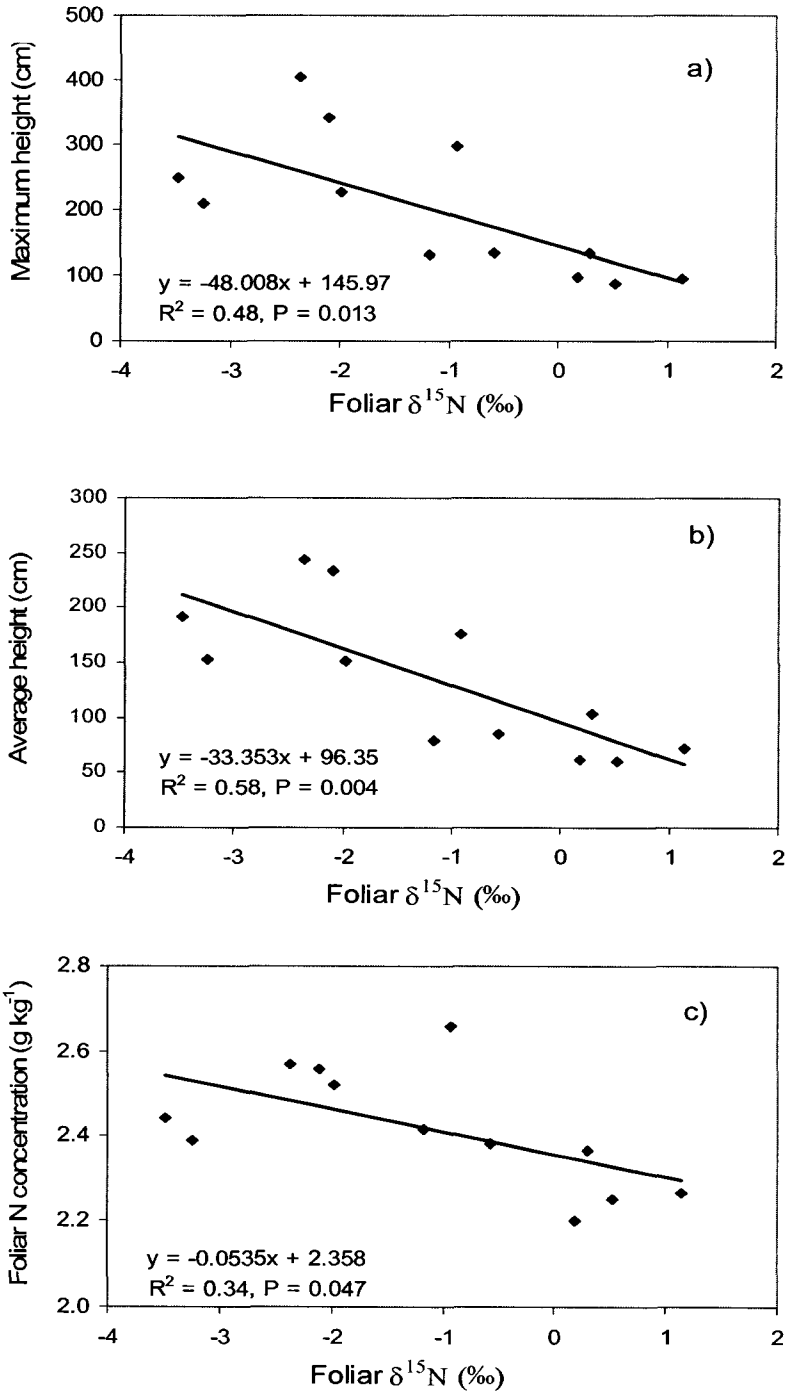


Figure V −5. Regression of aspen foliar $\delta^{15}N$ with a) maximum height; b) average height; and c) foliar N concentrations of aspen (n = 12).



Chapter 6. General discussion and conclusions

The objective of this study was to determine the effects of soil compaction and organic matter treatments on soil nutrient cycling and forest productivity in boreal forest soils. The focus was on 1) the effects of soil compaction and organic matter treatments on soil microbial properties, enzyme activities, and C and N transformations in boreal forest soils; and 2) the effects of soil compaction and forest floor removal on understory vegetation community structure, trembling aspen and white spruce foliar $\delta^{13}C$ and $\delta^{15}N$, and their growth in a boreal aspen dominated forest.

1. Most important findings

- Soil compaction reduced aeration porosity regardless of forest floor removal and reduced soil moisture content in the mineral soil after forest floor removal. Forest floor removal increased soil temperature but reduced moisture content during the growing season.
- Both soil compaction and forest floor removal reduced microbial biomass and the activities of enzymes such as protease and phosphatase.
- Soil compaction reduced net nitrification rates in both the forest floor and mineral soil, while forest floor removal increased net N mineralization and nitrification rates in mineral soil.

- The negative effects of soil compaction on microbial biomass and net nitrification rates were confirmed under controlled laboratory incubation conditions. Forest litter addition increased microbial biomass, and C and N mineralization rates in the early stage in a laboratory experiment.
- Reduced N and P availability after soil compaction and forest floor removal may be directly related to the reduced microbial biomass and protease and phosphatase activities.
- The highest total understory cover and species richness was found in the compacted soil with forest floor removal, caused by the increase in shrub and moss cover and moss species richness.
- Soil compaction reduced aspen and spruce foliar $\delta^{15}N$ when the forest floor was intact. Forest floor removal increased aspen foliar $\delta^{15}N$ regardless of soil compaction largely due to a shift in the N source from forest floor (with available N with low $\delta^{15}N$) to the mineral soil.
- Both soil compaction and forest floor removal reduced aspen maximum and average height, spruce unit leaf area and weight, and spruce height increment. Forest floor removal reduced aspen foliar N concentration.

2. Ecological and management implications

In boreal forests soils, compaction and organic matter treatments affected not only soil microclimatic conditions, but also soil biological/biochemical

properties and processes. Soil microbial properties and certain enzyme activities are sensitive to compaction and organic matter treatments and showed negative responses to compaction due to decreased aeration porosity, and to forest floor removal that reduces soil water and substrate availability as I found that 1167 kg N ha^{-1} was lost after the forest floor was completely removed. Microbial biomass and enzyme activities can be used as indicators of soil fertility changes caused by compaction and forest floor removal as microbial biomass and enzyme activities are positively correlated with N and P availabilities (Emmerling et al., 2002). If microbial populations and their function and enzyme activities could not recover as stands get established, diminished nutrient availability could limit the productivity of boreal forest ecosystems. Therefore, prevention of compaction and conservation of forest floor have great importance in maintaining soil fertility. Soil processes such as C and N transformations controlled by microorganisms and regulated by enzymes were also altered by soil compaction and organic matter treatments. Soil compaction slowed down organic matter decomposition and the nitrification process by shifting soil conditions toward an anaerobic state. Forest floor removal accelerated N mineralization and nitrification, causing N isotope discrimination and ^{15}N enrichment in the soil. Soil processes such as N transformations were sensitive to soil or site disturbances and determined the availability of nutrients for plant uptake. This may play an important role in the nutritional basis of sustained production and ecosystem function in boreal forests. Disturbed soil after compaction and forest floor removal was rapidly invaded by

shrubs and mosses (e.g., fire moss). These species may not only affect soil microclimatic conditions but also cause strong competition for nutrients and water with crop trees, thereby reducing target tree productivity (Matsushima, 2005). The most vigorous and productive aspen and white spruce were growing on the least disturbed sites. The detrimental effects on aspen and white spruce growth after soil compaction and forest floor removal at the early stages of tree growth could delay early stand development and canopy closure. Even if soil can eventually recover from compaction due to wetting and drying or freezing and thawing, and from forest floor removal after stand establishment and crown closure and trees start to return nutrients to the soil, the reduction of tree growth in the early years could be critical in determining long-term forest productivity (Greacen and Sands, 1980; Kowlowski, 1999). My findings are similar to results from some other LTSP with similar soil texture (Kranabetter, 1999; Gomez et al., 2002a; Li et al., 2003; Choi et al., 2005). Therefore, minimizing the extent of soil compaction and forest floor removal may be needed during forest operations in boreal forest ecosystems. If such disturbances occur, they may be ameliorated to some extent by treatments such as mechanically loosening soil and applying fertilizers that replace some of the nutrients lost off-site (Greacen and Sands, 1980; Kozlowski, 1999).

3. Recommendations for future research

Forest floor removal was found to increase net N mineralization and nitrification rates and reduce microbial biomass N. However, I found lower N availability and higher aspen foliar $\delta^{15}N$ after forest floor removal in my study between year 2002 and 2005. Is there a possibility that nitrate was lost due to leaching or denitrification? Further studies such as tracer experiments on denitrification or NO_3^- leaching are needed to clarify the effects of forest floor removal on N transformations.

In my study, the foliar $\delta^{13}C$ technique was not helpful for explaining aspen and white spruce water use efficiency response to soil compaction and forest floor removal because when the study was conducted it was a very wet year (Gomez et al., 2002b). High precipitation may have offset the effects of soil compaction and forest floor removal on soil water status and plant water use. Soil water availability might no longer be a limiting factor. Further studies, especially growth chamber experiments, are needed to clarify the effects of soil compaction and forest floor removal on plant water use efficiency by applying the $\delta^{13}C$ technique.

The failure of the $\delta^{13}C$ technique to reveal aspen and white spruce response to soil compaction and forest floor removal treatments may also be related to the sampling location within plants as different plant parts and their chemical components such as lignin and cellulose influence $\delta^{13}C$ signature and

interpretation of C assimilation because of their differences in C assimilation, reallocation, and utilization (Benner et al., 1987; Hansen et al., 1996). Fine roots may provide the most reliable information on $\delta^{13}C$ in the soil as aerobic root respiration is necessary for mineral nutrient uptake, synthesis of protoplasm, and maintenance of cell membranes (Hansen et al., 1996; Kozlowski, 1999).

Forest litter addition stimulated the growth of microorganisms at the early stage in the laboratory incubation experiment, but tended to reduce microbial biomass at the end of the incubation. I suspected that accumulated high N concentrations may inhibit microbial activity, which may not be the case in the real world. Growth chamber or field experiments may be needed to relate microbial properties and processes to tree growth in order to value the technique of mounding or mixing during mechanical site preparation.

My findings on the effects of soil compaction and organic matter treatments on soil biological properties and processes and tree growth may only be applicable to the boreal aspen forest. As the LTSP program is an international research network, further research is needed to see how well my findings apply to other soils and climatic regions as management practices are likely site and climate specific (Powers et al., 1990).

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