Changes in Soil Nutrient Status and Seedling Performance in Response to Harvest Intensity on Upland, Shallow Site Types in Northwestern Ontario: 10th Year Results

by

Andrea D.E. Wrigley

A Graduate Thesis Submitted in

Partial Fulfillment of the Requirements for the

Degree of Master of Science in Forestry

Faculty of Forestry and the Forest Environment

Lakehead University

August 8, 2007

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 978-0-494-31871-3
Our file Notre référence
ISBN: 978-0-494-31871-3

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

LIBRARY RIGHTS STATEMENT

In presenting this thesis in partial fulfillment of the requirements for the M.Sc.F. degree at Lakehead University in Thunder Bay, I agree that the University will make it freely available for inspection. This thesis is made available by my authority solely for the purpose of private study and research and may not be copied or reproduced in whole or in part (except as permitted by the Copyright Laws) without my written authority.

Signature ____ ____

Date

A CAUTION TO THE READER

This M.Sc.F. thesis has been through a semi-formal process of review and comment by at least three faculty members and an external reader. It is made available by loan by the Faculty of Forestry and the Forest Environment for the purpose of advancing the practice of professional and scientific forestry. The reader should be aware that opinions and conclusions expressed in this document are those of the student and do not necessarily reflect the opinions of either the thesis supervisor, the graduate advisory committee, the faculty, or Lakehead University.

ABSTRACT

Wrigley, A.D.E. 2007. Changes in soil nutrient status and seedling performance in response to harvest intensity on upland, shallow site types in northwestern Ontario: 10th year results. 153 pp + Appendix.

Key Words: black spruce, shallow soils, harvesting impacts, nutrient availability, ion exchange resins, site productivity

Although based on limited empirical data, concerns have been raised that increased nutrient removals associated with full-tree harvesting on shallow-soiled sites may result in reduced productivity in subsequent rotations. The objective of this study, therefore, was to compare and contrast the soil nutrient status and early stand development that resulted from a range of harvest intensities *(i.e.*, a gradient of biomass and nutrient removals), including a full-tree harvest treatment, to determine if such treatments did result in reduced site productivity. The sites (3) selected for the study were mature, fire-origin, black spruce-dominated stands with well-drained, shallow-to-bedrock (<20 cm of mineral soil overtopped by a moderately thin Fibrimor humus layer), coarse loamy soils. Experimental harvests were conducted in 1995 that consisted of five, replicated (3) treatments: **uncut (UC)**, **tree-length (TL)** - delimbed at the stump, **full-tree chipping (FTC)** - chipped debris was returned to the harvested plot, **full-tree (FTH)** - delimbed at roadside, **whole-tree (WTH)** - complete removal of vegetation and forest floor. In 2003-04, soil nutrient status (soil reserves and available pool) across the sites and harvest treatments was evaluated using both standard soil nutrient analysis and *in situ* ion exchange resins. Stand structure, early tree growth, and foliar nutrition were also assessed using a series of fixed area plots (48 per site) and individually tagged black spruce seedlings.

A gradient in the soil nutrient reserves was detected with declining pool sizes as the degree of organic matter removal increased. For example, the WTH plots had significantly less N (790 kg $\cdot ha^{-1}$) then the other harvest treatments (1018 - 1275 kg $\cdot ha^{-1}$). Estimates of the available nutrient pools derived from the ion exchange resins suggested similar patterns across harvest treatments and soil horizon for many of the macro-elements tested in both growing season and overwinter analysis. As would be expected, high seedling densities (7000 stems $\cdot$ ha^{-1}) were associated with the WTH treatment due to the large amount of mineral soil exposure. On the other hand, the heavy slash loading associated with the tree-length treatment provided a poor environment for seedling recruitment and survival (under 3000 stems $\cdot ha^{-1}$). Although individual tree growth (ht and rcd) appeared to be somewhat suppressed on the bladed plots, stand-level biomass followed a similar pattern to that of density, with the WTH treatment accruing over 5 T $\cdot$ ha^{-1} of total tree biomass over the 10 year period. Although foliar N and P content did decrease along the harvest intensity gradient, all values were well within the normal range reported for healthy black spruce seedlings. Based on the results of this study, there is no early evidence to suggest that harvesting shallow-soiled sites using the full-tree logging method would have an impact on tree productivity over the first 10 years after establishment.

CONTENTS

TABLES

FIGURES

Figure Page

ACKNOWLEDGEMENTS

Completing this thesis has encompassed a spectrum of emotions, and there are many people that have been there from the beginning that need to be thanked.

To my supervisor Dr. Dave Morris (OMNR), thank you for getting me started on this project and helping me through to the end. Thanks for all the support and suggestions, for the use of the equipment, and for the funding that you provided.

To my committee members Dr. W.L. (Leni) Meyer, and Dr. Nancy Luckai, both from Lakehead University's Faculty of Forestry and the Forest Environment, thank you for your support along the way, both in completing this Master's thesis, and during my undergraduate studies.

Thank you also to the CNFER crew: Abby, Allen, Bryce, Christine, Dan, Mike, Rob, and Terry for all your help in the field and the lab, I am indebted to all of you. Special thanks to Matt and Carole-Lynn for all the love and support, technical and emotional, and for all the coffees and chats along the way.

Special thanks to my family, especially my parents, Stephen and Donna Druhar, for EVERYTHING, and for always giving me more than I needed. Extra special thanks to my husband, Aaron, for always picking me up when I was down, and for not letting the tough times get the better of me. I appreciate all the love and support you have given me. I cheese-sandwich you.

Funding for this research project was provided by the Centre for Northern Forest Ecosystem Research (CNFER) and the Ontario Graduate Scholarship (OGS) and is gratefully acknowledged.

1.0 INTRODUCTION

The boreal forest region covers 11 % of the earth's terrestrial surface (Bonan and Shugart 1989), and contains 48 % of Ontario's forests (OMNR 1998). Characterized by cool temperatures and short growing seasons with strong seasonal variations (Bonan and Shugart 1989), the boreal forest in Ontario contains many valuable tree species. Black spruce (*Picea mariana* (Mill.) B.S.P.), jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), and white birch (*Betula papyrifera* Marsh.) are valued for both intrinsic and economic reasons, and are commonly extracted by timber harvesting regimes within northwestern Ontario. Currently, the most commonly used harvesting method in Ontario is full-tree harvesting, which delimbs the trees at the roadside instead of at the stump (Wiensczyk 1992). Past research has suggested that this harvest method has the potential to cause excessive nutrient losses within the site, a problem which remains a concern to researchers, foresters, and policy makers alike, and has been the subject of several studies within the forestry and scientific community (Gordon 1983, Kimmins *et al.* 1985, Wiensczyk 1992).

The changes occurring to both the soil nutrient reserves and the availability of nutrients over time are important aspects that need to be considered when monitoring the effects of timber harvesting on long-term site productivity and soil fertility. Standardized soil analysis methods such as ion exchange resins, can provide a reliable index of nutrient bioavailability and movement within forest soils (Dobermann *et al.* 1997). Ion exchange resins can be placed within the soil, and can be left *in situ* to collect nutrient ions dissolved in the soil solution. While buried within the soil, the resins become ion sinks, and are exposed to the same conditions as plant roots and soil colloids. Therefore, the same conditions that affect nutrient supply to the roots will also affect the resins and their ability to collect nutrients (Lundell 2001). For this reason, ion exchange resins have become a reliable and accurate way to estimate plant available nutrients located in the forest floor, which are products of the processes of both litter decomposition and mineralization.

Organic matter decomposition and mineralization rates are largely dependant on soil moisture and temperature regimes, as well as substrate quality. Modification of any or all of these factors induced by disturbances such as fire or timber harvesting, can have a profound effect on the cycling of nutrients within the boreal forest. Increases in decomposition and mineralization rates following disturbances can create a flush of nutrients, benefiting pioneering species, but can also lead to increased leaching rates and nutrient losses (Timmer *et al.* 1983). This can have a compounding effect on sites with inherently low soil nutrient reserves, specifically, shallow soil sites, which are common throughout northwestern Ontario. To address this concern the current research project was designed to evaluate the effects of harvest intensity (*i.e.,* degree of nutrient removals) on soil nutrient reserves, nutrient availability, and early seedling performance (*i.e.,* growth and nutrition) for shallow soil site types.

2.0 LITERATURE REVIEW

2.1 SILVICS OF BOREAL FOREST SPECIES

The boreal forest can be found across the world. In Canada, the boreal forest extends east to west throughout most of the country, and is home to a variety of diverse species. The tree species most commonly found in the northwestern Ontario section of boreal forest include, but are not restricted to: black spruce, white spruce (*Picea glauca* (Moench) Voss), jack pine, balsam fir (*Abies balsamea* (L.) Mill.), tamarack (*Larix laricina* (Du Roi) K. Koch), white birch, and trembling aspen (Kimmins 1997). Limited by harsh climatic conditions, the boreal forest has lower levels of natural diversity when compared to most other forest regions (Smith *et al.* 1997).

Nonetheless, the characteristic softwood-dominated forests are well suited to timber production, and the stands within are often dominated by one or a few tree species, mainly black spruce and jack pine. Able to tolerate poorer quality sites, black spruce is most commonly found in northwestern Ontario on poorly-drained sites or moist organic soils, while jack pine tends to occur in coarse sands, shallow soils, or on rock outcrops (Farrar 1995).

2.1.1 Black Spruce

Black spruce is an important pulpwood species found throughout Canada's boreal forests (Viereck and Johnston 1990). This spruce species usually grows on wet, cool, organic soil sites, such as peats and moist outwash sand plains, and commonly on shallow soil sites comprised of thin tills over bedrock in northwestern Ontario (Gordon 1983). Black spruce is able to survive and thrive in the shallow soil conditions due to its shallow rooting habit, which also provides the species with an advantage in conditions of permafrost. It most often grows as pure stands on organic soils, and as mixed stands with other softwood species such as white spruce, balsam fir and jack pine, and hardwood species such as paper birch and trembling aspen on mineral soil sites (Viereck and Johnston 1990).

Black spruce ground cover often consists of feather mosses (*Pleurozium schreberi*) and sphagnum mosses (*Sphagnum* spp.), with increasing amounts of the latter on wetter bog-type sites. Black spruce growing together with feather mosses are most common in the southern and central boreal forest (Viereck and Johnston 1990). The herb layer is enriched with species such as fireweed (*Epilobium angustifolium*), bunchberry (*Cornus canadensis*), and Canada mayflower (*Maianthemum canadense*), while the shrub layer varies across the country. In northwestern Ontario, species such as alder (*Alnus* spp.), raspberry (*Rubus* spp.), and beaked hazel (*Corylus cornuta*) are common, as well as Labrador tea (*Ledum groenlandicum*), and bog laurel (*Kalmia polifolia*). However, shrubs such as Labrador tea can reduce black spruce seedling establishment and survival rates (Arnup *et al.* 1995).

Black spruce is known as being a slow growing, moderately shade tolerant species, but not as shade tolerant as other softwood species such as white spruce and balsam fir. It can survive in as little as 10 % full light, with rapid growth occurring when it is totally free of competition (Buse and Bell 1992, Arnup *et al.* 1995). As a seedling, black spruce is a poor competitor against other boreal species and therefore, survival and growth are much better in open areas (Viereck and Johnston 1990, Arnup *et al.* 1995). The most productive black spruce stands grow on dark brown to blackish peats, which are fairly well drained, and usually in association with hardwood species (Viereck and Johnston 1990).

Nutritional requirements for black spruce are considered to be low, with low to moderate water demands (OMNR 1997a). Since it is most commonly found in nutrient poor areas in the boreal forest, black spruce's high level of nutrient use efficiency (NUE) makes it a strong species when competing against other species such as jack pine, and deciduous species such as trembling aspen and white birch, which all have low NUE levels. Robinson *et al.* (2001) add that the high NUE shown by black spruce is as a result of an adaptation to infertile soils, and the prevalence of the species in a nitrogen (N) poor environment.

2.1.2 Jack Pine

In the boreal forest, jack pine is often found in pure, even-aged stands, but can also grow in association with black spruce, balsam fir, birch, and aspen. Unlike black spruce, jack pine is well-adapted through characteristics such as serotinus cones, to invade areas of exposed mineral soil following disturbances such as fire. The conditions created by fire can open the cones to release the seeds, but dry, hot weather with temperatures nearing 30°C have also been known to open cones as they lay on the ground. This is prevalent especially after a disturbance such as harvesting. Cones may also open in very cold winters when the temperature nears - 50°C (Rudolph and Laidly 1990). The optimum conditions for the establishment of jack pine seedlings include exposed mineral soil that has some shading, with adequate moisture and limited competition from other species. Seedling growth is generally slow in the first three years, but increases rapidly within the fourth and fifth years (Rudolph and Laidly 1990).

Jack pine is the most widely distributed pine species in Canada, and is an important source of both pulpwood and lumber (Rudolph and Laidly 1990). Factors such as fire and drought determine the range for this species, and the area of optimum development is located north of the Great Lakes in Ontario, and Quebec (Rudolph and Laidly 1990). Common herb and shrub species include fireweed and Labrador tea, with feather moss and sphagnum. Lichens (*Cladina* spp., *Cladonia* spp.) are also commonly found growing near jack pine trees, usually on dry, shallow soil sites that overlie bedrock.

Jack pine gains a competitive edge over other boreal species due to its high level of water use efficiency, and its low water requirements (OMNR 1997a). It is known as a species that has a low to moderate nutrient requirement, with low amounts of nutrient cycling between soil and trees (Foster and Morrison 1976, OMNR 1997a). Jack pine can grow on a variety of soils, but is usually found on sandy soils, along with black spruce, or gravelly soils where other species could barely survive. Rudolph and Laidly (1990) add that it grows best on well-drained loamy soils. It is also able to thrive on shallow soil sites that have limited nutrient availability, such as dry, coarse, and acidic soils.

Seedlings require freedom from competing vegetation, but can grow beneath other species in the understorey. The shade provided is beneficial for germination and early survival, but can be detrimental after two years. Also, jack pine can outgrow competition on most sites, but increased height and survival require a large reduction in competition (> 50 %) (Buse and Bell 1992, Arnup *et al.* 1995). In parts of the boreal forest, jack pine is often succeeded by black spruce, white spruce, balsam fir, and paper birch.

2.1.3 Trembling Aspen and White Birch

Deciduous species such as trembling aspen and white birch are also common in the boreal forest. These hardwood species share many similar characteristics as they are both medium sized, fast growing trees, with short life spans. They are widely distributed throughout Canada, with trembling aspen favouring warm, dry sites, while white birch tend to occur on cool, moist sites.

Trembling aspen is one of the most common tree species in the boreal forest, with a wide geographic distribution. Growth is limited by low growing season temperatures, so optimum growth occurs on warm aspects (Chen *et al.* 2002). According to Radwan and Harrington (1986), nitrogen availability is also an important growth limiting factor in some trembling aspen stands. On the other hand, white birch is a northern species that is adapted to cold climates, and can often be found in conjunction with black spruce on north facing slopes (Safford *et al.* 1990).

Trembling aspen grows on many soils types, with poor growth on sandy soil sites (Perala 1990), and most productive growth on fresh to moist, porous, loamy, nutrient rich soils (Arnup *et al.* 1995, Chen *et al.* 2002). Well drained, moist soils are important to both species, but white birch tends to occur more on sandy loam sites (Safford *et al.* 1990). Disturbances such as fire are often the cause of seedling establishment for both species. Trembling aspen are quick to pioneer disturbed sites with exposed mineral soil, which creates ideal conditions for root sprouts, also known as suckers, to establish on the site (Perala 1990).

Both species are also shade intolerant, with trembling aspen being more intolerant of shaded conditions than white birch (Safford *et al.* 1990). Due to this intolerance, an important characteristic of these species, especially trembling aspen, is that they are pioneering species and can colonize areas after burns or harvesting (Perala 1990). Trembling aspen can deteriorate and die when overtopped by competition; growth increases rapidly following overstorey removal or thinning (Arnup *et al.* 1995).

After establishment, white birch is often found growing with beaked hazel, blueberries (*Vaccinium* spp.), raspberries, and bearberry (*Arctostaphylos uva-ursi*) (Safford *et al.* 1990). Trembling aspen are found with shrubs such as mountain maple (*Acer spicatum*), raspberry, willow (*Salix* spp.), rose (*Rosa* spp.), and herbs including large leaf aster (*Aster macrophyllus*), bunchberry, sedges (*Carex* spp.), and Canada mayflower (Perala 1990).

Rooting habits differ slightly between these species. Birch are shallow rooted, aspen have a short taproot; they can develop flat root systems in shallow or restricted soils (Perala 1990). These species both play important roles in nutrient cycling within the forest ecosystem. Nutrients such as phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) are returned to the forest floor through the enriched deciduous leaves (Safford *et al.* 1990). Aspen litter fall has been reported to have a high potassium content (Huang and Schoenau 1996), which is an important nutrient required for protein synthesis and translocation (Meyer *et al.* 1997).

Although all of the previously outlined species can be found thriving in the boreal forest, they are all very diverse in their water and nutrient requirements. Black spruce, when compared to trembling aspen, has a high NUE, mostly due to the retention of needles, and its slow growth rate. While black spruce and jack pine have low to moderate requirement levels for water and nutrients, trembling aspen and white birch have moderate to high requirement levels for water and nutrients (OMNR 1997a). Although very different in nutrient requirements and growing patterns, all these species have been able to adapt not only to each other, but to the various conditions that the boreal forest provides.

2.2 NUTRIENT CYCLING AND AVAILABILITY IN BOREAL FOREST ECOSYSTEMS

2.2.1 Litter Distribution and Decomposition

Available nutrients are provided by several sources including mineral weathering of rock and atmospheric deposition. It is estimated that in the past 50 years, weathering of igneous parent material has released 5 - 25 $kg \cdot ha^{-1}$ of phosphorus, 250 - 1000 $kg \cdot ha^{-1}$ of potassium, 150 - 1500 $kg \cdot ha^{-1}$ of calcium, and 50 - 500 $kg \cdot ha^{-1}$ of magnesium (Brady and Weil 1999). In boreal forest ecosystems, however, the forest floor is the principal reservoir of nutrients. For example, the boreal forest floor contains 600 - 1100 $kg{\cdot}ha^{-1}$ of nitrogen, 75 - 150 $kg{\cdot}ha^{-1}$ of phosphorus, 300 - 750 $kg{\cdot}ha^{-1}$ of potassium, and 150 - 500 $kg{\cdot}ha^{-1}$ of calcium (Brady and Weil 1999).

The largest amounts of available nutrients are sourced through the biogeochemical cycle, which is the cycling and flow of nutrients within the forest ecosystem (Kimmins 1997). As leaves, needles, bark, and twigs fall to the ground and start to decompose, vital nutrients are returned to the soil to be used once again by the surrounding vegetation. Not all litter decays at the same rate, nor does it provide the same quantities or qualities of nutrients, but all litter does contribute to the accumulation and pooling of nutrients by creating a humus or organic matter layer. Litter decomposition is a key process in the nutrient dynamics of forest ecosystems, as many nutrients are closely tied to organic matter and its decomposition (Federer *et al.* 1993). As such, nutrient release from decaying litter and soil organic matter is essential in maintaining the fertility of forests (Prescott *et al.* 1993). Organic matter is an important link in the biogeochemical cycling of nutrients and is essential for the nutrient status of forest stands (Raulund-Rasmussen and Vejre 1995), but the forest floor and decomposing litter that eventually forms the soil organic matter is dependant on environmental controls (*i.e.,* climate), litter quality, and soil characteristics to dictate the rate of decomposition (Moore *et al.* 1999).

2.2.2 Soil Nutrient Reserves and Nutrient Pools

Litterfall, as part of the biogeochemical nutrient cycle, is an important pathway in maintaining reserves of nutrients in the soil, as large amounts of organic debris are deposited on and in the mineral soil horizons (Foster and Morrison 1976). The release of nutrients within these reserves is closely tied to organic matter decomposition, which varies due to differences in temperature, moisture, pH, and soil aeration (Perala and Alban 1982). Boreal forests are known to be deficient, especially in nitrogen (Weetman and Algar 1983), which is, in general, due to the slow decomposition of organic matter because of cold temperatures (Perala and Alban 1982).

Mahendrappa *et al.* (1986) report that of the soil macro-nutrients (N, P, K, Ca, and Mg), plant available nitrogen is the most important factor limiting the growth of trees on forest soils. Nitrogen is required in the largest quantity by trees, and is considered by Klinka *et al.* (1994) to be the most limiting nutrient in forest soils. Most of the nitrogen that is in the soil is in organic form, and under normal conditions, only about 2 - 3 % of organic nitrogen is mineralized each year (Brady 1990).

Nitrogen deficiency is accentuated on poorer quality sites that have lower humus reserves, which is the most available source of nitrogen for trees and plants to utilize (Weetman and Algar 1983). Keeney (1980) adds that although total forest soil nitrogen pools can be quite large, estimated by Brady and Weil (1999) at 600 - 1100 $kg \cdot ha^{-1}$ in the boreal coniferous forest, nitrogen availability and uptake is often the limiting factor in forest growth and productivity. In boreal forest ecosystems, nitrogen uptake by trees and plants has been estimated at 22 $kg \cdot ha^{-1} \cdot yr^{-1}$, second lowest only to tundra ecosystems, in which nitrogen uptake is 10 $kg \cdot ha^{-1} \cdot yr^{-1}$. In comparison, temperate deciduous and coniferous forests have nitrogen uptake values in excess of 40 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Aber and Melillo 1991).

2.2.3 Nutrient Accumulation and Transfers Between Soil and Vegetation

The patterns and processes that are involved in the decomposition, decay, and accumulation of forest floor litter have major implications for tree and plant nutrition (Binkley 2002). Cation and anion exchanges occur mostly on the surfaces of the finer or colloidal fractions of both the organic and inorganic matter, including clays and humus (Brady 1990). Available cation nutrient elements (ammonium (NH_4^+), K^+, Ca^{2+}, and Mg^{2+}) are held in the soil by cation exchange capacity (CEC), which is the total negative charge of the soil, and is dependant on clay content and organic matter content (Meyer *et al.* 1997). Changes in CEC may also be related to changes in pH, and in most soils there is a positive relationship shown between these two parameters (Johnson *et al.* 1991b).

Soils with high organic matter content have more nutrient holding capacity, while acidic soils ($pH < 4.9$) usually have declining soil CEC (Meyer *et al.* 1997). Typically, loamy sands have the lowest CEC, compared with sandy loams, silt loams, and clay loams, all of which have less than 50 $cmol_c \cdot kg^{-1}$(lowest to highest). Soil humus has the highest exchange rate, varying from 150 to 250 $cmol_c \cdot kg^{-1}$ (Brady and Weil 1999). Compared to organic matter, which is responsible for 25 - 90 % of the total CEC of surface horizons, mineral soils have very low CEC (Van Dijk 1971, Oades *et al.* 1989).

Anion exchange capacity (AEC) exchanges anions (*i.e.*, NO_3^-, PO_4^{3-}, SO_4^{2-}) within the soil solution, but is generally much less than cation exchange (Kimmins 1997). It differs from cation exchange because soil AEC is very much pH dependent (Kimmins 1997), and generally decreases as soil pH increases (Brady and Weil 1999). According to Kimmins (1997), AEC is greater in acidic soils, where the negatively charged anions are attracted to positive charges in the soil, mainly on iron and aluminum oxides that may occur in both clay and organic colloids. The retention of anions through AEC is important for retaining negatively charged nutrients in the soil for plant uptake, and slowing leaching.

While there may be an abundance of nutrients within the forest ecosystem, they need to be in ionic form to be available for uptake and use. Nutrients cannot be absorbed by plant roots unless they are not part of the soil solution (Beyer 1998), or are mineralized into available forms as part of the organic matter decomposition process. In addition, nitrogen, calcium, and magnesium may form organic complexes in plant tissues and often require decomposition for release to an available form (Meyer *et al.* 1997). However, the release of potassium and magnesium is often quite fast compared to nitrogen and phosphorous release.

Nutrients play an important role in tree health and maintenance within the boreal forest. Once taken up by roots, nutrients are distributed in different concentrations throughout the tree. Generally, the foliage contains the greatest concentrations of nitrogen, phosphorous, and potassium (Foster and Morrison 1976, Wiensczyk 1992), while calcium and magnesium are concentrated in the stemwood, bark, and live branches

(Wiensczyk 1992). Also, Foster and Bhatti (2002) concluded that the availability of certain nutrients, such as nitrogen, phosphorous, and potassium, in forest soils largely determine the leaf area, photosynthetic rate and net primary production of forest ecosystems.

2.2.4 Nutrient Cycling Processes Within the Soil

2.2.4.1 Nutrient Mineralization. Nutrients in organic form are returned to the forest floor as litterfall and are converted into plant available forms through a microbial process called mineralization, which relies on saprophytic micro-organisms to convert organically complexed nutrient elements into an available form (Huang and Schoenau 1997, Vervaet *et al.* 2002). Mineralization rates, and the nutrients that are released, are influenced by the quantity and quality of soil organic matter, soil temperature, soil moisture content, and by tree species type (Raulund-Rasmussen and Vejre 1995, Vervaet *et al.* 2002). Studies by Huang and Schoenau (1997) have also shown that variations in type and rate of mineralization are reflected during different seasons, and different temperature and moisture regimes. Nutrient availability for trees after mineralization also depends on competition from other plants and soil microbes, which can utilize nutrients before roots have absorbed them. Soil insects can also affect mineralization due to their role in soil structure maintenance, decomposition, and nutrient cycling rates (Knoepp and Swank 2002).

Mineralization, when discussed in scientific papers, concentrates on the mineralization of nitrogen. Nitrogen mineralization can be defined as the conversion of organic nitrogen into inorganic nitrogen (Hart *et al.* 1994). After mineralization occurs, nutrient elements are available for plant use, but can also be immobilized through uptake by micro-organisms, which return the nitrogen back into an organic form.

Mineralization in the soil can be measured in different ways. Gross mineralization measures the actual amount of nitrogen that is mineralized in the soil, while net mineralization measures the difference between the actual amount of nitrogen mineralized (gross) and the amount of nitrogen that is used by microbes (immobilization) (Hart *et al.* 1994). Net mineralization is also referred to as plant available nitrogen, as it is the amount of nitrogen remaining in the soil for plant uptake. Many studies have focused primarily on measuring the levels of total soil mineralizable nitrogen because it is a good single measure of soil nutrient conditions (Klinka *et al.* 1994), and because nitrogen availability is crucial in maintaining long-term site productivity (Binkley *et al.* 1990).

The mineralization of nitrogen from organic matter can be viewed as a two-step process, which includes: ammonification ($R\text{-}NH_2 \rightarrow NH_3$ (or NH_4^+)), followed by nitrification ($NH_4^+ \rightarrow NO_2^- \rightarrow NO_3^-$). Both of these forms of nitrogen are important for plant growth, but studies by Huang and Schoenau (1997) have shown that high soil moisture contents have inhibited nitrification processes. This leads to a high uptake of ammonium, especially in conifer forests, which has conditions favourable for ammonifiers, which exist in acidic soils (Ohlund and Nasholm 2002). According to Nadlehoffer *et al.* (1984) plant uptake of ammonium is more important in conifer stands than in deciduous stands. Ohlund and Nasholm (2002) have also reported that a number of studies have shown that conifers prefer ammonium over nitrate, and that under certain conditions, ammonium may inhibit the uptake of nitrate by the plant roots. Forest ecosystems growing on acid soils may function with a nitrogen cycle dependant only on ammonium (Stottlemyer and Toczydlowski 1999).

Cool soil temperatures and excessive moisture inhibit mineralization, while maximum mineralization occurs when soil temperatures are between 25 and 35 °C (Nicolardot *et al.* 1994, Stark and Firestone 1996) and soil moisture is near field capacity (Stanford and Epstein 1974). These conditions, while optimal, are rarely reached in the field (Knoepp and Swank 2002). For example, mean summer soil temperatures for the boreal forest in the Thunder Bay area are between 15° and 18 °C, with mean annual soil temperatures between 5° and 8 °C (Environment Canada 2005). In field studies, Stottlemeyer and Toczydlowski (1999) found that nitrogen mineralization rates increased as soil temperature increases, but that soil moisture had little effect on mineralization rates.

Mineralization rates vary, and Persson and Wiren (1995) have estimated that 78 % of the net nitrogen mineralization in coniferous forests occurs in the organic horizons, and in the upper 10 cm of mineral soil (Federer 1983). In addition, Huang and Schoenau (1997) found further differences in the mineralization rates between the L, F, and H organic horizons, all of which are in different stages of decomposition. The highest mineralized nitrogen rates are generally found in the lower organic horizons of F and H, with the lowest mineralization occurring in the surface horizon, L, which is least decomposed (Huang and Schoenau 1996). Vitousek (1981) reports that the amount of nitrogen cycled between soil, plants, and micro-organisms can range from less than 10 kg·ha^{-1}·yr^{-1} in infertile boreal forests, to as much as 350 - 600 kg·ha^{-1}·yr^{-1} in very rich tropical forests (Bernhard-Reverstat 1977, Pfadenhauer 1979).

2.2.4.2 Nutrient Unavailability and Leaching. While there may be an abundance of nutrient elements within the soil and more specifically, the organic matter layer, they are not commonly available for plant use. Nutrient elements that have been immobilized by microbial micro-organisms are unavailable to plants until the organism is decomposed, and the nutrients are recycled back into the soil. Also, nutrient elements that have not been mineralized or have been leached past the rooting zone are largely unavailable to plants.

Nutrient loss through leaching is a problem that is often enhanced after a disturbance such as wildfire or timber harvesting. Anions (*e.g.*, nitrate) are more susceptible to leaching after disturbance as the forest canopy is removed, thereby increasing the amount of precipitation that reaches the forest floor, which results in greater runoff and filtration through the soil profile. Due to low AEC, anions tend to be highly mobile, are more soluble in water, and can by easily leached out of the system (Gordon 1983). Cations, including potassium, calcium, and magnesium, on the other hand, are principally lost through biomass removal (*e.g.*, timber harvest removal), as well as some enhanced leaching following disturbances (Romanowicz *et al.* 1996). For example, Likens *et al.* (1970) reported that potassium was readily leached or released from living and non-living biomass after a harvest. This loss was likely due to low retention of potassium by geochemical processes, such as cation exchange, but could also be explained by the fact that potassium is most often mobile in tree sap and is not incorporated into plant tissues (Morris, *pers. comm.* March 7, 2005). Nutrient losses from leaching are often greatest in the first two years following harvesting (Likens *et al.* 1970). This loss of nutrients, however, could prove to be detrimental in forest ecosystems that are nutrient limited, or that have a low available nutrient supply, such as forests with low turnover rates.

2.2.5 Environmental Drivers of Nutrient Cycling

2.2.5.1 Effect of Moisture and Temperature on Nutrient Fluxes. Litter decomposition rates are important in determining soil fertility and stand productivity. Since tree productivity is directly related to nutrient availability, it is important to identify the processes and environmental factors that control the rate at which nutrients become available for use within forest ecosystems. The litter and the soil organic matter that eventually decomposes on the forest floor is affected by factors such as climate, temperature, freezing and thawing of soils, and moisture regimes.

Soil temperature is an important factor in the decomposition rate of boreal forest organic matter. As would be expected, warmer soils tend to have higher decomposition rates. For example, Bonan and Van Cleve (1992) found that a 5 °C increase in mean annual air temperature caused soils to warm by 300 - 500 growing degree days. Using a 25-year warming simulation model, they discovered that the net effect of 25 years of soil warming resulted in less forest floor mass and higher tree biomass. Specifically, this warming action caused increased mineralization and nitrogen availability resulting from an increase in microbial activity. They also found that under warmed soil conditions, decomposition rates in black spruce forests increased 17 - 45 %, while tree production increased up to 65 %. This study supports the generalized statement that warmer soils lead to increased decomposition rates and that warm temperatures can have a positive effect on productivity in boreal forest ecosystems.

From the plant perspective, cooler soil temperatures can affect metabolic rates and inhibit water uptake. The slow decomposition rates that are associated with cooler temperatures can also restrict nutrient availability to the plant, and cause nutrients and biomass to accumulate in the forest floor (Bonan and Shugart 1989). Overall, the cool temperatures often found in areas of the boreal forest result in reduced organic matter decomposition and restricted nutrient cycling.

Cold temperatures that freeze the soil, however, can have a positive effect on decomposition rates through cycles of freezing and thawing. For example, Harris and Safford (1996) found that alternating cycles of freezing and thawing of newly fallen leaves disrupted plant cells and thus enhanced the release of soluble components. Freeze and thaw cycles generally occur in the late winter and early spring, and also late fall, and can cause a flush in nitrogen mineralization 2 - 3 fold (Herrmann and Witter 2002), but these increased inputs of nutrients are short lived (Skogland *et al.* 1988, Herrmann and Witter 2002). These cycles can cause nutrient elements in organic matter to become more available by physically disrupting the soils, and by changing their physical properties, such as size distribution and stability of soil particles (Edwards 1991). The effects of the freeze and thaw cycles on these properties are dependant on both frequency and duration of freeze and thaw periods, temperature changes and shifts, soil moisture content, bulk density values, coarse fragment content, and the number of cycles that occur.

Soil moisture content and temperature are also important factors to consider, as they can directly affect microbial activity, and therefore control seasonal variations in the mineralization rate of soil organic matter (Herrmann and Witter 2002). Soil moisture can help regulate soil temperature, but can also hinder microbial organic matter decomposition. If there is excess moisture in the soil, temperatures will be cooler, and with little oxygen, result in anaerobic conditions which are unfavourable for microbial processes and can lead to denitrification. Nitrate is not usually created under these conditions, but ammonification can still occur. Colder environments and cooler soil temperatures usually lead to slow rates of decomposition and decreased rates of mineralization (McFarland *et al.* 2002). Under these conditions organic matter often builds up and creates thick organic horizons on the forest floor, which further lowers the soil temperature and impedes water infiltration (Bonan and Shugart 1989).

2.3 MEASURING SOIL NUTRIENT AVAILABILITY WITH ION EXCHANGE RESIN BAGS

2.3.1 Introduction to Ion Exchange Resins

Estimating the amounts of nutrients that are available in forest soils is often a difficult task, due to high spatial variability, seasonal fluctuations of the nutrient pools, and the problems that arise when trying to distinguish between the available and unavailable nutrient fractions (Krause and Ramlal 1987). Ion exchange resins, hereon in referred to as resins, are part of a suite of soil analysis methods which can provide a reliable index of nutrient bioavailability and movement within forest soils (Dobermann *et al.* 1997), and have been proved to be a useful means of assessing soil nutrient status (Sibbesen 1977). They are useful for estimating nutrient supply rates within soils because of their ability to simulate nutrient fluxes to plant roots (Huang and Schoenau 1997).

The rate of adsorption by a resin, when placed in the soil, depends on factors and processes that regulates the supply of nutrient elements to the root (Sibbesen 1977), including soil temperature and moisture. The factors that can influence the amount of ions that are adsorbed by the resin include: the concentrations of ions in the soil solution, the flow rates of the soil solution through the resin, the rates of ionic diffusion in their surroundings and types and quantities of surrounding vegetation (Skogley and Dobermann 1996). Since the resins are also exposed to the same conditions as the roots while *in situ*, the resins are able to provide an estimation or index of nutrient levels in the soil that are available for plant use.

Available in several different forms, and widely used in research for both forestry and agriculture, resins have the ability to estimate the types and amounts of nutrients that are available for plant uptake and use within the soil. It is important to understand and to be able to predict the amount of nutrients available to the plant relative to the total amount of nutrients in the soil (Abrams and Jarrell 1992), and resins can be used for this purpose.

It is also important when studying nutrient cycles to have accurate measurements of nutrient bioavailability and to know and understand the nutrient transfers that occur in forest ecosystems, especially after disturbances, such as harvesting, which alter forest floor input and mineralization rates. As a result, resins can provide vital information about any treatment-induced change in nutrient status of a forest ecosystem.

Used for both long- and short-term studies, resins act as a sink for ions. Available as either anion- or cation- resins, the resins are saturated accordingly with a counter-ion so they act as a strong sink for other ions. For example, cation exchange resins would be saturated with H^+, while an anion exchange resin would be saturated with OH^- (Skogley and Dobermann 1996). The resins would then release these counter-ions in exchange for other nutrient ions that are diffused through the resin in the soil solution. Sherrod *et al.* (2003) performed experiments to determine which counter-ion yielded the most nutrients, and stated that resins that are saturated using hydrochloric acid (HCl) yielded the most net ion exchange when compared with other counter-ions such as sodium bicarbonate ($NaHCO_3$).

Furthermore, the resins will only function as sinks for the ions present in the soil solution if the resins have a greater affinity for those ions compared with the counter-ion that is initially placed on the resin (Skogley and Dobermann 1996). Thus, the ions that are absorbed by the resin can reflect the nutrient status of the soil (Lundell 2001), but, if used improperly, resins can become sources of nutrient ions for surrounding vegetation, instead of being a nutrient sink. This may occur if the wrong resin type is chosen, or if the wrong counter-ion is used to saturate the resin.

2.3.2 Methodology Associated With This Technique

Different studies have used different resin forms accordingly depending on their study objectives, but resin beads are most widely used in soil nutrient research (Qian and Schoenau 2002). They have been used in many studies to create resin bags, which are created by placing a specific amount of the resin beads into pre-sewn bags made out of various mesh materials or even nylon stockings (Binkley and Matson 1983). The most common material used to create the resin bags seems to be nylon, which when sewn into the bags, allows for good separation of the resin from the soil (Sibbesen 1977).

Depending on which type of resin is used, the resins are soaked in either a $NaHCO_3$ or sodium chloride (NaCl) solution to saturate the resins with the counter-ions that will be exchanged with ions from within the soil solution. Anion resins are saturated with the sodium bicarbonate solution to convert the resins to a bicarbonate form (HCO_3^-) (Huang and Schoenau 1996, Huang and Schoenau 1997), and the cation resins are saturated using sodium chloride solution to convert the resins into sodium form (Krause and Ramlal 1987, Beyer 1998).

Once placed in the soil, it is important for the resins to maintain a flat surface area. This ensures rigid and constant contact surface with the soil and soil solution, and allows for maximum ion exchange to occur (Dobermann *et al.* 1997). The resin bags, if positioned carefully into the soil, can be inserted with minimal soil disturbance, which is important if a natural state is to be evaluated. If the resins are positioned properly within the soil column, ions in the soil solution can then diffuse through the soil to accumulate on the resin. This diffusion sensitive method of putting the resin bags *in situ* is advantageous as it provides information about initial ion concentrations, the dynamics of ion release, and ion diffusion (Skogley and Dobermann 1996).

The resins are analysed after the incubation period in a laboratory using an extraction technique known as desorption. Also called elution, desorption is a counter-ion exchange, in which the nutrient ions that are held by the resin are displaced by ions in the eluting solution (Qian and Schoenau 2002). The eluting solution must be selected based on the ion strength of the resins, but it is common that this solution is the same solution that was used for initial saturation of the resin. HCl and potassium chloride (KCl) are commonly used to recover the nutrients from the resin (Binkley and Matson 1983, Dobermann *et al.* 1997).

2.3.3 Advantages of Using Ion Exchange Resin Bags to Measure Nutrient Availability

Chemical extractions are common for measuring nutrient availability, but according to Sherrod *et al.* (2002), resins may be preferable. Chemical techniques can be tedious and time consuming, while resins are simple to use, cost effective, inexpensive, and are applicable in many regions on many different soil types (Skogley and Dobermann 1996, Sherrod *et al.* 2002). Unlike chemical extractions, using resins does not require the collecting and processing of soil samples. The resins provide a simple, reliable means to measure multiple nutrient elements in the soil environment (Schoenau *et al.* 1993), and provide an index of nutrient availability allowing for comparisons across different treatments and sites. The resin method overcomes the disadvantage of chemical extractions which are inherently static and do not account for the kinetics of nutrient release and transport, and which may mobilize nutrients that are not truly available to plants, thereby over-estimating the true available nutrient fraction (Abrams and Jarrell 1992). The method also provides a better relationship of plant uptake of nutrients than chemical extraction and allows comparisons of results across locations, between samples, and over time (Skogley and Dobermann 1996).

Since resin bags are often placed *in situ* within the soil, they are exposed to the same conditions to which the soil colloids and roots are exposed. *In situ* measurements are accurate because physical and chemical soil disturbances are minimized and the resin bags are sensitive to the on-site conditions (Dobermann *et al.* 1997). Therefore, *in situ* resin bags are believed to reflect the conditions that are experienced by the roots (Lundell 2001), and are considered to be one of the best methods to provide a measure of nutrient supply in soils (Huang and Schoenau 1996). Qian and Schoenau (2002) have reported that ion supply rates decrease as soil moisture decreases, which shows the relationship between soil moisture and the diffusive flux of nutrient ions. The advantages and ease of use of the resins are important characteristics and features if one is trying to study the movement and supply of different types of nutrients in a forest ecosystem that has been disrupted by disturbances such as fire or timber harvesting, both which can have negative effects on nutrient supply.

2.4 BOREAL FOREST HARVESTING TREATMENTS

2.4.1 Full-Tree Harvesting

2.4.1.1 Effects on Nutrient Supply and Losses Within Harvested Areas. Full-tree harvesting is a technique that removes the entire above-ground portion of the tree to the roadside, including the branches and foliage (Wiensczyk 1992). Trees are delimbed at roadside instead of at the stump. Full-tree harvesting is also often referred to as whole-tree harvesting, but in Ontario, whole-tree harvesting refers to the complete removal of vegetation and the forest floor (Duckert and Morris 2001). This method is not in operational use (Greenwood 1988), and full-tree harvesting is by far, the most widely used method (> 90 % of all operations).

It has been suggested that since a significant portion of aboveground biomass is being removed from the site during full-tree harvest, reductions in site fertility may occur, particularly on poor sites (Weetman and Algar 1983, Wiensczyk 1992), ultimately resulting in severe implications on long-term site productivity (Wiensczyk 1992). By removing the nutrient-rich crown material, not only are greater quantities of nutrient elements being removed, but the regenerative capability of the forest ecosystem may also be impacted (Johnson *et al.* 1991b).

Nutrient loss after full-tree harvesting depends on several factors including the species being harvested, the extent of crown development, the amount of foliar biomass, and the level of re-distribution of roadside slash after harvesting has occurred (Kimmins 1977). Although effects may not be immediately apparent, it has been suggested that full-tree harvesting could result in deficiencies in nutrient amounts of phosphorus, potassium, and calcium (Timmer *et al.* 1983) after several rotation periods. Different biomass components have varying concentrations of nutrient elements (Kimmins 1977), with large concentrations of nutrient elements often located in the tree foliage and bark. High concentrations of nitrogen, phosphorus, and potassium are found in the foliage and branches, while high concentrations of calcium and magnesium are located in the bole and bark of the tree (Maliondo *et al.* 1990).

It would be expected that full-tree harvesting would have a larger effect on sites where the trees have well developed crowns and high foliar biomass. For example, nitrogen losses from full-tree harvesting increased 288 % in a 65-year-old spruce forest, when compared to conventional harvesting (Weetman and Weber 1972), and a 65-year-old jack pine forest showed a 120 % increase (Morrison and Foster 1979). The average loss increase for nitrogen in the boreal forest after full-tree harvest was estimated at 115 % (Marion 1979). Species type and needle retention is important, as species such as spruce, have high foliar nutrient concentrations, resulting in higher amounts of nutrient loss than species with lower foliar concentrations (Kimmins 1977).

Full-tree harvesting may also result in increased soil temperatures and available moisture due to the lack of slash and canopy cover on the site. This often leads to an increase in decomposition rates after the harvest and therefore, an increase in available nutrients. This is known as the *assart effect* (Kimmins 1997), which is a flush of nutrients into the system. Prescott *et al.* (1993) have reported that the nutrient increase after harvest can occur for two to three years before declining. The increases in soil temperature and moisture could, however, also lead to rapid seed germination accompanying the increase in available nutrients (Wiensczyk 1992). If plant uptake of nutrients does not increase as well, the difference could lead to increased leaching from the site. If nutrients are being leached away from the site after a full-tree harvest, one can anticipate a compounding loss of nutrients from the site, in addition to the losses associated with the removal of forest biomass (Gordon 1983). This could result in site productivity reductions on sensitive sites, such as shallow soil sites, which are more susceptible to nutrient depletion after full-tree harvesting than deeper soil sites (Timmer *et al.* 1983).

2.4.1.2 Site Impacts of Full-Tree Harvesting. Full-tree harvesting leads to greater exposure of the forest floor and increased disturbance of the remaining organic and mineral soil horizons by the harvesting operations (Hendrickson *et al.* 1989). Physical soil disturbances can have negative effects on long-term forest health and productivity, and can include soil compaction through increases in soil bulk density values, reductions in soil air spaces, and changes to soil structure. The degree to which soil compaction occurs depends on the type of equipment that is used, the types of soils involved, the condition of the soil, and the season in which the harvest occurs (Wiensczyk 1992). Soil compaction can be reduced by placing slash over trails used frequently by harvesting machinery, through careful planning and scheduling of operations, and by following the Best Management Practices outlined by Archibald *et al.* (1997). The redistribution of slash can also to help reduce rutting, which also destroys soil structure, creates trenches in the soil, and disrupts drainage patterns (Grigal 2000).

These ruts often fill with water to create puddles, discourage seedling growth, and alter the water table. Soil texture and moisture can influence the impacts from harvesting, as finer-textured mineral and organic soils are more susceptible to compaction and rutting, while coarse-textured or clayey soils, with dry moisture regimes, or frozen soils, have minimal risks of being compacted or rutted during harvest operations (Archibald *et al.* 1997).

There are also concerns regarding the dislocation of soil materials, which involves the mixing of surface soils, and the redistribution of nutrient pools laterally and vertically within the soil profile (Martin 1988). These cumulative effects generated by the full-tree harvesting method have important implications concerning site fertility and nutrient cycles. It has thus been suggested that full-tree harvesting has a greater potential impact on nutrient cycling than tree-length harvesting (Hendrickson *et al.* 1989, Johnson *et al.* 1991a), which only removes the stem and bark (or bole) from the site.

Other impacts that have been suggested to occur after full-tree harvesting include soil acidification that may occur as a result of nutrient loss following the harvest. Since full-tree harvesting removes the branches and foliage of trees, it also removes cations that normally buffer acid inputs from organic matter decomposition (Maliondo *et al.* 1990). Organic matter decomposes at a faster rate after harvest due to increased soil moisture and temperature, and the resulting increase in site acidity can displace ions, leaving them vulnerable to leaching (Maliondo *et al.* 1990). This is a problem that could become more prominent after several rotations of full-tree harvesting.

Full-tree harvesting also reduces the amount of slash and organic matter that is left on the site. This reduction in slash does allow for easier planting after harvest (OMNR 1997a), but could eventually lead to lower levels of available nutrients for on-site vegetation or seedlings that are trying to establish on the site. The remaining slash, (*i.e.*, coarse slash) does help to shade seedlings and retain soil moisture, as well as representing an important source of nutrient elements that, over time will replenish the soil reserves. Slash also plays an important role in protecting the forest floor from temperature extremes, that often lead to increased drying. Also, wind and water erosion can easily degrade any exposed or vulnerable mineral soil that is disturbed during harvest. Water erosion increases with slope and Archibald *et al.* (1997) indicate that slopes greater that 30 % have moderate to high site damage hazard ratings, depending on the soil texture, type, and depth. Mineral soils have the highest risk of erosion after harvest occurs.

Harvesting impacts can be reduced by harvesting during winter months when the ground is frozen or by redistributing the slash over the site during the harvest. Both of these methods can help to reduce the impacts of rutting, puddling, and compaction of soils. It is also important to use full-tree harvesting with caution on sensitive sites, such as shallow soil sites. In the northwestern Ontario Silviculture Guide (OMNR 1997b), full-tree harvesting is not recommended (NR) for use on soils (mineral and surface organic) that are less than 20 cm deep. Based on this recommendation, other harvesting techniques, such as tree-length harvesting, may be more appropriate on these types of sites in northwestern Ontario.

2.4.2 Tree-Length Harvesting

2.4.2.1 Site Impacts of Tree-Length Harvesting. Tree-length harvesting, which is recommended for use on shallow soil sites (OMNR 1997b), is a harvesting operation in which the trees are delimbed at the stump and all slash and debris is left on the site. The assumption is that the slash will protect the organic and mineral horizons from soil disturbance effects, such as compaction, that often occur as a result of harvesting. Also, nutrient elements found in the tree crown components remain on the site to help maintain the nutrient status of the soil and provide, via mineralization processes, inputs to the available nutrient pool. But, leaving all of the slash on the site can also cause some problems to occur, especially by inhibiting natural regeneration of some tree species, and serving as a food source for forest pests such as weevils. For example, exposed mineral soil provides an excellent seedbed for jack pine, but these conditions may not largely be present after tree-length harvesting with the slash and debris covering the forest floor.

It is important to add that all forest management activities, including full-tree and tree-length harvesting, affect soils and alter soil properties which can directly or indirectly affect site productivity (Grigal 2000). Soil physical properties are easily altered and are not easily repaired, therefore extreme care should be taken to minimize site impacts that occur during harvesting. Nutrients are always removed from the site through the removed timber, but the type and intensity of harvest method will dictate the amount of additional nutrients that are removed during the harvest. Negative effects of forest harvesting and management can be reduced through proper planning (Grigal 2000). This is because some site are more sensitive to harvesting impacts than others, such as shallow soil sites, and caution needs to be exercised accordingly on these sites. Forest ecosystems are dynamic and resilient, so continued research is needed to fully comprehend how forests respond to impacts and changes in nutrient storage and supply (availability) related to harvest intensity (*i.e.,* levels of biomass removal).

2.5 PROBLEM FORMULATION

There are many issues surrounding the effects that timber harvesting has on boreal forest ecosystems, ranging from wildlife dislocation, habitat destruction, natural disturbance emulation, and economical sustainability. This study aims to focus on one of the larger pieces of the puzzle, nutrient retention and cycling, and thus, forest stand productivity. By examining several different kinds of harvesting techniques that are employed in the boreal forest, and including a reference stand that has not been harvested, comparisons can be made between the different harvest intensities.

As already mentioned, full-tree and tree-length harvesting will be examined, as well as whole-tree (blading) harvesting, and chipping. By using *in situ* techniques such as ion-exchange resins, amounts of plant available nutrient ions can be estimated, and correlations between nutrient element concentrations and stand productivity can be made. The critical question addressed by this study relates to the effect that harvest intensity has on nutrient pool size and availability on upland shallow soil sites, and how these changes relate to seedling growth and productivity.

All of the harvest types being examined have differing degrees of biomass removal and are expected to have different impacts on the nutrient status of shallow soils. The relevant question is: does the logging method that removes the most forest biomass have the greatest effect, in terms of lower nutrient reserves after harvest, and are these levels linked to reduced growth and productivity of the regenerating forest?

Specifically, the questions addressed by this project are: *1) is there a difference in seedling growth and the nutrient status of the forest floor when harvesting occurs?, 2) does the amount of slash (i.e., fine and coarse (tree-length) vs. coarse only (full-tree)) influence nutrient availability and seedling growth?, 3) does the type of slash (chipped vs. regular) influence nutrient availability and seedling growth?, and 4) does the additional removal of the forest floor compound the effect on nutrient availability and seedling growth?*

3.0 METHODS AND MATERIALS

3.1 STUDY SITE DESCRIPTIONS

The boreal forest study sites are located in northwestern Ontario (49° 03' - 49° 04' N, 89° 23' - 89° 24' W), approximately 70 kilometres north of Thunder Bay, Ontario (Figure1) on the Spruce River Forest (Abitibi Consolidated SFL) (Duckert and Morris 2001). Three replicate sites represent the upland, mixed conifer, shallow, coarse loamy site type, which is characterized by a moderately thin organic horizon (< 11 cm) over a shallow mineral Bm horizon (< 20 cm). For this paper, the three sites will be called Site 1, Site 2, and Site 3. Site descriptions for all three sites can be found in Table 1.

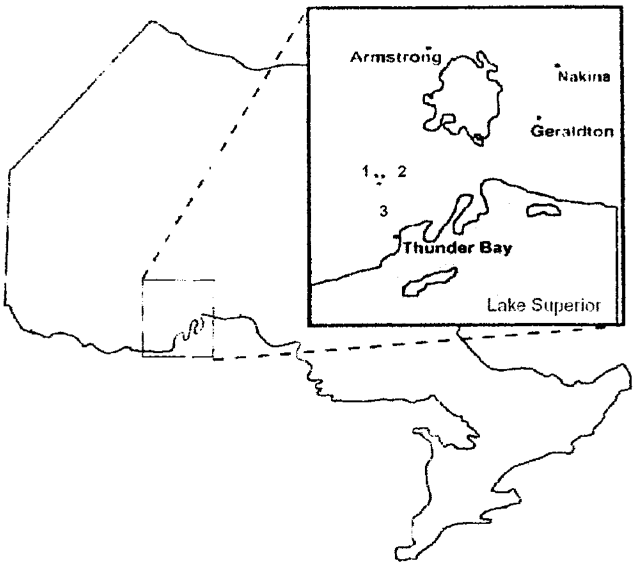


Figure 1. Location of the three study sites in northwestern Ontario (Duckert and Morris 2001).

Table 1. Site descriptions of the three study sites (Duckert and Morris 2001, Racey *et al.* 1996).

	Tree Species Composition (%)					
Site	Sb	Pj	Po	Ecosite Class	Soil Type	Moisture Regime
1	70	20	10	20	SS6	Very Fresh (3)
2	80	20	0	20	SS6	Fresh (2)
3	100	0	0	26	SS7	Moist (4)

Being part of the boreal forest, all sites experience cold and dry winters, with relatively short, moderately moist and warm growing seasons (Morris *et al.* 2003). The mean annual temperature is 2 °C, with a mean annual precipitation of ~ 67 cm (Environment Canada 1982). According to Morris *et al.* (2003), a high percentage (~60 %) of the precipitation falls as rain during the months of May to September.

All sites have Dystric Brunisol profiles (weakly developed mineral horizons with a pH < 5.5) and lack a well-developed mineral-organic surface horizon. At Site 1 and Site 3, the mineral profile is overtopped by a moderately thin Fibrimor humus organic horizon with average depths of 8 and 10.6 cm, respectively. Site 2 is characterized by a HumiFibrimor humus organic horizon, averaging 10.5 cm in depth. Site 1 and Site 2 both have cobblely, sandy loam mineral soils, with Site 3 being dominated by silty loam substrate (< 15 cm). There are slight differences in topographic position and mode of deposition, but all sites are characterized by shallow, but variable soil depths, with exposed patches of bedrock throughout (Duckert and Morris 2001).

The terrain across all three sites is strongly glaciated with rolling topography; the soil mantle consists of thin, coarse textured soils over granitic Precambrian bedrock (Rowe 1972). The stands are natural, fire origin stands, with a mean age of 110 years at time of harvest. Stem density on Sites 1 and 2 is just under 2100 trees·ha^{-1}, with a higher density on Site 3 of 3170 trees·ha^{-1} (Duckert and Morris 2001). Site index (base age 50) was slightly over 13.5 m. Species composition among the three sites is very similar, as all are dominated by black spruce (70 - 100 %) (Table 1). A scattering of trembling aspen, white birch, and understorey balsam fir can also be found on the sites (Duckert and Morris 2001).

3.2 HARVEST TREATMENTS

A series of replicated, experimental harvest treatments were conducted on all three of the study sites, in the winter of 1995 (February - March) (Duckert and Morris 2001). The harvest treatments included: chip (slash retained and chipped), tree-length (slash retained), full-tree (slash removed), whole-tree (vegetation and forest floor removed), and an uncut/reference condition. Figure 2 provides examples of the harvest operations associated with the four harvest treatments.

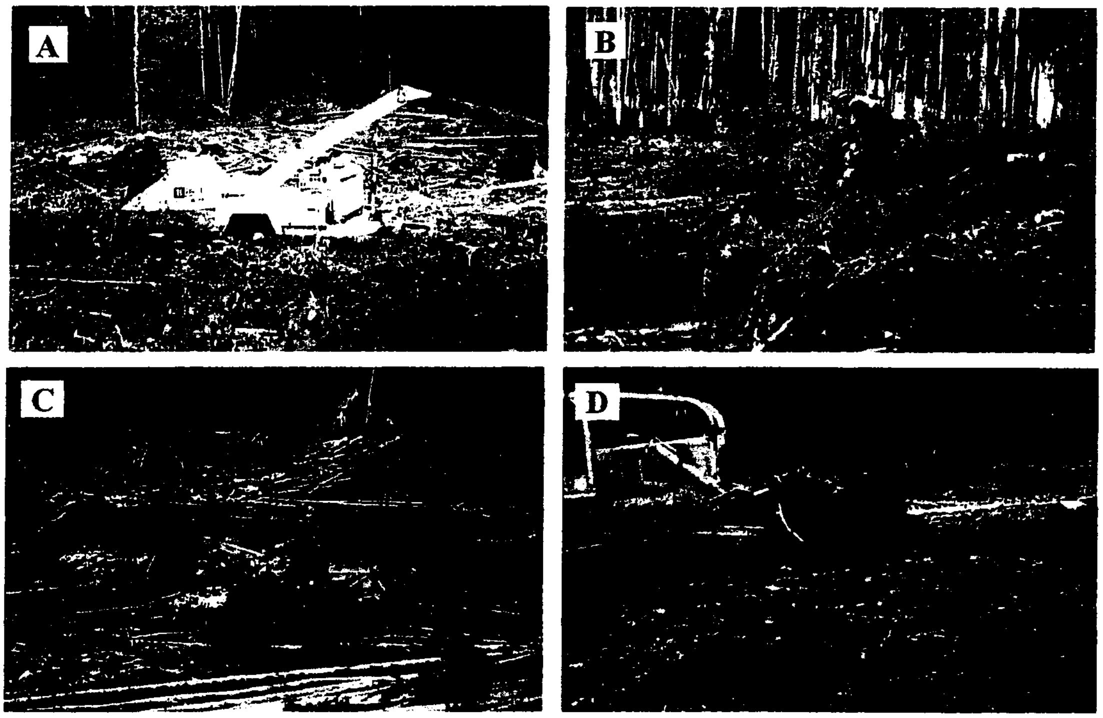


Figure 2. Examples of the four experimental harvest treatments. Plate A: chip Plate B: tree-length, Plate C: full-tree, and Plate D: whole-tree.

The harvest operations were done mechanically using a feller buncher, grapple skidder, and a delimber. On the tree-length harvested plots, a mechanical delimber distributed slash on the site as it was operating, but some manual distribution of slash was required to ensure uniform distribution across the plots (Figure 2 - Plate B). The slash from the chip sites was processed using a 12-inch gas-powered brush chipper (Chipmore Model TM-120-G2) (Figure 2 - Plate A), and the chipped material was weighed and spread uniformly across the plot manually. A D8 bulldozer was used in the whole-tree harvest treatment (Figure 2 - Plate D) to remove the slash and duff organic horizon after the plots were harvested (Duckert and Morris 2001). Each treatment represents different organic matter removals and levels of disturbance (Table 2).

Table 2. Descriptions of the differences between harvest treatments.

Harvest Treatment	Description of Disturbance
Chip	Similar to tree-length harvesting, but branches and foliage were chipped at the site, and redistributed on the harvest plot
Tree-Length	Trees are delimbed at the stump, branches and foliage remain at point of harvest
Full-Tree	Trees delimbed at the roadside, branches and foliage remain at roadside
Whole-Tree (Bladed)	After harvesting, all remaining vegetation and forest floor organic matter are removed using mechanical means

Buffer strips of at least 20 m were placed between the harvest plots and at least 5 m between the uncut plots. Each site was divided into 16 plots, with four replicates of the uncut plots (50 x 50 m) and three replicates of each of the four harvest treatments (30 x 30 m) (Figure 3) (Duckert and Morris 2001). Each plot was then divided into four quadrants, and approximately 50 black spruce seedlings were planted in three of the four quadrants. Buffers were also planted with black spruce to minimize the potential for edge effect. Natural regeneration has been monitored/documented in the unplanted quadrant (Duckert and Morris 2001).

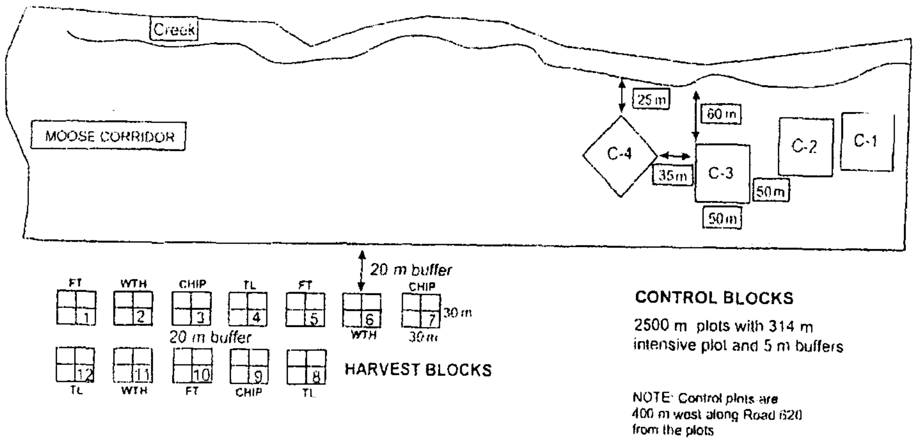


Figure 3. As an example, plot layout of the harvest treatment plots at Site 1 (Duckert and Morris 2001).

3.3 DETERMINING SOIL NUTRIENT RESERVES

3.3.1 Field Procedures

Soil samples were collected both pre- and post-harvest, with post-treatment re-assessment being conducted in 2002, eight years after treatment. The organic horizon pre-harvest data included two sampling periods, one in 1992, three years before harvest, and one in 1995, directly after the harvest. No differences were noted in the soil nutrient reserves between these two sampling periods, so in addition to the slash and moss reserves on the sites, these two periods were combined to provide an estimate of the plot-level organic horizon nutrient pool immediately after harvest (Morris, *pers. comm.* September 28, 2005). The pre-harvest mineral soil nutrient pool was based on the 1992 sampling year. Mineral soil depth is considered a static (or unchanging) variable, therefore, the mineral soil depths collected in 1992 during pre-harvest sampling were used for the other two sampling periods. (Morris, *pers. comm.* September 28, 2005).

Mineral soil depths averaged between 15 and 20 cm, with slight variations in depth occurring across the three sites.

Both the physical and chemical soil properties resulting from the various harvesting treatments imposed on the sites, and their relation to early seedling growth and nutrient status, were assessed through time. A total of three soil pits were excavated and assessed in each of the experimental harvest treatment plots in 1992 as well as the uncut/reference plots. In 2002, 36 small pits were dug into the mineral layer, based on a diagonal grid pattern, with nine pits in each quadrant (Figure 4). Samples for nutrient determinations were taken at pit numbers 1, 5, and 9, in each quadrant (12 per plot), at a depth of 10 - 15 cm, with bulk density samples in all pit number 5's (4 per plot). All pits (36 per plot) also had organic horizon depths recorded. Collected samples were placed in labelled plastic bags, and kept cool until being processed.

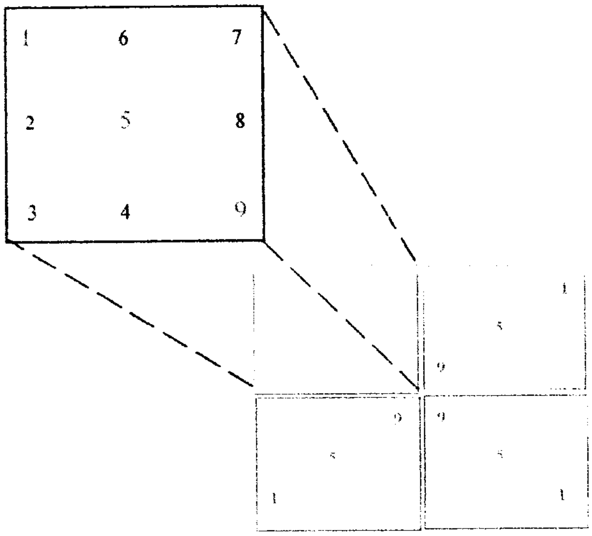


Figure 4. Example of the diagonal grid pattern of pits within each plot, with quad pit numbers and layout.

3.3.2 Laboratory Procedures

Upon returning from the field, bulk density samples were placed in a drying oven set at 70°C until constant weight was achieved. Organic samples were weighed; bulk densities were calculated as sample weight per sampler volume ($g \cdot cm^{-3}$). All mineral soil samples were then sieved (2 mm), and the fine fraction weighed. The volume of the coarse fraction (gravel) was determined and subtracted from the bulk density sampler volume.

Nutrient samples were allowed to air-dry on labelled disposable plastic plates. Once dry, mineral samples were sieved (2 mm), placed in clean and labelled paper bags, and stored awaiting nutrient analysis. Organic samples, once dry, were ground using a Wiley mill (20 mm mesh) after coarse debris such as sticks, cones, and bark were removed from the sample. Similar to the mineral samples, the ground organic samples were placed in labelled paper bags awaiting nutrient analysis.

3.3.3 Analytical Chemistry

All samples (soils, resin extracts, foliage) for this thesis were sent to Sault Ste. Marie, Ontario, to the Ontario Forest Research Institute (OFRI) to be analysed. Both the organic and mineral soil samples were analysed for moisture content (air to oven dry conversions), total C, total Kjeldahl nitrogen, potassium, phosphorus, calcium, magnesium, manganese, sodium, iron, and aluminum (Duckert and Morris 2001). Morris (2000) includes more in-depth details regarding the analytical procedures used to make these nutrient determinations. As an example, a short summary follows.

3.3.3.1 Total Carbon and Nitrogen. Total carbon was measured using a LECO analyser through infrared absorption. Dry combustion of the samples was used in this process. Total nitrogen was determined using a modified Kjeldahl method (semi-microKjeldahl), which incorporates a permanganate-reduced Fe modification technique. The sample is thus pre-treated with $KMnO_4$ and H_2SO_4 before Kjeldahl digestions. This step oxidizes nitrite (NO_2) to NO_3^-, and then with the added reduced Fe, NO_3^- is reduced further to NH_4^+.

3.3.3.2 Extractable Phosphorus (Bray P). All soils were extracted using an acid fluoride (Bray No. 1) extractant. This extract was then analysed by automated wet chemistry using an adaptation of the Bran+Luebbe TP method 365.4, which has been widely used as an index of available P in soils.

3.3.3.3 Exchangeable Cations (K, Ca, Mg). All soils were extracted using neutral normal ammonium acetate. The resulting solution was analysed for the above cations by Atomic Absorption Spectroscopy using a Varian SpectrAA - 400. All samples were analysed in duplicate for Quality Assurance (QA), and an in-house standard was incorporated every 10 samples for Quality Control (QC).

3.3.4 Data Synthesis and Statistical Analysis

Using both the field and laboratory data, nutrient pools could be calculated for both the organic and mineral horizons. In order to calculate the nutrient pool, information such as horizon depth (cm), soil moisture content (%), soil coarse fragment

(%), bulk density ($g \cdot cm^{-3}$), and nutrient concentration (% or $mg \cdot kg^{-1}$) was required. For this study, results are reported in $kg \cdot ha^{-1}$ (based on ~10 cm organic and ~15 cm mineral horizon depths), and are reported according to harvest treatment and site.

The calculations for both the organic and mineral soils are based on the same equation, with the exception that the mineral soil calculation needed to consider soil coarse fragment (*i.e.,* the inert portion of the soil profile volume). Soil coarse fragment (cobble-size and greater), as a percent was applied to each mineral soil calculation based on an average for each of the three sites. Sites 1, 2, and 3 had 25.2 %, 14.4 %, and 10.5 % soil coarse fragment, respectively (Morris, *pers. comm.* September 13, 2005).

Soil nutrient pools (organic and mineral horizons) were calculated by applying horizon bulk density to soil volume, minus the coarse fragments (mineral), and then multiplying by the nutrient concentrations, adjusted for air dry moisture content (Duckert and Morris 2001). After the calculations were completed, Analysis of Variance (ANOVA) was run using the statistical software Data Desk, Version 6.0 (Velleman 1997). The experiment was designed as a completely randomized design (CRD), with replication. The pre-harvest data set employed a one-way ANOVA, whereas the post-harvest data set utilized a two-way ANOVA.

Results for the pre-harvest nutrient pools from both the organic and mineral soil horizons were considered separately, but employed the same General Linear Model (GLM) (Equation [1]). Estimated Mean Square (EMS) tables were also very similar, but with different total observations. The EMS for the pre-harvest period is presented in Table 3. The GLM contains a restriction error on Site Type (T), as all three areas represent an upland-shallow soil conifer dominated site, and since only one Site Type was considered in this study, this factor carries zero degrees of freedom, and had no test. The GLM for the pre-harvest sampling periods only contains one term, Site (S), which has three levels, representing the three study sites. Forty-eight observations were used in this ANOVA.

The GLM for the pre-harvest nutrient pool sampling period is as follows:

$$Y_{ijk} = \mu + T_i + \delta_{(i)} + S_j + \varepsilon_{(ij)k} \qquad [1]$$

$$i = 1 \quad j = 1 - 3 \quad k = 1 - 16$$

where:

Y_{ijk} = the measurement of nutrient pool content from the k^th^ replicate of the j^th^ site and the i^th^ site type

μ = the overall mean

T_i = the fixed effect of the i^th^ site type

$\delta_{(i)}$ = error associated with the restriction on randomization within the i^th^ site type

S_j = the fixed effect of the j^th^ site

$\varepsilon_{(ij)k}$ = the random effect of the k^th^ replicate of the j^th^ site and the i^th^ site type

The $\varepsilon_{(ij)k}$ are assumed to be i.i.d. N $(0, \sigma^2)$.

Table 3. The EMS table associated with the pre-harvest soil sampling period for nutrient pool calculations.

Level		1	3	16		
F/R		F	F	R		
Subscript	df	i	j	k	EMS	TEST
T_i	0	0	3	16	$\sigma^2 + 48\ \Phi_\delta + 48\ \Phi\ (T)$	--------
$\delta_{(i)}$	0	1	3	16	$\sigma^2 + 48\ \Phi_\delta$	--------
S_j	2	1	0	16	$\sigma^2 + 16\ \Phi\ (S)$	MS(S)/MS(E)
$\varepsilon_{(ij)k}$	45	1	1	1	σ^2	
Total	47					

The post-harvest nutrient pool ANOVA's utilized a similar GLM (Equation [2]), but with an added term representing the Harvest Treatments (H) used on the three sites, with five levels, representing chip, tree-length, full-tree, whole-tree harvesting, and the uncut/reference state. The organic and mineral horizon results were studied separately. The EMS table for the post-harvest sampling period can be seen in Table 4, and the ANOVA was run with 45 observations. Equation [2] is used for all subsequent analysis, with some changes to levels and reps, depending on the application.

All data sets were checked to ensure that they complied with the ANOVA assumptions of normal distribution and equal variance (Lorenzen and Anderson 1993). Response residuals were used to generate normal probability plots to check the residuals for departure from normality and homogeneity of variance was assessed by plotting the residuals side-by-side in dot plots. The residuals appeared to be in compliance, but further testing using the *W* Statistic test for normality and Bartlett's test for homogeneity (Lorenzen and Anderson 1993) was done to determine whether or not the data met the assumptions. It was concluded that the ANOVA assumptions had been met and the data sets did not require transformation. SNK tests were also completed following significant ANOVA results to identify differences between Site means (Zar 1999).

The GLM for the post-harvest nutrient pool sampling period is as follows:

$$Y_{ijkl} = \mu + T_i + \delta_{(i)} + S_j + H_k + SH_{jk} + \varepsilon_{(ijk)l} \qquad [2]$$

$$i = 1 \quad j = 1 - 3 \quad k = 1 - 5 \quad l = 1 - 3$$

where:

Y_{ijkl} = the measurement of nutrient pool content from the lth replicate of the kth site in the jth harvest treatment and the ith site type

μ = the overall mean

T_i = the fixed effect of the ith site type

$\delta_{(i)}$ = error associated with the restriction on randomization within the ith site type

S_j = the fixed effect of the jth site

H_k = the fixed effect of the kth harvest treatment

SH_{jk} = the interaction effect of the jth site and the kth harvest treatment

$\varepsilon_{(ijk)l}$ = the random effect of the lth replicate of the kth harvest treatment in the jth site and the ith site type

The $\varepsilon_{(ijk)l}$ are assumed to be i.i.d. N $(0, \sigma^2)$.

Table 4. The EMS table associated with the post-harvest soil sampling period for nutrient pool calculations.

Level		1	3	5	3		
F/R		F	F	F	R		
Subscript	df	i	j	k	l	EMS	TEST
T_i	0	0	3	5	3	$\sigma^2 + 45\ \Phi_\delta + 45\ \Phi\ (T)$	--------
$\delta_{(i)}$	0	1	3	5	3	$\sigma^2 + 45\ \Phi_\delta$	--------
S_j	2	1	0	5	3	$\sigma^2 + 15\ \Phi\ (S)$	MS(S)/MS(E)
H_k	4	1	3	0	3	$\sigma^2 + 9\ \Phi\ (H)$	MS(H)/MS(E)
SH_{jk}	8	1	0	0	3	$\sigma^2 + 3\ \Phi\ (SH)$	MS(SH)/MS(E)
$\varepsilon_{(ijk)l}$	30	1	1	1	1	σ^2	
Total	44						

3.3.4.1 Constructing Linear Contrasts for the Comparisons of Means. Since harvest type was the factor driving this experiment, analysis was completed on the post-harvest data to investigate for any differences between the different harvest types and their associated levels of biomass removal and site disturbances. This was done using a series of orthogonal contrasts, also called comparisons (Snedecor and Cochran 1989, Lane 1999) (Table 5). Since there are k = 5 harvest types, it is possible to have a maximum of (k - 1) = 4 linear contrast comparisons (Snedecor and Cochrane 1989).

Table 5. Orthogonal contrasts for the effect of harvest type on nutrient element concentrations.

L_i	Contrast	Treatment Coefficient					
		λ_1	λ_2	λ_3	λ_4	λ_5	$\Sigma\lambda$
1	Reference vs. Harvested	-4	+1	+1	+1	+1	0
2	Chipped slash vs. Original slash	0	-1	+1	0	0	0
3	Blading after harvest vs. Harvested	0	+1	+1	+1	-3	0
4	Coarse and fine slash retained vs. Coarse slash retained	0	0	+1	-1	0	0

λ Subscripts refer to: 1 - Reference (no treatment/uncut), 2 - Chip,
3 - Tree-Length, 4 - Full-Tree, 5 - Whole-Tree (Bladed)

The contrasts and ecological questions that are addressed by them are as follows: L_1 - is there a significant change in the size of the nutrient element pool resulting from timber harvesting (reference *versus* harvested), L_2 - is there a significant change in the size of the nutrient element pool when the slash left from the harvest is chipped or left in the original state (tree-length *versus* chip), L_3 - is there a significant change in the size of the nutrient element pool when both the overstorey and the organic matter on the forest floor is removed during harvesting (whole-tree (bladed) *versus* full-tree, tree-length, chip), L_4 - is there a significant change in the size of the nutrient element pool when different amounts and sizes of slash remain on the site after harvesting (tree-length *versus* full-tree).

Linear contrasts were applied to both the organic and mineral data sets. The full suite of comparisons were made as some of the comparisons might identify significant differences that the initial ANOVA *F* tests showed as being non-significant (Snedecor and Cochran 1989). According to Snedecor and Cochran (1989), ANOVA is only the first step of statistical analysis, the next step being examination of the class means, and any differences that may exist between them.

3.4 ESTIMATING AVAILABLE NUTRIENT POOL (ION EXCHANGE RESINS)

3.4.1 Field Procedures

3.4.1.1 Installing the Ion Exchange Resin Bags. At each plot, four resin bags (two anion and two cation) were placed in pits in quads one, two, and four, unless one of those quads was unrepresentative of the overall site. Some pit locations were moved slightly to avoid any large roots or rocks, but generally, pits were dug approximately 50 cm apart and were located in the centre of the quadrant, corresponding to pit number 5 (Figure 4). Care was taken to ensure that the resin bags were not placed in a pit which had been sampled previously, and also to keep the organic and mineral horizons separate while excavating the pits. Instructions were also given to ensure that any excavated soil was not placed on top of the location where the resins were under the soil.

Two pits were excavated, with one pit designated for the fall resin bags (growing season) and the other pit for the spring resin bags (overwinter). Pits were only big enough to be able to work in and place the bags in the two horizons. Two mineral soil resin bags were first placed in the pit at a depth of 10 cm, with the two organic bags staggered above them at the interface to avoid overlapping (Figure 5). Care was also taken to ensure that bags were not touching, crumpled, or placed under rocks or roots.

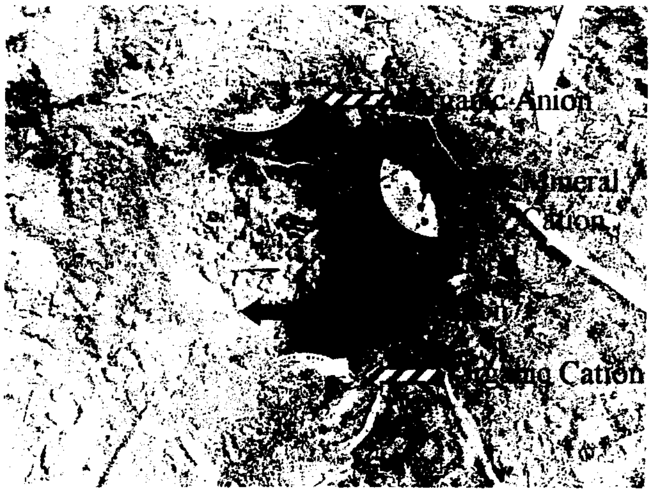


Figure 5. Overhead picture of a typical pit with staggered resin bags.

In order to prevent the crumpling or bunching of the bags, 4.25 inch wide plastic canvas disks (available at craft stores) were utilized to stabilize the resin bag (Figure 6). The disks were approximately 2 mm thick with 674 holes on the surface (2 mm x 2 mm), which allowed for water to pass through the disks, and percolate through the resin bag itself. The disks were often reused, but were thoroughly cleaned between uses.

Figure 6. Resin bags were supported with plastic disks while *in situ*.

In the field, the disks were also used to evenly spread out the resin within the bag. Typically, each mineral resin bag was sandwiched between two disks and slid into the soil after making a slit with a trowel. Generally, only one disk was needed to stabilize the bags placed in the organic horizon, with the disk being placed underneath the bag. It was found that a square Bricklayer's trowel worked the best for inserting the disks into the soil.

After placing both mineral bags in the Bm horizon, the organic bags were placed in the organic-mineral interface. This depth varied from pit to pit, and all placement depths were recorded on tally sheets. Most often, the organic LF horizon was lifted with the trowel, the bag and disks were placed on the top of the mineral horizon, and the organic matter was lowered back down onto the bag. The soil was then returned to the pit, and was gently hand-pressed, but not compacted. The location was marked with a coloured plastic stake to indicate if it was to be recovered in the fall or the following spring (Figure 7).

Figure 7. A new pit being dug, with coloured stakes marking other resin pits.

The second pit was then dug, being careful not to stand on or place any soil on the location where the first bags were placed. This pit would also be marked with another coloured plastic stake. Since the stake was placed in the centre of the pit, contamination was not likely to occur, as the bags were on the outside of the pit and would collect nutrient elements that percolated downwards through the soil column. Contamination was also avoided by the use of latex gloves, which were worn at all times when handling the resin bags.

3.4.1.2 Removing the Ion Exchange Resin Bags. Using the coloured stakes as not only indicators of extraction periods, but of resin locations, the best technique for extraction was to first locate and remove the organic horizon resin bags. This was done by scraping away the organic matter around the stake with a small trowel or your hands to reveal the bags. This was done carefully as many of the organic bags only had one disk to stabilize them (Figure 6), and the shovel could sever the bags and spill the resins. Once the organic bags were recovered, the mineral bags were removed by excavating the pit with the shovel, and since these bags were sandwiched between two disks, there was less chance of damaging the bags. The pit was essentially dug out again, and the mineral soil was dug away until the disks could be retrieved.

Once the resins were removed from the pit, each was cleaned with either a small, clean paintbrush or deionized water, and each resin bag was placed in a clean zipper freezer bag as per Beyer (1998) and Dobermann *et al.* (1997). The sample number on the resin bag was also written on the outside of the bag. The resin bags were kept cool in transit back to the lab and placed in the refrigerator at 4°C where they were stored until being extracted. Most extractions were completed within two to three days of collection, but past studies have suggested that they can be stored in the refrigerator or the freezer until they can be analysed (Dobermann *et al.* 1997, Beyer 1998).

3.4.2 Laboratory Procedures

3.4.2.1 Preparing the Ion Exchange Resin Bags for Use in the Field. Before being placed in the field, the resin bags needed to be created and chemically treated in the lab. The actual resin bags, each measuring 6 cm by 6 cm, were constructed out of a fine screen or mesh material, also known as "no-see-um" screen. This material was used to ensure that the resin beads would not be able to seep out of the bag, but that water could still percolate through. After the material had been sewn into a square with three of the sides sutured shut, it was ready to be filled with the resin beads.

Two resins were used in this experiment, anion and cation. Both resins were made by Sigma-Aldrich, under the brand name *Amberlite*. The anion resin was a strong base, called IRA 400 (Cl^-, 16 - 50 mesh), and the cation resin a strong acid, which was called IR 120 Plus (H^+, 16 - 50 mesh). The resins were weighed out in one gram quantities and all weights were recorded. The anion and cation resins provided 3.8 $meq \cdot g^{-1}$ and 4.4 $meq \cdot g^{-1}$ of exchange capacity, respectively. One gram of resin was adequate as CEC is typically lower than 1 $meq \cdot g^{-1}$ in most Canadian forests (Meyer *et al.* 1994).

After one gram of either the anion or cation resins was placed in the prepared mesh bags, the open panel was folded over 1 cm and then stapled shut (Binkley and

Matson 1983). Once the resins were evenly spread out within the mesh bag, each resin bag and the resins within provided a functional surface area of 4 cm by 5 cm (20 cm^2) to allow for ion exchange. The filled and sealed bags were then labelled using a colour coded vinyl tag that had an identification number written on it. The type of resin could be identified by the colour of the tag or the identification number on the tag, which was also coded to identify field location and sampling period. The label was affixed to the bag and the bag was then moistened with deionized water and placed in zipper freezer bags. The resin bags were kept cool and moist by being stored at 4 °C until they were saturated with counter-ions.

All anion bags were saturated using the same methodology and chemicals from the same batch and lot number. Fresh chemicals were mixed for use for each time period. Anions were saturated using $NaHCO_3$ which was purchased in powder form from Fisher Scientific and mixed to a 0.5 M solution (Sibbesen 1978, Krause and Ramlal 1987). In order to convert the resins to a bicarbonate form, which has low attraction to the positive resins and will be easily exchanged for other elements, the bags were soaked in the 0.5 M $NaHCO_3$ solution. This was done by placing the chemical in clean large plastic Rubbermaid tubs, using the equivalent of 100 ml per bag. Two saturation periods of one hour each with gentle agitation at time zero and thirty minutes were employed (Sibbesen 1978, Krause and Ramlal 1987). Chemicals were not reused when saturating the bags.

After being in the second bicarbonate saturation for an hour, the bags were transferred to a tub of deionized water, where they remained for one hour, and were then transferred to a second tub of deionized water for another hour (Sibbesen 1978). The bags were allowed to drip the excess water off, but were not allowed to completely dry, and were returned to the zipper freezer bags and put in the refrigerator at 4°C until being used in the field.

Similar to the anion bags, the cation bags were separated into large batches, and all bags were treated in the same manner regardless of time period. The cation bags were cleaned in 1 M HCl overnight using 50 ml per bag and were rinsed in deionized water for one hour, being stirred at half hour intervals, before being saturated using 50 ml per bag of 1 M NaCl (Krause and Ramlal 1987) in three saturation periods of one hour each (Beyer 1998). These were also agitated at time zero and at thirty minutes. After the third hour of saturation, the bags were rinsed in deionized water for three rinsing periods of one hour each (Beyer 1998). Similar to the anion bags, the cation bags were drained of excess water before being placed in zipper freezer bags and stored in the fridge until being used in the field. As noted for the anion bags saturation procedure, each saturation period used fresh chemical batches.

3.4.2.2 Extracting the Resin Bags After the In Situ Sampling Period. Both sets of resins were extracted using the same methodology but with different molar strengths of HCl for the anion and cation extractions. The anion and cation bags were extracted separately to avoid accidental mixing up of the bags during extraction. Mineral and organic resin bags were also separated into groups for extraction. Before extraction, the resin bags were thoroughly cleaned with three separate deionized water baths to remove any remaining dirt or debris (Krause and Ramlal 1987, Cooperband and Logan 1994, Huang and Schoenau 1996, Dobermann *et al.* 1997, Huang and Schoenau 1997, Beyer 1998). This is an important process because ion adsorption from the remaining soil particles may continue beyond the sample period (Dobermann *et al.* 1997, Qian and Schoenau 2002).

It is also preferable not to over handle the resins before they are placed in containers, and direct handling of the resin should be limited and avoided if possible (Sibbesen 1977). Cleaning the resins was done by gently agitating the bags in a Rubbermaid tub using a gloved hand. Roots were carefully removed from the bags using tweezers and scissors, and careful attention was paid to avoid damaging the bag. Once the bags were cleaned in the baths and allowed to drip dry for a few minutes, they were placed in clean plastic pill bottles.

The anion resin bags were extracted using 50 ml of 0.5M HCl (Sibbesen 1978, Lajtha 1988, Schoenau and Huang 1991, Huang and Schoenau 1996, Qian and Schoenau 1997). Cation resin bags were extracted using 50 ml of 0.1M HCl (Krause and Ramlal 1987). Clean plastic pill bottles with tight fitting lids were used. After the resin bag and the chemicals had been added to the bottle, it was shaken for one hour on a shaker table at 180 rpm. After shaking, the solution was filtered using a vacuum flask and Buchner funnel with Fisherbrand's Q2 filters (John Perron, *pers. comm.* September 12, 2003) (Figures 8 and 9). The filtered solution was placed in 50 ml centrifuge tubes (Figure 10) and placed in the freezer until samples were analysed. All lab equipment was thoroughly washed three times to avoid contamination between extractions.

Figure 8. Front view of the vacuum flask and Buchner funnel apparatus used in the resin bag extractions.

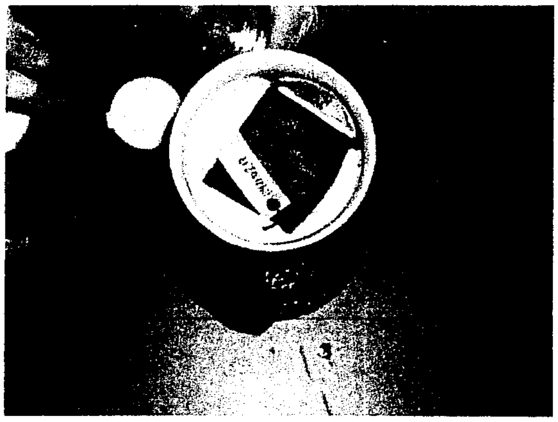


Figure 9. Overhead view of a resin bag and extract solution being filtered.

Figure 10. After filtering, the solution was stored in 50 ml centrifuge tubes.

3.4.3 Analytical Chemistry

While two separate kinds of resins were placed *in situ* in conjunction with each other, only cation results will be presented in this paper. The anion resins were analysed along with the cation resins, but during the anion analysis process problems were encountered with the extract solution. Unusual results and spikes of unwanted and unanticipated ions delayed the anion results. The extract samples are currently being re-filtered and re-analyzed to try and normalize the results into a workable data set. Such problems were not encountered with the cation ion exchange resin extract samples. All resin results are reported in $kg{\cdot}ha^{-1}$ after converting from ppm (see Appendix I).

The cation resin bags were analysed for Ca^{2+}, Mg^{2+}, K^+, aluminum (Al^{3+}), iron (Fe^{3+}), ammonium (NH_4^+), and manganese (Mn^{2+}) levels. Ammonium was determined using 5 - 10 ml of the extract sample using a modification of the classic Kjeldahl method, adapted for TrAAcs automated wet chemistry (Bran+Luebbe Method 351.2). SPEX QC aqueous control (4-15 NUT-1 and 5-10 ANIONS - NIST) material was incorporated every 10 samples. The other cations were determined by Atomic Absorption Spectroscopy. The volumes used for each sample taken depended upon expected elemental content and sample amount. SPEX QC aqueous control (4-12 TMAA-3, from NIST) material was incorporated every 10 samples.

3.4.4 Data Synthesis and Statistical Analysis

In total, over 1600 resin bags were installed over two field seasons representing three sampling periods (Growing Season - 2003; Growing Season - 2004; Overwinter

2003/2004, by subtraction). For each sampling period, 540 resin bags were created (270 anion + 270 cation), with varying amounts actually being needed once in the field, due to missing horizons or unsuitable conditions for burial (*i.e.,* water, excessive roots or rocks in pit).

The first period was over the growing season of 2003 (June 2003 to September 2003) with 246 anion and 247 cation resin bags being buried for an average of 111 days. The second period included the summer of 2003 and carried over to the spring of 2004 (June 2003 to June 2004) with 249 of each the anion and cation resin bags being used for an average of 366 days. The third and last period was during the growing season of 2004, with 259 of each the anion and cation type resin bags. These bags were *in situ* from June 2004 to September 2004, for an average of 109 days. A timeline (Figure 11) is shown to simplify the dates of installation and extraction.

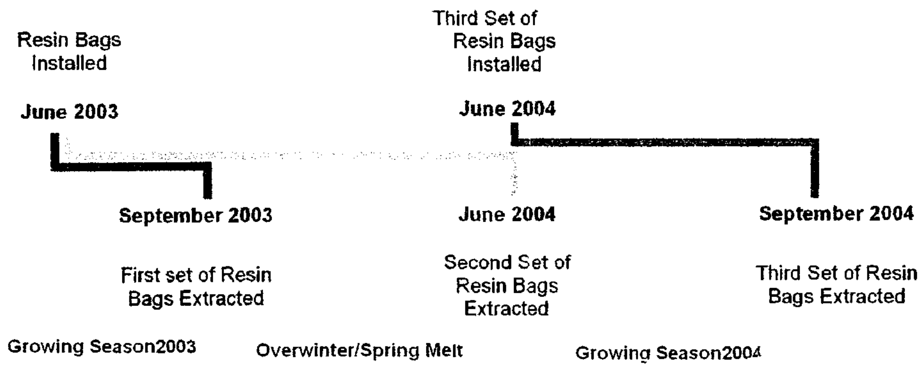


Figure 11. A timeline showing the dates of installation and extraction of the resins.

For analysis, the two growing season periods were combined together to provide one estimate of the available nutrients during the growing season. This was done to simplify the analysis, as the two growing season periods had similar nutrient concentrations. These values were then subtracted from the overwinter period to provide an estimate of the contribution of nutrients to the ecosystem by the spring flush. The organic horizon tests had 135 observations for the growing season, and 131 observations for the overwinter period, while the mineral test had 128 and 114, respectively. Observation numbers differed because different numbers of bags were used due to the variations that occur across the plots and sites. For example, these sites have exposed bedrock areas where there tends to be little or no organic and/or mineral soil to sample.

Resin extraction results were considered separately for each horizon and sampling period, but employed the same GLM and EMS table, which was similar to Equation [2]. The EMS table was similar to Table 4, but had different epsilon repetitions and degrees of freedom for error. The experimental design is the same as the nutrient pool experiment, considered as a completely randomized design (CRD) with harvest treatment replication, with analysis again utilizing ANOVA run with Data Desk, Version 6.0 (Velleman 1997). All data sets were checked for compliance with the ANOVA assumptions of normal distribution and equal variance as well as being tested for normality and homogeneity (Lorenzen and Anderson 1993). It was concluded after computing these tests that the ANOVA assumptions had been met and the data sets need not be transformed. Student-Newman-Keuls (SNK) tests were also completed (Zar 1999).

3.4.4.1 Constructing Linear Contrasts for the Comparisons of Means. Harvest type was again compared using linear contrasts to investigate for differences between the different harvest types and their associated levels of biomass removal (Snedecor and Cochran 1989, Lane 1999). The same contrasts were used as introduced for the nutrient pool sampling, with k = 5 harvest types, and a maximum of (k - 1) = 4 linear contrast comparisons (Snedecor and Cochran 1989) (Table 5). The contrasts and ecological questions used in these contrasts were outlined previously (Section 3.3.4.1). Both the organic and mineral data sets were included in the linear contrasts to capture any significant differences not identified by the initial ANOVA *F* tests (Snedecor and Cochran 1989).

3.5 ESTIMATING STANDING CROP AND EVALUATING CROP TREE PERFORMANCE

3.5.1 Collecting Tree Inventory Data

During the summer months of 2003, tree inventory plots were completed in all four quadrants in all plots harvested on all three study sites as part of a bioassay of the treatments. From the centre of each quadrant, a 3.99 m radius was measured, and any tree within that radius with a total height greater than 30 cm was included as part of the inventory. Quad centres (equivalent to pit 5) were used as a plot centre (Figure 4).

Measurements taken included: species type, root collar diameter (RCD) and diameter at breast height (DBH), both measured using digital calipers, total height, four growth increments, and crown widths and lengths, all of which were measured using either metre sticks or height poles. Crown density percentages were measured by visual estimation. All measurements were recorded on tally sheets, and later entered and verified in an Excel spreadsheet to be used to calculate species composition, stand density, and applied to local "small tree" biomass equations, used to estimated standing crop across sites and harvest treatments. Species densities were also calculated by Site and Harvest Treatment using this information.

3.5.2 Derivation of "Small Tree" Aboveground Biomass Equations

In the fall of 2004, destructive sampling of the dominant tree species (black spruce (Sb), jack pine (Pj), and trembling aspen (At) was completed to develop a relationship between RCD and biomass, in order to use the stand inventory data to estimate standing crop. A total of 30 trees covering the full range of diameter classes from each of three tree species were taken from within the buffers between harvest treatments (10 per species per site). Diameter classes were determined from the tree inventory data that was collected the previous year.

The trees were measured similarly to the intensive trees which were part of the tree inventory, but instead of just clipping samples of the current growth, the whole tree was brought back to the lab to be weighed and measured. The tree was cut down using a small hand saw, and tagged with an identification number. Roots were not included as part of the collected components due to the difficulty associated with removing them at that time.

Upon returning to the lab, all 90 trees were placed in a walk-in cooler set at 4 °C, until processing a few days later. Tree components separated and weighed included:

(total) foliage (F), current foliage (CF) and twigs (CT), branchwood (BW), and stemwood and bark (SB). Each component was placed in a labelled paper bag, oven dried at 50°C to constant weight, and then weighed. Ages were determined from cookies taken from the base of the stem of each tree.

After entering and checking the data, two black spruce and two jack pine trees were removed from the data set due to inconsistencies that could not be explained or corrected by the original tally sheets. In total, 28 black spruce and jack pine trees, and 30 trembling aspen trees were used.

Curvilinear regression equations were generated to determine component biomass (dependant variable). RCD was used as the independent variable in a generalized, two parameter power function:

$$\text{Mass} = B1 * \text{RCD}^{B2} \tag{3}$$

Using this function, individual equations were developed for each tree component based on the measurements obtained from the destructive sampling. Total weight was also included in the calculations, which were performed using the PROC NLIN procedure on SAS/STAT software (SAS Institute Inc. 1987). The multi-variate secant method (Ralston and Jenrich 1978) was applied to the model-building data set.

Evaluation of the fitted model was based on the coefficient of determination (R^2), the asymptotic standard errors of B1 and B2, the asymptotic 95 % confidence intervals of the estimated parameters (B1 and B2), the Mean Square Error (MSE), and the scatterplots of the regression residuals (Appendix II). Standing crop values for the tree strata were then generated by combining the regression equations, by each component, with the stand table information, in this case, the RCD of all trees from the known plot areas of collection, as per the procedure outlined in Baskerville (1972).

3.5.3 Black Spruce Seedling Intensive Inventory

After harvesting, three of the four quads per plot were planted with black spruce seedlings at a 2 m x 2 m spacing. After Year One, several (to a maximum of 45 per plot) planted black spruce seedlings were randomly selected and tagged. In addition, nine of these trees (three per quad) were also selected for foliar nutrient analysis. In the late summer/early fall of 2003, all tagged trees were measured for total height (10th year) and RCD. In addition, current foliage samples were collected from the predetermined foliar trees. It is preferable to use current foliage in the assessment of foliar nutrition due to the high correlation between the nutrient concentration of the current year's foliage and the availability of soil nutrients (Leyton 1958, Lavoie *et al.* 2007). The leaf (or needle) is also the focal point for many plant functions, and, as such, is an excellent indicator for those mineral elements that directly affect internal processes, such as photosynthesis, as well as being a convenient portion of the plant to sample and handle (Smith 1962).

Samples were placed in labelled paper bags, and upon returning to the lab, were placed in a drying oven where they were force-draft oven dried at 70 °C to a constant weight. After drying, 100 needles were counted and weighed, after which the whole needle sample was finely ground (to pass a 20-mesh sieve) using a Wiley mill. Ground samples were then transferred to air-tight, moisture-proof polyethylene containers and stored for further analysis. Macro-nutrient analysis completed at OFRI measured for total N, P, K, Ca, and Mg.

3.5.4 Analytical Chemistry

Total Kjeldahl Nitrogen (TKN) was determined on 0.2 - 0.5 g of needle sample using a modification of the classic Kjeldahl method, as outlined for the soil samples (see sec. 3.3.3.1), adapted for TrAAcs automated wet chemistry (Bran+Luebbe Method 351.2). Total Phosphorus was also determined by using automated wet colorimetric analysis (Bran+Luebbe Method 365.4) on the same digest obtained for TKN determination. All foliar samples were analysed in duplicate, and NIST (National Institute of Standards and Technology) standard reference material (Pine 1575) was incorporated into the sample runs as a QC (Quality Control) check every 10 samples.

Total P, K, Mg, and Ca were determined by Atomic Absorption Spectroscopy on a mixed acid (H_2SO_4, NHO_3, $HClO_4$) digest (Grimshaw *et al.* 1989 - method 12.5). Again, standard reference material (Pine 1575) was incorporated as a QC check every 10 samples.

3.5.5 Data Synthesis and Statistical Analysis

3.5.5.1 Biomass Component ANOVA and Linear Contrasts. After the biomass equations had been applied to the tree inventory data, and standing crop estimates were calculated, ANOVA was run using Data Desk, Version 6.0 (Velleman 1997). It used a similar GLM to Equation [2], using only four levels for harvest treatment as the uncut/reference stand was not included, and was calculated on a quad level. The standing crop data was analysed as a group with all species combined, as well as by individual species. Combining all species yielded 144 observations, with 129 for black spruce, 102 for jack pine, and 117 for trembling aspen. As done previously with all data sets, checks were completed to ensure compliance with the ANOVA assumptions of normal distribution and equal variance (Lorenzen and Anderson 1993). It was concluded after computing these tests that the ANOVA assumptions had been met and the data sets need not be transformed. Linear contrasts using the last three of the four contrasts outlined in Table 5 were also calculated.

3.5.5.2 Height, RCD, and Foliar Concentration and Content ANOVA's.

Nutrient concentrations and the 100 count needle weights were used to calculate nutrient contents for each macro-element. Data Desk, Version 6.0 (Velleman 1997) was used, using similar GLM's to the other experiments (Equation [2]), and similar EMS tables (Table 4). The foliar tests each had 319 observations, while total height (10th year) and RCD each had 1137 observations. Linear contrasts were also calculated for the height and RCD data sets, using the last three of the four contrasts (Table 5). After running the ANOVA's for all the foliar nutrient element concentrations and contents, linear contrasts were calculated to compare and check for differences between harvest treatments. The last three contrasts will be used, as the reference/uncut state was not included in foliar sampling.

4.0 RESULTS AND DISCUSSION

4.1 CHANGES IN SOIL NUTRIENT RESERVES IN RESPONSE TO HARVEST INTENSITY

Timber harvesting on shallow soils has been the cause of concern for many years due to the removal of nutrients during clearcut harvesting. Although these concerns have triggered several extensive long-term studies (Morris 1997, Gordon *et al.* 2001), many intensive harvest treatments, such as full-tree harvesting, are still recommended practices on shallow soil, conifer dominated sites (OMNR 1997b). Since harvest treatments such as full-tree and whole-tree harvesting are the most intense and remove the most nutrients from the site, it is expected that these treatments will result in greatly reduced nutrient pools for several years after harvest. Removal of crown and forest floor biomass such as that seen in these harvest types has the potential to alter the biogeochemical cycle of the sites (Johnson *et al.* 1991b), thus compromising site fertility.

Soil nutrient reserves were evaluated across three sites by comparing and testing differences between the pre-harvest and post-harvest pool (8 years). Both organic and mineral horizons were tested, as both play integral roles in nutrient cycling. For example, organic horizon materials have a greater capacity to mineralize nutrient elements per unit mass than the mineral horizon, but mineral soil can store larger amounts of nutrients on a per unit area basis (Mahendrappa *et al.* 1986). All results are presented in $kg \cdot ha^{-1}$, with the exception of carbon which is presented in $T \cdot ha^{-1}$.

4.4.1 Organic Soil Horizon

Pre-harvest carbon and macro-nutrient pools varied across the study sites, and Table 6 provides an estimate of these pool sizes. Of the macro-nutrients examined, only nitrogen pre-harvest pools varied significantly ($p = 0.015$) across the study sites (Table 7), with pool sizes ranging from 730 - 1000 $\text{kg}\cdot\text{ha}^{-1}$ (Table 6).

Table 6. Pre-harvest pool sizes from the organic horizon across the three study sites (letters denote significant SNK results, $p < 0.05$).

Site	C	N	P	K	Ca	Mg
	$\text{T}\cdot\text{ha}^{-1}$	$\text{kg}\cdot\text{ha}^{-1}$				
1	28.91	736.1 **a**	14.22	66.04	190.5	66.06
2	38.84	1012.0 **b**	11.52	69.25	211.4	65.52
3	30.28	794.7 **a**	12.24	61.64	219.2	64.01

Table 7. P-values from the organic nutrient pool ANOVA, for both sampling periods (significant values are in **bold**, $p < 0.05$).

Pre-Harvest	C	N	P	K	Ca	Mg
Site (S)	0.0622	**0.015**	0.4570	0.6128	0.6109	0.9682

Post-Harvest	C	N	P	K	Ca	Mg
Site (S)	0.6703	0.4602	**0.0435**	0.4232	**0.0147**	**0.0404**
Harvest Treatment (H)	0.1667	0.0984	**0.0001**	**0.0001**	**0.0021**	0.2171
S*H	0.7948	0.8008	0.4815	0.8445	0.6234	0.7465

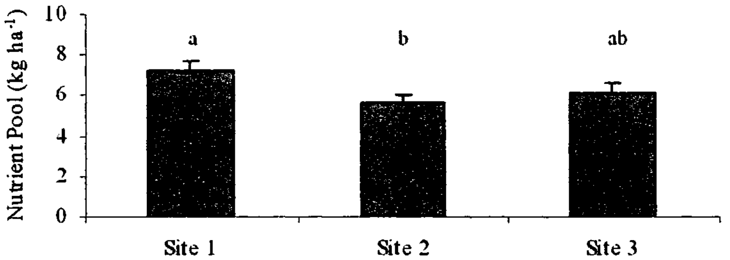
The pre-harvest site differences in pool sizes of nitrogen (Table 6) can be explained by the differences in the organic matter located on the sites. Site 1 and Site 3 have a moderately thin Fibrimor humus organic horizon, while Site 2 is characterized by a slightly deeper HumiFibrimor humus organic horizon (Duckert and Morris 2001). Humus type, according to Richards *et al.* (1985), is one of the most important factors affecting the amounts, forms, and mineralization/immobilization processes of nitrogen in forest soils. Forest humus horizons are recognized as being a major nutrient reservoir in boreal ecosystems (Krause *et al.* 1978).

This HumiFibrimor, or humus (H) organic horizon, typically is more decomposed than the Fibrimor (F) horizon. The H horizon is generally darker and moister, and made up of well-decomposed material whose origins are unidentifiable (Kimmins 1997). Birch (1958) adds that organic matter in the humus form accounts for the largest proportion of soil nitrogen. Research by Huang and Schoenau (1996) also found that the humified H horizon had the highest ammonium supply rates, followed by the F horizon, and then the L, or surface litter horizon. Several other studies, including those by Boone (1992) and Persson and Wiren (1995) have also found that the highest amounts of mineralized nitrogen are generally found on the lower forest floor horizons, such as the F and H horizons.

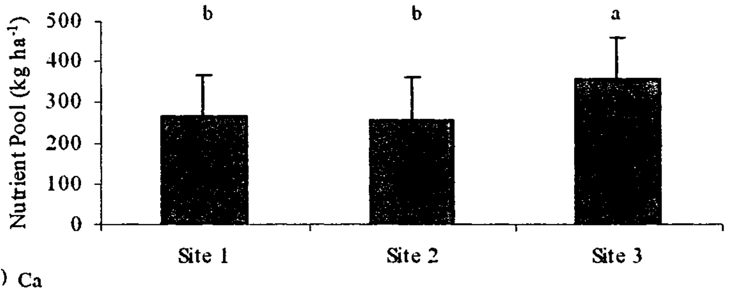
Although interactions were not a significant source of variation, main effects were found to be significant in several cases (Table 7). Phosphorus, calcium, and magnesium, all had significant tests for site (Figure 12), suggesting differential shifts in nutrient pool sizes have occurred after harvesting. For example, phosphorus pools were higher on Site 1, whereas calcium and magnesium were highest on Site 3, with SNK tests showing significant differences between sites (Figure 12). When comparing the harvest treatments using ANOVA testing, phosphorus, potassium, and calcium pools were significantly different across the treatments (Table 7). Both phosphorous and potassium pools have dropped substantially for all of the harvest treatments when compared to the uncut condition (Figure 13). Calcium, on the other hand, increased (Figure 13 c). Linear contrasts (as described in Table 5) revealed similar trends for these elements, with significant results for contrasts L_1 and L_3 (Figure 13).

Although carbon, nitrogen, and magnesium pools were found to be non-significant sources of variation by ANOVA testing (Table 7), linear contrasts were able to identify significant differences in L_3 for both carbon and nitrogen, and L_1 in regards to magnesium (Figure 14). A clear gradient is noticeable in all pools across the harvest treatments, with the largest occurring in the least intense treatments (chip and tree-length), and the lowest in the whole-tree treatment (Figures 13 and 14). This pattern was expected, as higher biomass removals leave less nutrient bearing slash on the site, and as such, are anticipated to contribute less nutrients to the soil nutrient reserves. No linear contrast results were significant for two of the four linear contrasts, and thus, no differences were found between the full-tree and tree-length harvesting treatments (L_4), or between the chip and tree-length treatments (L_2) (Figures 13 and 14).

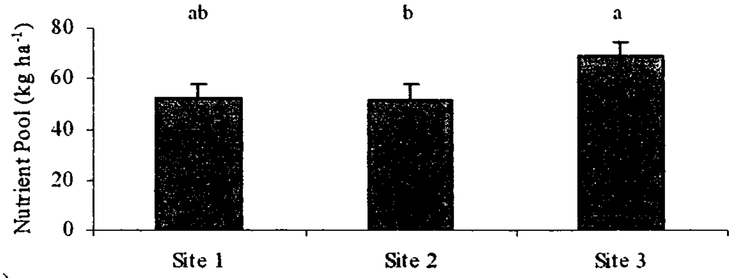
Oddly, calcium and magnesium did show larger pool sizes after blading had occurred, compared to the uncut stands (Figures 13 c and 14 c). This is an unusual result, and while unique to this project, data were checked for accuracy and uniformity, and were included after no sampling or inputting errors could be detected. However, it is expected that since blading removes the organic horizon, a reduction in pool size would occur.



(a) P



(b) Ca



(c) Mg

Figure 12. Post-harvest organic nutrient pools across sites for phosphorus (a), calcium (b), and magnesium (c). Different letters denote significant site differences, based on the SNK tests ($p < 0.05$).

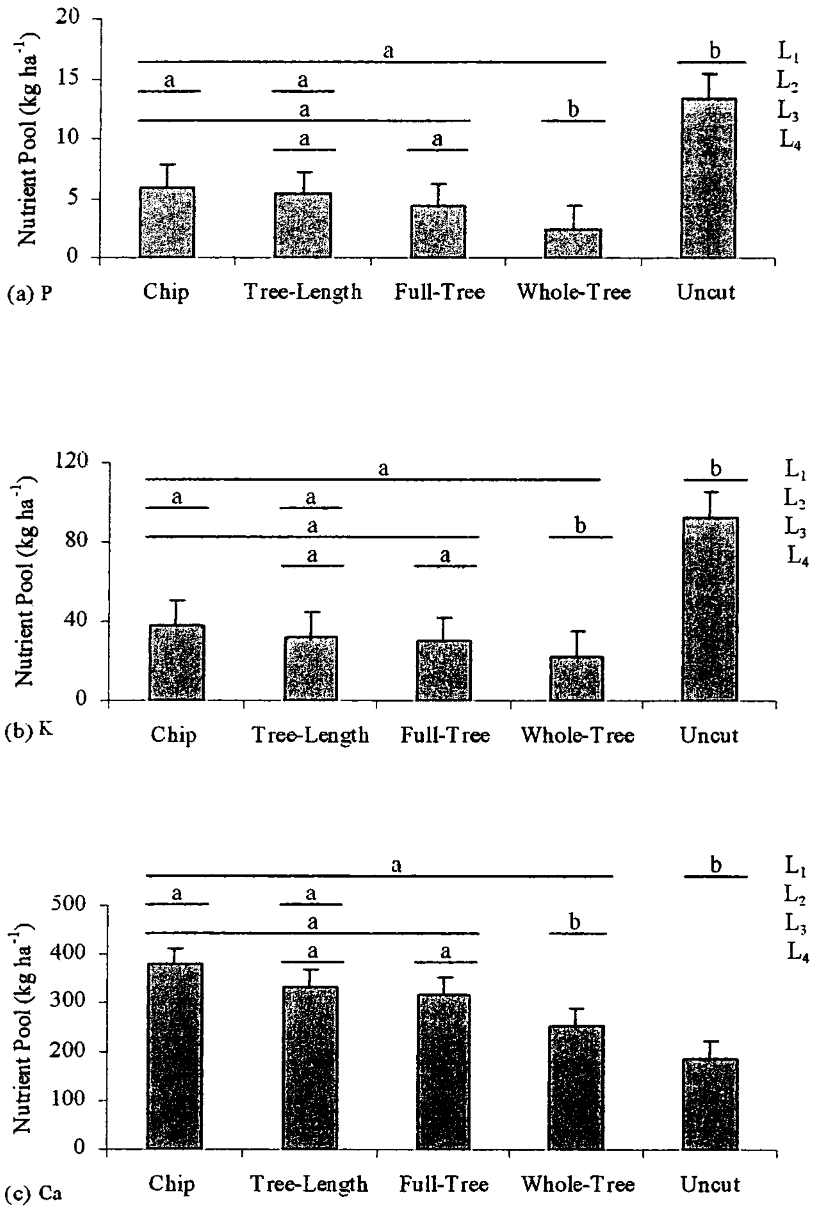


Figure 13. Post-harvest organic nutrient pools with linear contrast comparisons for phosphorus (a), potassium (b), and calcium (c). Different letters over the underlined groupings denote significant differences for the various linear comparisons ($p < 0.05$).

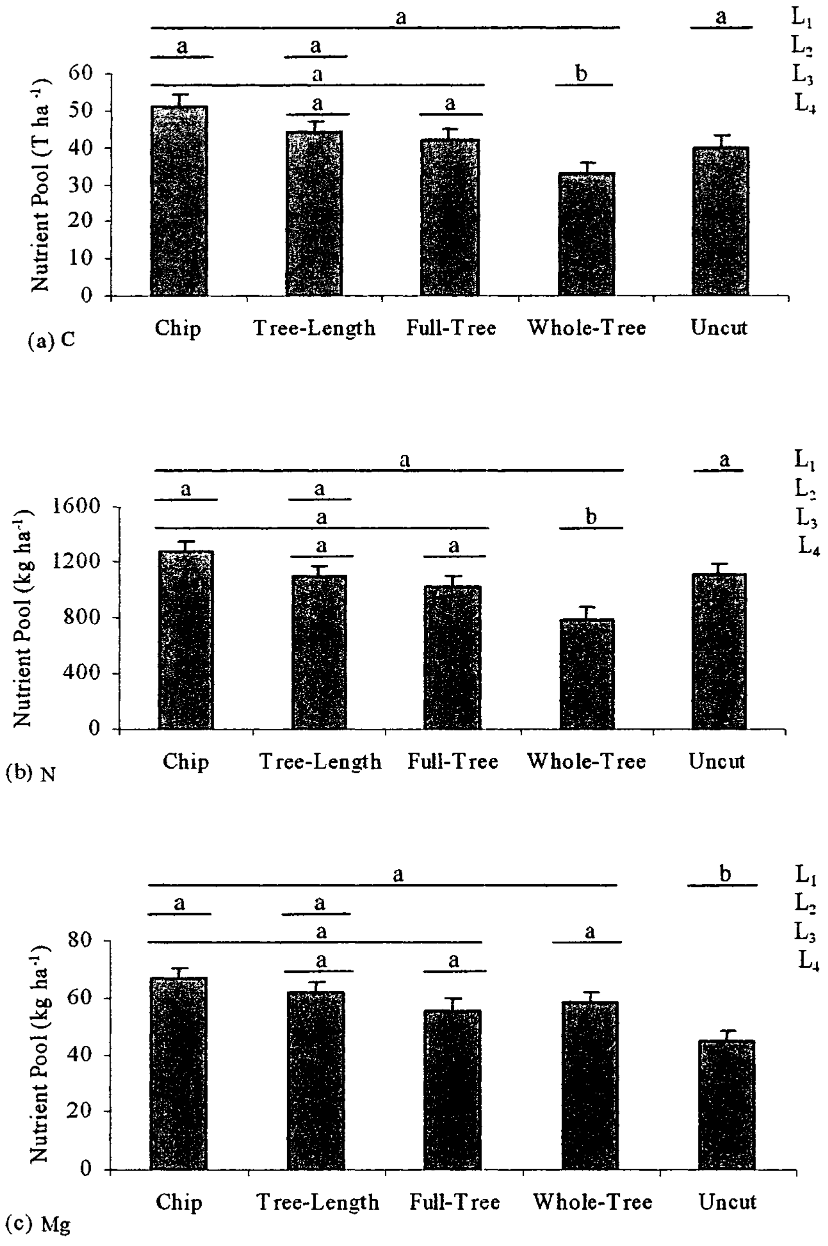


Figure 14. Post-harvest organic nutrient pools across harvest treatments for carbon (a), nitrogen (b), and magnesium (c). Different letters over the underlined groupings denote significant differences for the various linear comparisons ($p < 0.05$).

Phosphorus and potassium decreased after harvesting (Figure 13), while calcium and magnesium significantly increased (Figure 14), with greater nutrient reserves of both phosphorous and potassium in the uncut stand (Figure 13 a, b). Bradley *et al.* (2001) also found that potassium concentration was higher in old stands than in harvested plots, adding that potassium is very mobile and is easily leached from living and decomposing plant tissues compared to other nutrients. Potassium is also readily lost because of its relatively low retention by processes such as cation exchange (Likens *et al.* 1970, Gosz *et al.* 1976). Romanowicz *et al.* (1996) suggest that several nutrient cations including potassium, calcium, and magnesium are lost from forested ecosystems by harvesting through biomass removal, post-harvest treatments, and enhanced leaching. While potassium did decrease, both calcium and magnesium increased in all treatments after harvesting, following the pattern of harvest intensities, with chip and tree-length having greater pools.

Phosphorus is rapidly taken up by growing seedlings, as it is needed in relatively large amounts and is essential for plant growth (Meyer *et al.* 1997). Most of the readily available phosphorus is found in the forest floor (Kimmins *et al.* 1985), as it is primarily recycled by microbial decomposition of organic matter such as litter, and by plant uptake (Cade-Menum *et al.* 2000). It is also present in humus, mainly in the organic form, of which only a small fraction is soluble (Bradley *et al.* 2001). Thus, since uncut stands often have larger and deeper organic matter pools, it makes sense that these elements are found in greater amounts in these stands compared to harvested stands, which generally had thinner forest floors.

Calcium (Figure 13 c) and magnesium (Figure 14 c) had greater reserves on the harvested sites compared to the uncut stand (L_1), which could be attributed to the litter inputs and any decomposing slash that might still remain, even eight years after harvest. Calcium, and to some extent magnesium, are found in recalcitrant plant tissues (Morris 2000), which could explain the increases. Calcium is also relatively immobile when in litter and organic matter, where it is found mainly as a complex within plant cell walls, which makes foliage litter an important source of calcium in forest floors (Bradley *et al.* 2001). Hendrickson *et al.* (1989) found levels of these nutrients to be high in tree-length sites because of the logging slash, which correlates to the high reserves on harvest treatments that had the largest amounts of slash remaining on the site, such as the tree-length and chipped treatments.

With the exception of magnesium, blading caused organic nutrient pools for all elements to be much smaller, compared to pools associated with other harvesting types where the forest floor was not removed (L_3 - Figure 13 and 14). This result is not unexpected. This method effectively removes the forest floor and associated nutrients. It is important to note that this was an experimental treatment, and is not an operational practice in Ontario (Morris, *pers. comm.* March 7, 2006), and was incorporated in the design as an extreme example of biomass removal.

Full-tree harvesting, often the treatment that generates the most concern due to increased biomass removals, did not result in lower organic nutrient pools when compared to the less intense tree-length treatment (L_4 - Figure 13 and 14). In fact, the pools associated with these two treatments are quite similar. While this treatment has been suggested as having a greater potential for negative impact on organic matter and nutrient cycles than stem-only harvesting, due to the additional removals of live crown biomass (Aber *et al.* 1978, Hendrickson *et al.* 1989, Johnson *et al.* 1991a), this paradigm was not supported by this study.

4.1.2 Mineral Soil Horizon

Significant differences were seen in the organic horizon after harvesting had occurred, so it might be expected that the mineral horizon would experience similar responses, but no significant effects were found in either the pre- or post-harvest ANOVA tests (Table 8). The mineral horizon pools did not experience a significant change in size, as they were constantly being recharged by the inputs from the decomposing upper organic horizons. However, the nitrogen and potassium pools, although not significantly different, were consistently higher across all three sites in post-harvest measurements. Romanowicz *et al.* (1996) also found increases in potassium in mineral soil after harvesting had occurred.

Table 8. P-values from the mineral nutrient pool ANOVA, for both sampling periods (significant values are in **bold**, $p < 0.05$).

Pre-Harvest	C	N	P	K	Ca	Mg
Site (S)	0.1247	0.1547	0.2004	0.6693	0.4027	0.4328
Post-Harvest	C	N	P	K	Ca	Mg
Site (S)	0.2491	0.3297	0.3434	0.6146	0.2353	0.5424
Harvest Treatment (H)	0.0781	0.2746	0.1757	0.1493	0.366	0.1165
S*H	0.9536	0.993	0.9908	0.9825	0.902	0.9497

The harvest treatment responses in the mineral nutrient pools were also compared using the linear contrasts outlined in Table 5. In this case, no contrasts were found to be significant. The lack of any significant tests in both the ANOVA and linear contrasts indicated that harvesting may not affect the mineral soil reserves in the same manner or magnitude as it does in the organic horizons, or at least within the time frame of the current study.

4.2 DIFFERENCES IN AVAILABLE NUTRIENT POOLS IN RELATION TO HARVEST INTENSITY

While boreal forest nutrient pools can be large (*e.g.,* estimated in this study at 1360 - 1860 $kg \cdot ha^{-1}$ for nitrogen), only a small portion of these large reserves is turned over annually and made available for plant uptake. The cation resins have provided an index of nutrient availability, which differs after harvest, and may be influenced by harvest intensity. Whole-tree harvested sites that have had the majority of organic matter removed would be expected to have smaller available nutrient pools, especially when compared to the other treatments which have varying amounts of slash and leaf litter left remaining on the site after harvesting has occurred. Organic and mineral soil horizon results are shown in Table 9, both with growing season values (June - October) and overwinter values (November - May). These data will allow an estimate of spring flush contributions to the available nutrient pool.

4.2.1 Organic Soil Horizon

In this horizon, site significantly affected both potassium and calcium availability; while harvest treatment only significantly affected ammonium (Table 9). Available nutrient pools of potassium were greatest on Site 1 (4 kg·ha^{-1}·growing season^{-1}), with Site 2 and Site 3 having smaller and similar pools (2 kg·ha^{-1}·growing season^{-1}) (Figure 15). In contrast, availability of calcium was greatest on Site 3 (8.5 kg·ha^{-1}·growing season^{-1}), with Site 1 and Site 2 having smaller available pools (< 4 kg·ha^{-1}·growing season^{-1}) (Figure 16).

Table 9. P-values from the organic resin ANOVA, for both growing season and overwinter (significant values are in **bold**, $p < 0.05$).

Growing Season	NH_4^+	K^+	Ca^{2+}	Mg^{2+}
Site (S)	0.665	**0.0009**	**0.0103**	0.1964
Harvest Treatment (H)	**0.0017**	0.0806	0.0955	0.0828
S*H	0.898	0.103	0.2568	0.382

Overwinter	NH_4^+	K^+	Ca^{2+}	Mg^{2+}
Site (S)	0.1448	**0.003**	**0.0166**	0.3141
Harvest Treatment (H)	0.301	0.8996	0.8204	0.4647
S*H	0.6686	0.971	0.4129	0.3141

The difference in available calcium pools across the study sites could be explained by the site differences that were highlighted both in the site descriptions and in Table 1. Site 3 has a slightly deeper organic horizon, with a higher moisture regime (Table 1). Krause and Ramlal (1987) found increased calcium values on sites with higher soil temperatures and moisture, and added that while soil temperature might not

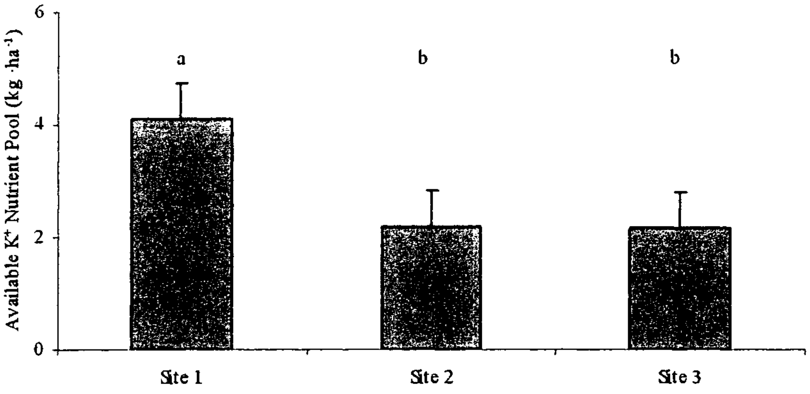


Figure 15. Available potassium nutrient pools during the growing season for the organic horizon, depicting significant differences between sites. Different letters denote significant site differences, based on the SNK tests ($p < 0.05$).

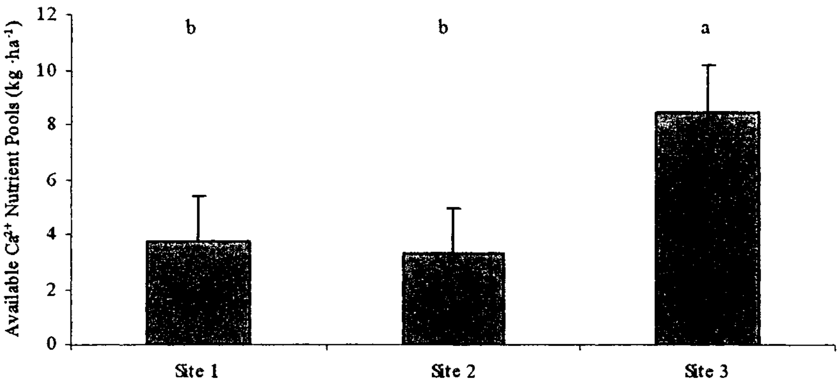


Figure 16. Available calcium nutrient pools during the growing season for the organic horizon, depicting significant differences between sites. Different letters denote significant site differences, based on the SNK tests ($p < 0.05$).

vary that much across sites which are close to one another, soil moisture can vary considerably. Pre-harvest differences in moisture regimes (MR 2 - 4), are likely to be maintained or even enhanced post-harvest, therefore, affecting nutrient availability.

Potassium availability could be higher on Site 1 as a result of the presence of trembling aspen, which comprised 10 % of the pre-harvest stand composition (Table 1). This deciduous component provides nutrient rich foliar litter that may enhance nutrient cycling on the site. It has been demonstrated that deciduous leaves, such as that from aspen, are more easily decomposed and digested by micro-organisms than acidic conifer litter (Kimmins 1997). Any aspen suckering occurring post-harvest may also be important in contributing nutrients such as potassium and calcium back into the system (Morris 2003).

With available calcium pools nearly doubling those of potassium, once again, the mobility of the latter is asserted. Compared to potassium, calcium is more tightly held on cation exchange sites, and is relatively abundant in most soils as a result (Meyer *et al.* 1997). Ammonium, on the other hand, is weakly held on cation exchange sites, which can be seen in the harvest treatment results (Figure 17), and the small range in the available nitrogen pools across treatments (0.06 - 0.21 $\mathrm{kg \cdot ha^{-1} \cdot growing\ season^{-1}}$). These pools were small, even though the nitrogen nutrient reserve pools ranged from ~790 $\mathrm{kg \cdot ha^{-1}}$ after whole-tree and ~1300 $\mathrm{kg \cdot ha^{-1}}$ after chip treatments (Figure 14 b).

Other studies have found limitations of ion exchange resins in reflecting the actual soil nitrogen supply through the growing season (Stark and Hart 1997, Driscoll *et al.* 1999). Instead, it is proposed that the resins only give a static measure of available soil nitrogen at a single point in time (Hangs *et al.* 2004), thus underestimating the total available pool. Kjonaas (1999) also tested nitrogen stability with Amberlite IR 120 ion exchange resins, and found that resins that had dried contained less ammonium than resins that remained moist, suggesting that drying may cause an irreversible absorption of ammonium in the cation exchange potential of the resins. The low amounts of ammonium measured by the resins could also be the result of increased nitrification, which can occur after harvest (Lindo and Visser 2003). Unfortunately, the anion component of this experiment was not completed, and therefore, no direct link or comparison can be made at this time.

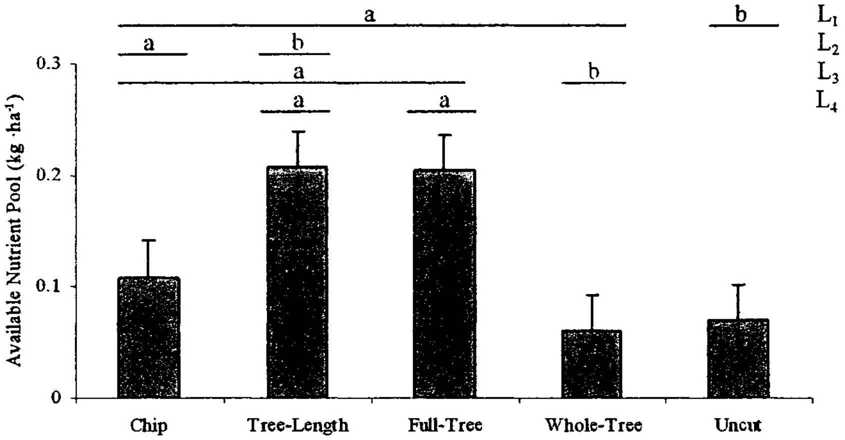


Figure 17. Available ammonium nutrient pools during the growing season for the organic horizon, depicting significant differences between harvest treatments. Different letters over the underlined groupings denote significant differences for the various linear comparisons ($p < 0.05$).

Studies by Carlyle and Malcolm (1986), however, using 20 grams of the IR 120 resins in spruce stands found, *in situ* for periods of 120 and 200 days, that the resins yielded between 10 - 20 and 10 - 17 μg N $\cdot g^{-1}$, respectively. The resins in this study were the same and yielded much lower amounts of ammonium (0.457 - 1.786 $\mu g \cdot g^{-1}$), but employed much smaller amounts of resin (1 gram). Due to the low amount of resin/exchange sites, the stronger bonds formed by calcium, and the generally high abundance of calcium in the soil solution, the exchange sites might have been differentially "saturated" in favour of calcium. More resin may have been needed, providing more exchange sites to allow other nutrients to attach to the exchange sites without being displaced by calcium ions. It does seem reasonable, however, to consider the resin results as an "index" of availability to compare across harvest treatments.

Linear contrasts were found to be significant except for L_4, which compares full-tree versus tree-length harvesting. This indicates that, although reduced, the slash loading associated with full-tree harvesting is sufficient to generate equivalent available nutrient levels when compared to the tree-length treatment. While the first three contrasts were significant for ammonium (Figure 17), only the first or third contrast was significant for calcium and magnesium, and potassium, respectively (Figure 18). These elements were tested using the linear contrasts after ANOVA testing found no significant sources of variation between treatments (Table 9).

Generally, availability increased after harvest for ammonium, calcium, and magnesium (L_1), with greater ammonium availability after tree-length harvesting when compared to chipping (L_2). Blading generated the lowest nutrient availability for both ammonium and potassium (L_3).

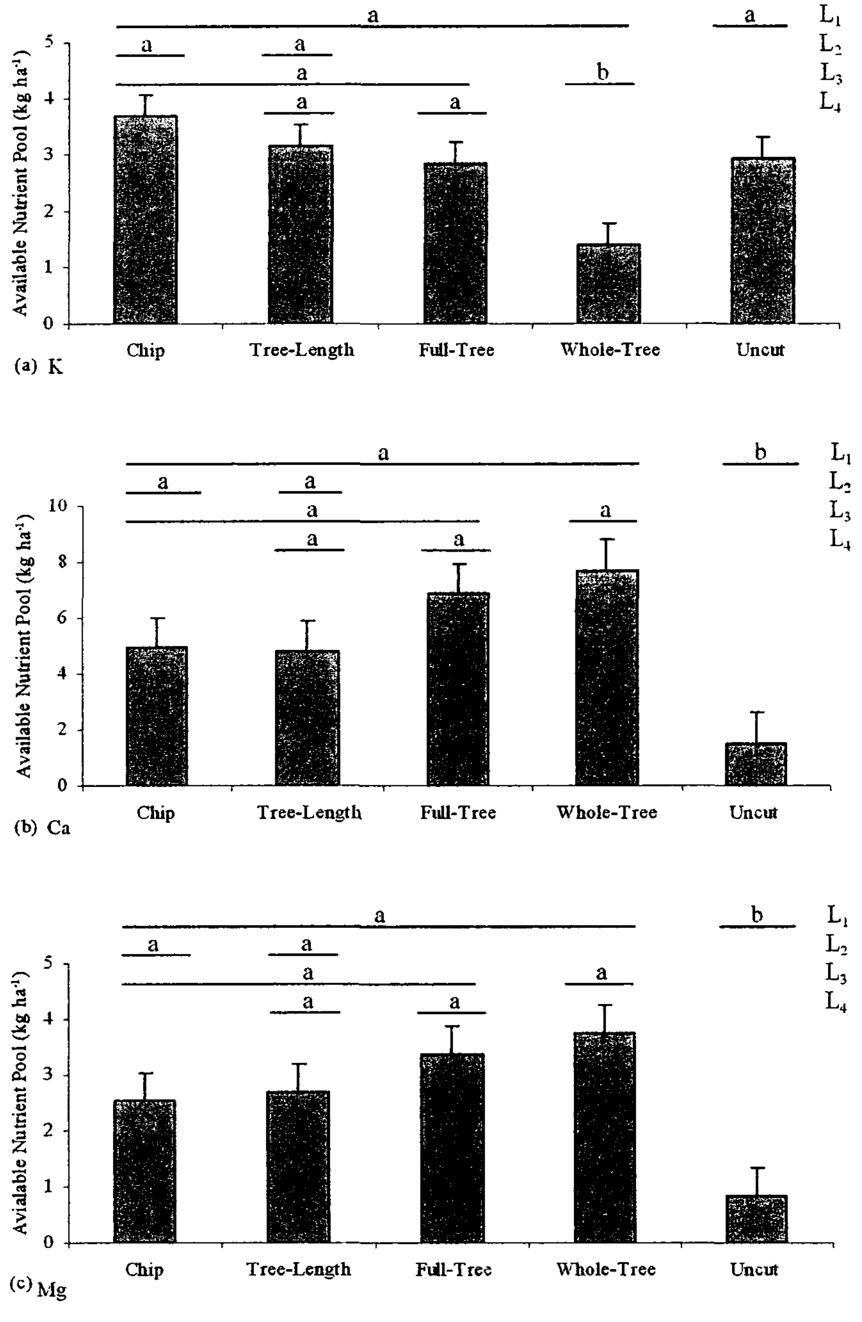


Figure 18. Post-harvest available organic nutrient pools during the growing season, depicting significant differences between harvest treatments for potassium (a), calcium (b), and magnesium (c). Different letters over the underlined groupings denote significant differences for the various linear comparisons ($p < 0.05$).

In other studies, nitrogen levels have been found to increase following harvesting, even after five to ten years has passed (Paul and Clark 1989). The increase was mainly attributed to increased organic matter decomposition (Paul and Clark 1989). The addition of live leaves, which have a lower C:N ratio than senescing or dead leaves, could also be an important factor (Vitousek 1981). In ten-year-old cedar (*Thuja* spp.) and hemlock (*Tsuga* spp.) stands, Chang *et al.* (1995) did report lower amounts of available nitrogen in the forest floor than on three-year-old sites. This difference was accounted for through greater competition of available nitrogen from both the microbial community and the vigorous growth of competing understory vegetation. This finding indicates that the year of testing post-harvest nutrient availability is also an important consideration due to the dynamic nature of this flux.

As previously noted, chipping resulted in lower ammonium availability than the tree-length treatment (Figure 17 - L_2). Considering both of these treatments yield the same amount of slash, the slash composition appears to have a larger effect on mineralization/immobilization processes than other factors. Chipping could result in nitrogen deficiencies over time through immobilization, induced by slow decomposition and high C:N ratios (White and Harvey 1979). For example, Tappeiner (1971) estimated that less than 10 % of jack pine chips are decomposed after several seasons.

Tree-length harvesting, while having the ability to provide an immediate source of cations on site by leaving rapidly decomposing components, such as tree crowns which included leaves and small twigs (Abbott and Crossley 1982), can also immobilize nutrients. The small branches left on the site following this treatment, in addition to the roots, which are also left after the chip and full-tree treatments, represent a longer-lived source of nutrients and organic matter, and could be responsible for the increased pools almost ten years since harvest. These components tend to initially immobilize some nutrients during the earlier stages of decomposition, but later release them (Abbott and Crossley 1982, Fahey *et al.* 1988). This delayed release may limit the nutrient losses following harvest (Knoepp and Swank 1997).

Overwinter resin results showed both potassium and calcium differences across the study sites (Table 9). These results are similar to those obtained for the growing season period, with potassium having the greatest amount of availability on Site 1 (Figure 19), and calcium on Site 3 (Figure 20). Growing season, overwinter, and annual available pools are shown across sites (Figure 21 a - d) and treatments (Figure 22 a - d). Site and pool size differences are shown between the growing season and the overwinter period. For ammonium, most of the annual available nitrogen results from the overwinter period, particularly on Site 2 and Site 3 (Figure 21 a).

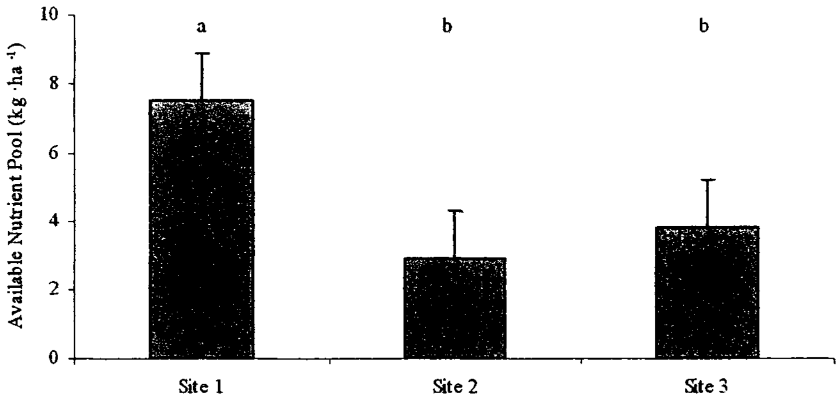


Figure 19. Available potassium nutrient pools during the overwinter period for the organic horizon, depicting significant differences between sites.

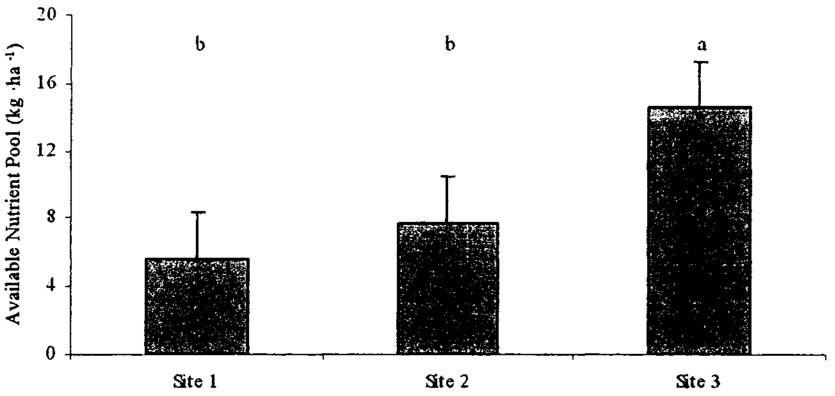


Figure 20. Available calcium nutrient pools during the overwinter period for the organic horizon, depicting significant differences between sites.

Annual available potassium was greatest on Site 1 (Figure 21 b), probably related to inputs from trembling aspen found on the site. Calcium and magnesium availability was greatest on Site 3. In most cases, the overwinter values are greater than those calculated for the growing season, indicating that the spring flush of available nutrients makes an important contribution to the annual available pools.

Harvest treatment response in the ammonium available pool was greatest in both the tree-length and full-tree treatments (Figure 22 a). The whole-tree harvest treatment yielded the greatest availability for both calcium and magnesium in both periods, but the least amount of potassium and ammonium. Krause and Ramlal (1987) also found that potassium was constantly lower in their resin studies on whole-tree harvested sites than other harvest treatments, such as full-tree.

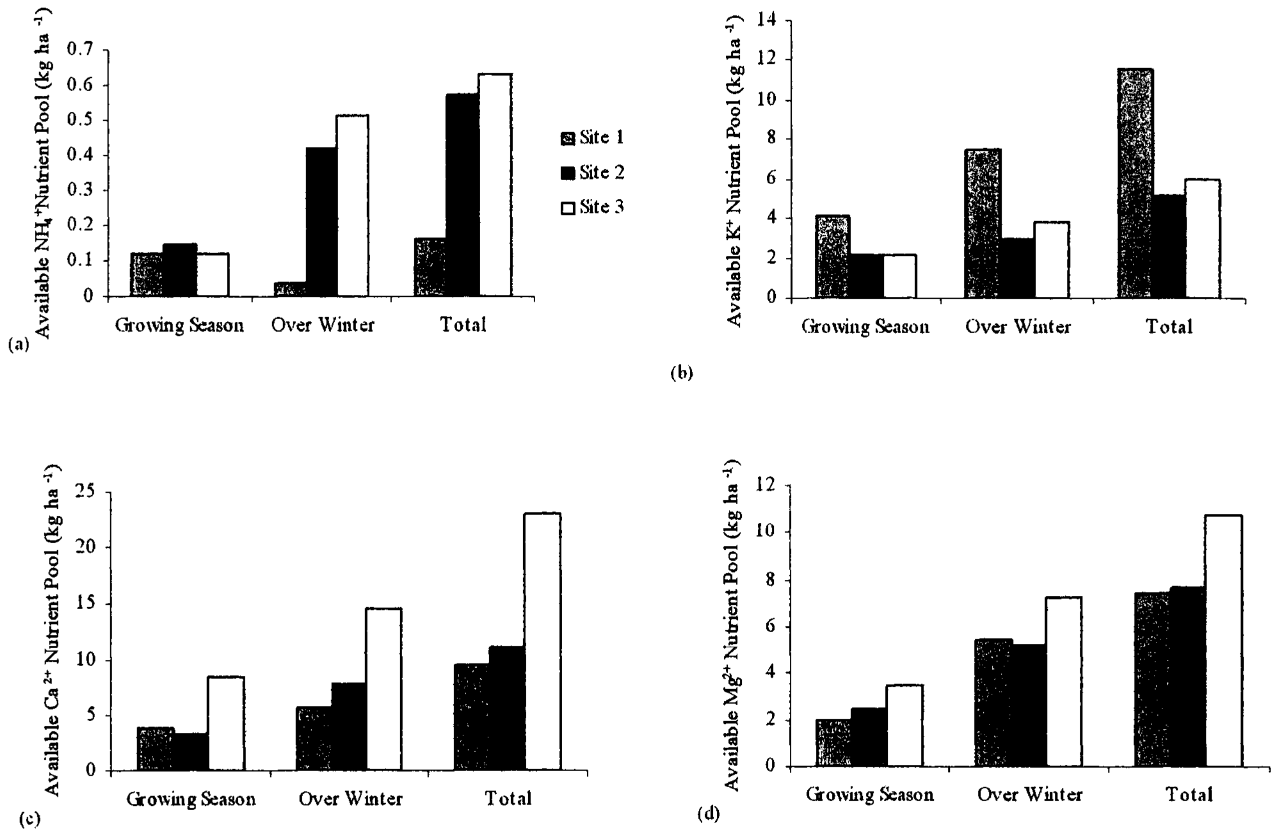


Figure 21. Available nutrient pools during the growing season and overwinter period for the organic horizon across sites for ammonium (a), potassium (b), calcium (c), and magnesium (d).

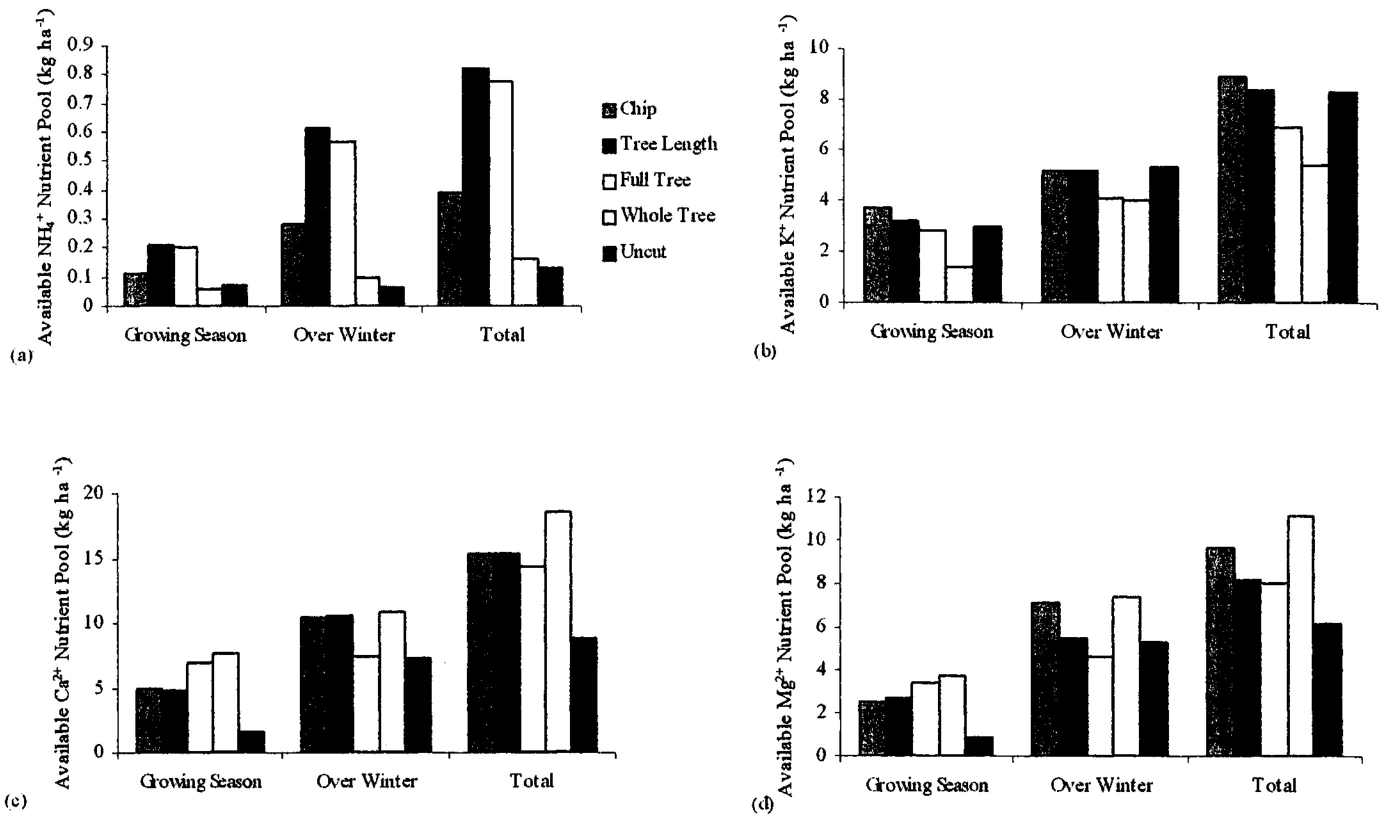


Figure 22. Available nutrient pools during the growing season and overwinter period for the organic horizon across harvest treatments for ammonium (a), potassium (b), calcium (c), and magnesium (d).

Overall, availability for nutrients such as ammonium, calcium, and magnesium after tree-length and full-tree harvesting were not significantly different (L_4 - Figure 17 and 18), resulting in similar annual available pools (Figure 22). One might expect that due to the high degree of biomass and organic matter removal associated with whole-tree harvesting that this harvest treatment would have the lowest available pools for all nutrients. The significantly lower ammonium availability after whole-tree harvesting could be a result of low organic matter levels, in conjunction with the effect of soil moisture regime on ammonium values (Binkley 1984a). Whole-tree harvested plots may exhibit drier soils due to increased surface soil temperatures, as well as increased water runoff and evaporation. As noted earlier, resin ammonium values do not necessarily reflect ammonium content, but rather the effect of soil water regime (Gibson 1986), so it is important to use these estimates merely as an index of soil nutrient availability.

Seasonal effects are shown in the variability of the soil nutrient availability across the sites and treatments (Figures 21 and 22, respectively). Greater nutrient availability during the overwinter period is a result of the resin bags that were *in situ* during this time being exposed to larger amounts of water from both autumn rain, and winter snow melt. Other resin studies, such as those by Lundell (1989) also found that overwintered bags adsorbed larger amounts of ions than those not overwintered. Lower summer concentrations could be a result of the resins being ineffective competitors for nutrients against roots, mycorrhizal hyphae and other soil micro-organisms (Lundell 1989). Lower soil moisture levels during this period could also lead to a lack of ion sorption by the resins.

The growing season linear contrasts (Figure 18) as well as the available pool graphs for both periods (Figure 22), consistently show that harvesting resulted in increased availability for ammonium, calcium, and magnesium, compared to the uncut stand (L_1). It is possible that potassium availability did not increase after harvesting due to its high mobility compared to divalent ions such as calcium and magnesium, and poor retention on the exchange sites. Although not measured in this study, the low recovery of potassium by the resins could reflect greater losses in the soil through leaching or assimilation by vegetation compared to calcium or magnesium (Olsson *et al.* 1996). Potassium is readily lost from both living and dead biomass, also contributing to losses (Romanowicz *et al.* 1996). Morris (1997) suggests that potassium lost due to harvesting, especially from whole-tree harvesting, may not be replaced over a rotation on shallow soil sites in Ontario. Uncut stands also have lower nutrient availability because prior to cutting, gross mineralization is assumed to be equal to immobilization plus plant uptake (Vitousek 1981), and following cutting, mineralization and immobilization increase while plant uptake decreases.

Canopy removal through harvesting can increase the amount of solar radiation and precipitation that reach the soil surface, thereby, increasing soil temperature and moisture and increasing nutrient mineralization (Keenan and Kimmins 1993). While nutrient availability in this study increased, Lindo and Visser (2003) found ammonium in forest floors to be lower in clearcut treatments three years after harvest compared to uncut stands. Schmidt *et al.* (1996) also found that nutrients, especially nitrogen, decrease in the forest floor after harvesting has occurred. This response, however, is not consistent, as other studies have reported increases in nutrients after harvesting (Vitousek and Matson 1985, Frazer *et al.* 1990), while others showed no significant differences between cut and uncut forests (Maynard and MacIssac 1998). Collectively, this may suggest that no definitive negative impact on long-term site productivity can be expected (Knoepp and Swank 1997).

Once again, the removal of the forest floor associated with the whole-tree harvesting treatment significantly reduced the amount of available ammonium and potassium, when compared to the other harvest treatments (L_3) (Figure 18). On the other hand, calcium and magnesium availability was greater after whole-tree treatments, which could be a result of the retention of these divalent ions (Olsson *et al.* 1996). Similar results were reported by Frey *et al.* (2003) in a white spruce-dominated forest in Alberta, where blading had increased calcium and magnesium, but depleted potassium. Frey *et al.* (2003) and Verburg *et al.* (1999) related the increases to enhanced mineralization, due to increased temperatures in the exposed upper mineral soil and organic matter remaining on the site. Generally, the low nutrient availability associated with the whole-tree treatment is accounted for by limited mineralization due to the small amount of organic material remaining (F or H horizon).

The resin results have not only provided indices of the availability of nutrients such as ammonium and potassium (based on concentration levels, not soil mass), but have also shown the effect, or lack there of, that harvesting has on available nutrient pools. Again, contrasts were significant in cases where harvesting was compared to the uncut stand, and after whole-tree harvest treatments, similar to earlier contrasts which compare total nutrient pools. The available pool contrasts also saw one example of significance for the chip versus tree-length harvesting contrast, but no significant contrasts for the full-tree versus tree-length harvesting comparisons. As noted earlier, full-tree harvesting has been the subject of concern for many years regarding its potential for detrimental nutrient removals. The current results, however, clearly indicate that there is no significant difference in the available nutrient status for the shallow-soiled sites used in this study.

4.2.2 Mineral Soil Horizon

Resins bags in the mineral horizon were placed at a depth of 10 cm to obtain an index of available nutrients from within the rooting zone. Most nutrients in the mineral horizon are believed to be leached if not used by plants or retained by exchange sites, however, due to inputs from the decomposing organic horizon, the pool is considered to be relatively stable over time (Morris, *pers. comm.* September 28, 2005). This was the case for the total pools, but regardless of this steady recharge, available mineral pool concentrations (as measured by the resins) are expected to be lower than the organic horizon because of plant uptake by roots and lower CEC values.

ANOVA results over the growing season for the mineral horizon available pool (Table 10) identify at least one significant source of variation for each macro-nutrient. Only ammonium was significantly affected by the Site*Harvest Treatment interaction. It should be noted that the p-value for the interaction was 0.0152 (Table 10), which can be considered to be a high value. As a result, it can be interpreted that the interaction is subtle, and finding some sound ecological significance rather than just sampling variability can generally be difficult. However, it appears that ammonium increased for Site 1 thru 3 under full-tree harvesting, but peaked on Site 2 under tree-length harvesting (Figure 23). This peak could be a result of the nutrient inputs from remaining litter resulting from tree-length harvesting, combined with the HumiFibrimor humus organic horizon on Site 2. The differences between harvest treatment response across sites are subtle, and are simply a shift in tree-length and full-tree harvesting, which have the higher ammonium values.

Table 10. P- values from the mineral horizon resin ANOVA, for both growing season and overwinter (significant values are in **bold**, $p < 0.05$).

Growing Season	NH_4^+	K^+	Ca^{2+}	Mg^{2+}
Site (S)	**0.0097**	0.0711	**0.0068**	**0.0054**
Harvest Treatment (H)	**0.0002**	**0.0005**	0.1905	0.1508
S*H	**0.0152**	0.4908	0.2477	0.1281
Overwinter	NH_4^+	K^+	Ca^{2+}	Mg^{2+}
Site (S)	0.4085	0.15	0.0842	0.2488
Harvest Treatment (H)	0.662	0.1759	0.9306	0.7465
S*H	0.556	0.8459	0.4806	0.148

Calcium and magnesium were both significantly affected by site (Table 10), with Site 3 again having the largest available pool for both elements (Figures 24 and 25), an occurrence which could be due to the higher moisture regime that is found on that site, which would influence post-harvest moisture conditions to also be high. Both ammonium and potassium were significantly affected by harvest treatment (Table 10), with availability higher after both full-tree and tree-length harvesting, with the smallest

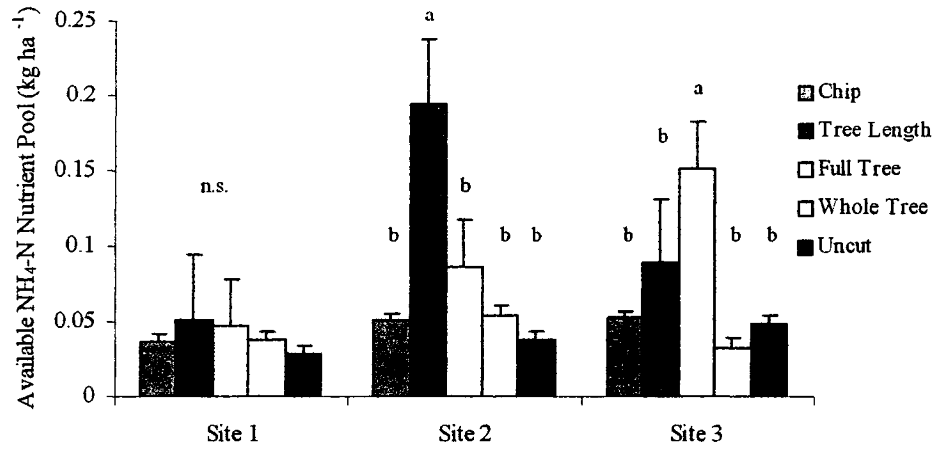


Figure 23. Available ammonium nutrient pools during the resin growing season. Results depict a Site*Harvest Treatment interaction in the mineral horizon. Different letters denote significant differences, based on the SNK tests ($p < 0.05$).

available pool after whole-tree harvesting (Figure 26 and 27). The increase in potassium could be a result of live litter inputs into the organic horizon, and the high mobility of potassium ions, which cycle through vegetation and soil as an unbound ion (Bradley *et al.* 2001). Linear contrasts did not find any additional sources of variation not already detected through the initial ANOVA testing. The first three contrasts were significant for ammonium (Figure 26), with the last three contrasts significant for potassium (Figure 27). Similar to the organic horizon contrasts, no overwinter contrasts were found to be significant for the mineral horizon.

Consistent with the organic horizon results, the harvest treatments provided greater available ammonium pools than the uncut stands (L_1) (Figure 26). In all likelihood, this increase was a result of increased mineralization that typically occurs after harvesting. Both ammonium and potassium availability were reduced on the chipped treatment plots when compared to tree-length harvesting (L_2). The lower

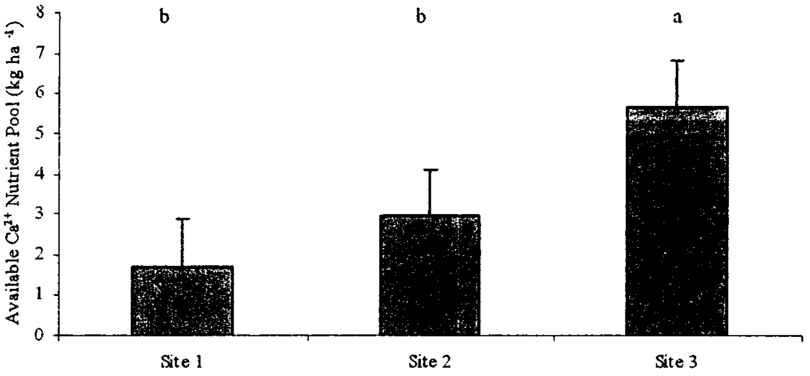


Figure 24. Available calcium nutrient pools during the growing season for the mineral horizon, depicting significant differences between sites. Different letters denote significant site differences, based on the SNK tests ($p < 0.05$).

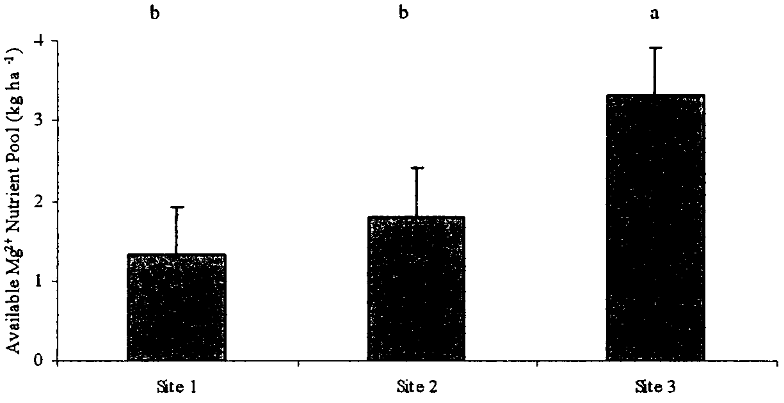


Figure 25. Available magnesium nutrient pools during the growing season for the mineral horizon, depicting significant differences between sites. Different letters denote significant site differences, based on the SNK tests ($p < 0.05$).

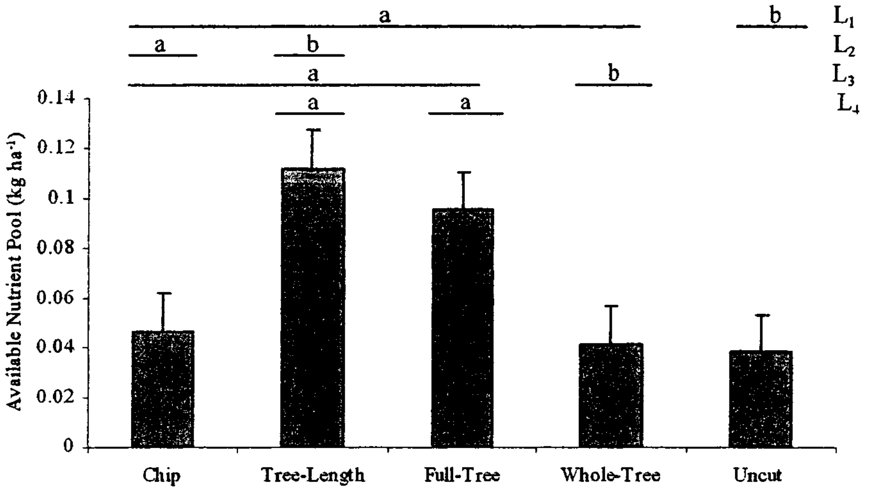


Figure 26. Available ammonium nutrient pools during the growing season for the mineral horizon. Significant harvest treatment effects are illustrated using linear contrast comparisons ($p < 0.05$).

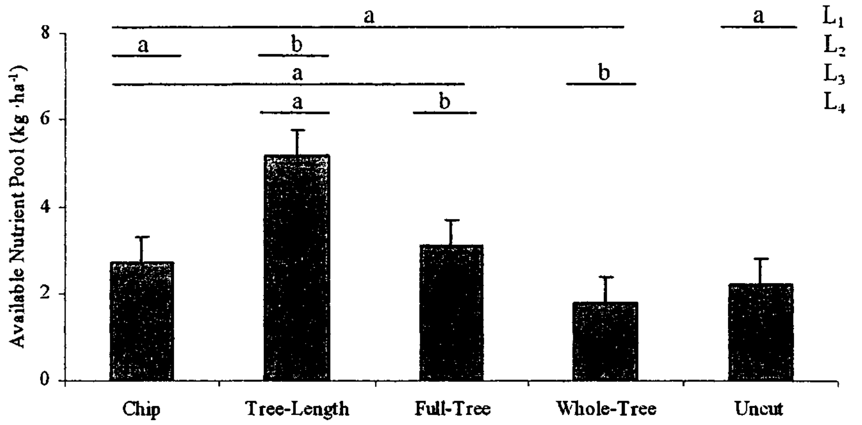


Figure 27. Available potassium nutrient pools during the growing season for the mineral horizon. Significant harvest treatment effects are illustrated using linear contrast comparisons ($p < 0.05$).

amounts of ammonium could be attributed to the high C:N ratios of the chips, and while the organic horizon showed increased values of potassium after chipping, losses in the mineral horizon could be associated with the inherent mobility of potassium, and its poor retention on exchange sites (Bradley *et al.* 2001). Whole-tree harvesting also significantly reduced the availability of these two elements in the mineral horizon compared to the other types of harvesting (L_3), and was comparable to the uncut treatment, a result that is due to the increased removals associated with this treatment.

Of all the contrasts that were calculated thus far, only potassium had a significant test for the full-tree versus tree-length comparison (L_4), from the mineral horizon during the growing season (Figure 27). In this case, tree-length harvesting resulted in greater potassium availability than did full-tree harvesting, suggesting a potential impact on the level of available potassium in the mineral horizon. Belanger *et al.* (2003) also reported higher exchangeable potassium concentrations in mineral soil after tree-length harvesting. In addition, Olsson *et al.* (1996) described findings showing that full-tree harvesting resulted in lower CEC and pools of exchangeable ions, such as potassium, than did tree-length harvesting. This element is released quickly from decomposing slash, has high mobility, and makes a high contribution to overall ionic activity in the mineral soil compared to other base cations (Edmonds 1987, Fahey *et al.* 1991, Staaf and Olsson 1994). These factors may explain the absence of a treatment effect on other elements (*i.e.*, Ca, Mg).

Overall, tree-length harvesting had the least impact on the available nutrient pools of this site type, and, as expected, whole-tree harvesting had the greatest impact. Tree-length harvesting is recommended on this site type (OMNR 1997a), and while full-tree harvesting is not recommended on very shallow soils (< 20 cm of organic and mineral soil), the results presented in this study have shown that there is little difference between tree-length and full-tree harvesting from an available nutrient perspective, particularly when combining the organic and mineral soil horizons.

Comparison of growing season, overwinter, and annual available pools for site (Figure 28) and harvest treatment (Figure 29) suggested the overwinter period contributed greater amounts of available calcium and magnesium when compared to the growing season period. Availability between periods was reasonably similar for ammonium and potassium (Figure 28 a, b). This trend was comparable across all sites and range of harvest treatments.

In summary, annual available pools of ammonium were greatest in the tree-length treatment, followed by full-tree, with whole-tree and the uncut/reference stand having the lowest means (Figure 29 a). Tree-length harvesting also resulted in the greatest availability of potassium and calcium, and not surprisingly, whole-tree harvesting consistently resulted in the lowest amounts of available cations.

Although the resin results from this study are merely being used as an index of available pools, additional research should be considered as it is questionable as to whether the resins used here provided the best index of available nutrient pools on these sites, and if the results shown here are truly reflective of the available nutrient pools. It is possible that the resins are not efficient competitors for nutrient cations, as suggested by Lundell (1989), and that they could possibly lose efficiency by reacting with low

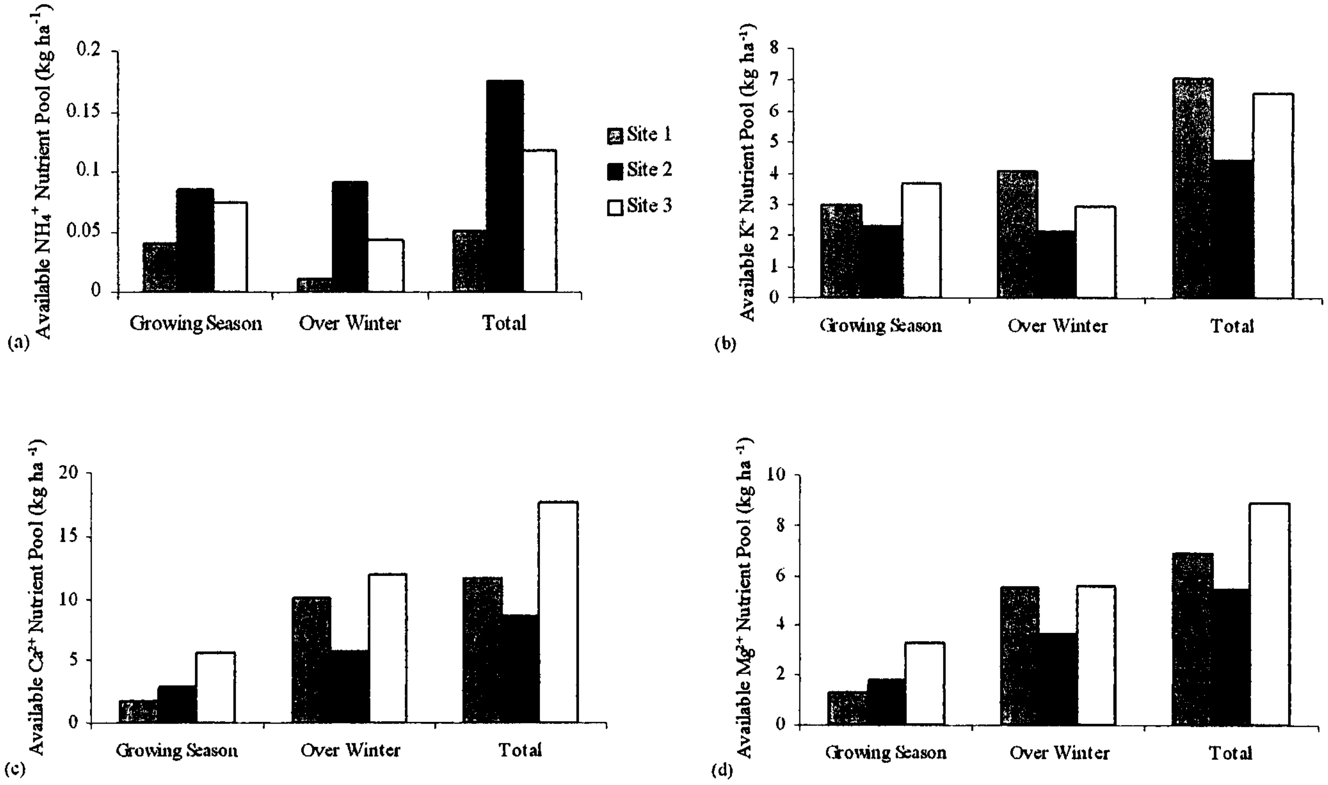


Figure 28. Available nutrient pools during the growing season and overwinter period for the mineral horizon across sites for ammonium (a), potassium (b), calcium (c), and magnesium (d).

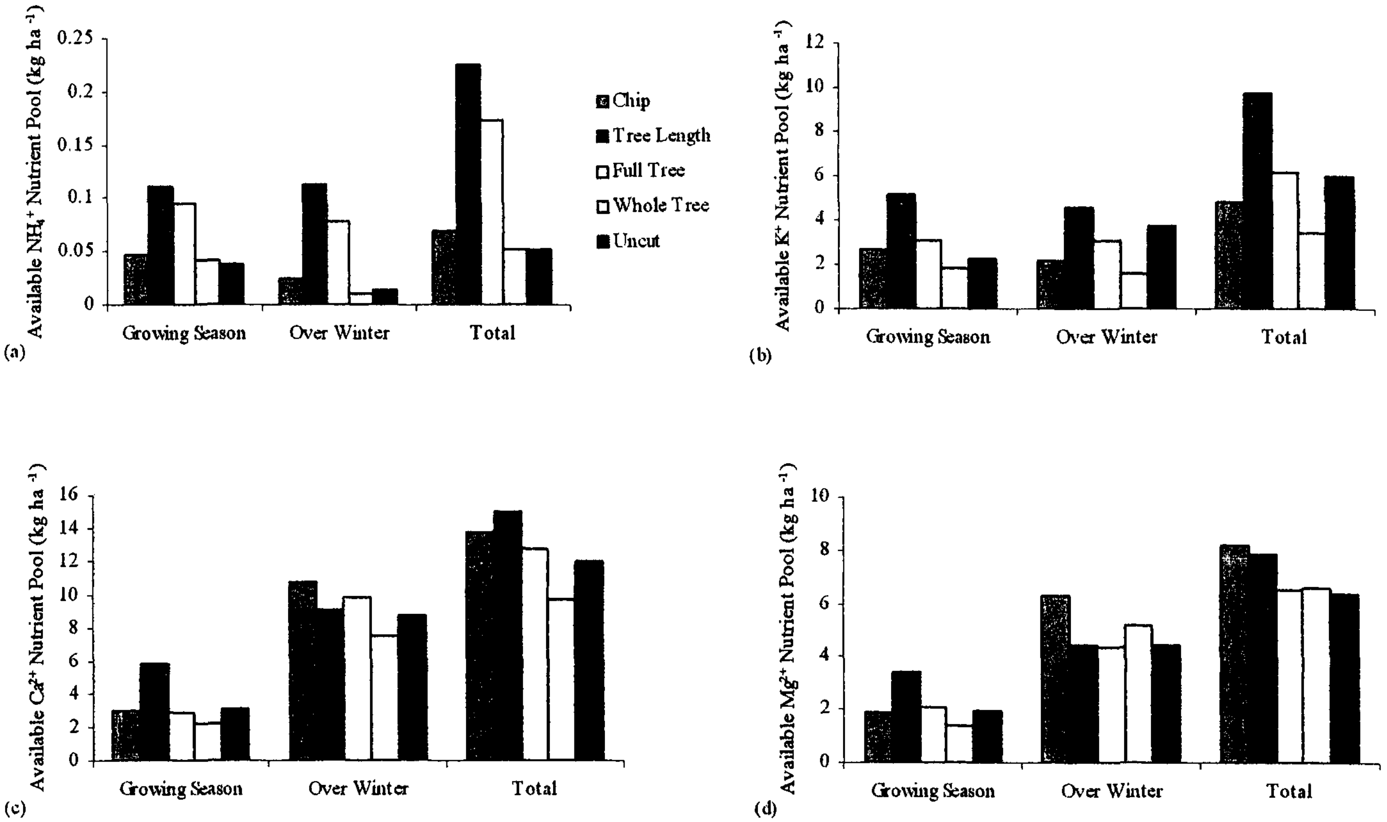


Figure 29. Available nutrient pools during the growing season and overwinter period for the mineral horizon across harvest treatments for ammonium (a), potassium (b), calcium (c), and magnesium (d).

molecular substances or organo-complexes, both which are common in solutions from acidic forest soils (Krause and Ramlal 1987). In addition, since it is possible that plant and microbe competition may reduce the ion supply in the resin bags (Binkley 1984b), the resins may not be effective in showing the differences in the available nutrient pool between the harvest treatments.

4.3 STAND-LEVEL RESPONSE TO HARVEST INTENSITY: REGENERATION POTENTIAL AND CROP TREE PERFORMANCE

4.3.1 Species Composition

Forest floor disturbance through harvesting not only affects nutrient pools and nutrient availability, but also directly affects seed availability, seedbed receptivity, and environmental factors that control germination, seedling survival, and early growth (Roberts and Dong 1993). The study sites are representative of an upland site type, characterized by shallow, coarse to fine loamy soils and supporting mixed conifer stands, with high probabilities of natural ingress of these species following harvesting. Although black spruce recruitment would occur over an extended period of several years, viable seed is located both within the logging slash and the adjacent uncut stands. For this site type, conventional clear-cutting is recommended, and both tree-length and full-tree are recommended logging practices, with a high natural regeneration potential (OMNR 1997b).

Almost ten years after harvesting had occurred, species densities varied across the three study sites. In a mature state (*i.e.,* late successional stage), the stands were dominated by black spruce. After disturbance (natural or harvesting), however, these site types are dominated by pioneering species, primarily jack pine (Figure 30). While site did not significantly affect total stand density, the sites did significantly differ with respect to black spruce and jack pine densities (Table 11). Based on the regeneration survey data completed in 2004, all three study sites had high regeneration densities, ranging from over 4400 stems·ha^{-1} (Site 1) to 7200 stems·ha^{-1} (Site 2).

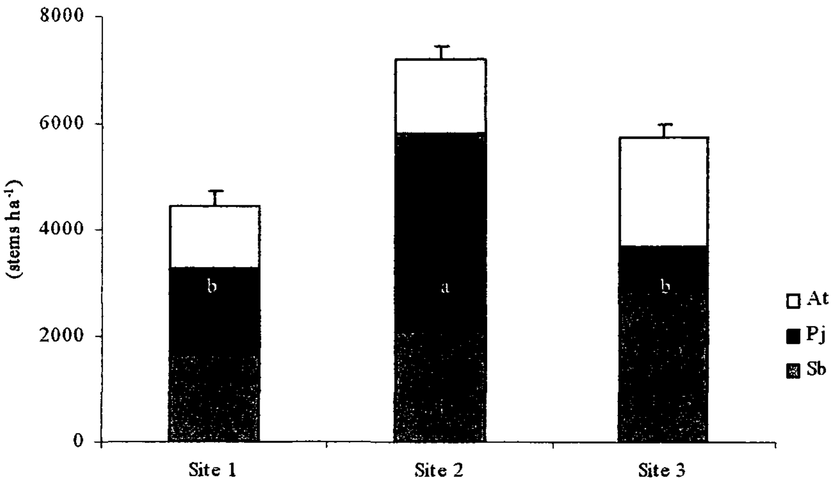


Figure 30. Tree densities by species, across the study sites ten years after harvest. Different letters denote significant site differences, based on the SNK tests ($p < 0.05$).

Table 11. P-values from the species density ANOVA tests for all species (significant values are in **bold**, $p < 0.05$).

	Total Density	Black Spruce	Jack Pine	Trembling Aspen
Site (S)	0.0567	**0.0419**	**0.0293**	0.079
Harvest Treatment (H)	**0.0371**	0.2152	0.2971	**0.0202**
S*H	0.3719	0.6081	0.6205	**0.0276**

As expected, the species composition was a mix of black spruce, jack pine, and trembling aspen, but was dominated by the conifer component (64 - 81 %). Black spruce regeneration would be expected to be a significant contributor to the total stand density as it was not only the dominant species in the pre-harvest stand (*i.e.,* large seed source), but also as it was planted (2 m spacing) on all treatment plots. The high occurrence of the other two species (Pj and At), however, was not unexpected as both jack pine and trembling aspen are pioneering species, geared toward rapid re-colonization following a disturbance. It is not uncommon for upland black spruce dominated stands to regenerate into mixedwood stands after harvesting (Brumelis and Carleton 1988, Hearnden *et al.* 1993). Bowling *et al.* (1997) indicate that upland black spruce sites will often likely develop into a two storied condition, with an overstorey of relatively quick growing aspen and jack pine, and an understorey of slower growing black spruce.

Small occurrences of other species such as balsam fir, tamarack, white birch, and willow were recorded as well, in isolated patches, so these species were not included in the standing crop estimates. For this study, density was tested by species, as well as by total stand density. In addition to site affecting both black spruce and jack pine (Figure 30), the different harvest intensities generated conditions that significantly impacted the regeneration potentials that, in turn, resulted in differences in total stand density (Table 11). Only trembling aspen was significantly affected by the Site*Harvest Treatment interaction (Table 11).

On these sites, the tree-length treatment generated the lowest densities (~ 3000 stems·ha^{-1}) compared to the other three treatments (6000 - 7000 stems·ha^{-1}) (Figure 31). The harvest treatments all leave different and unique seed bed conditions after harvesting. At the initial stages of regeneration and seedling establishment, seed bed receptivity overshadows soil nutrient status (Kimmins 1997).

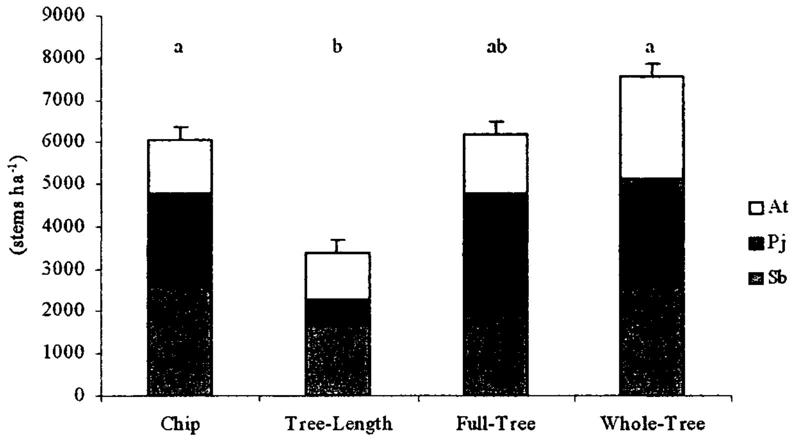


Figure 31. Total tree densities across treatments ten years after harvest. Different letters denote significant harvest treatment differences, based on the SNK tests ($p < 0.05$).

As a result, the tree-length treatment, which was shown to have the greatest nutrient pools, had the lowest density. In contrast, the whole-tree treatment had the highest densities even though it resulted in the lowest nutrient pools. The bottom line is that whole-tree harvesting provided the best seed bed due to the high level of mineral soil exposure; whereas tree-length harvesting leaves the greatest amount of logging debris on the site. Waters *et al.* (2004) indicate that post-harvest regeneration after tree-length harvesting will likely be affected by the considerable amount of logging slash remaining, compared to full-tree harvesting which leaves minimal slash at the site. The full-tree and chip treatments have very comparable densities (~6000 stems·ha^{-1}), with the grinding and even distribution of the chips allowing for good regeneration (Figure 31).

Moist mineral soil or mosses are very suitable for black spruce germination (Viereck and Johnston 1990), and for trembling aspen establishment, because of its shade intolerance and aggressive pioneering qualitites (Perala 1990). Trembling aspen regenerated well in this study, particularly on the moister, finer textured soils of Site 3 after whole-tree harvesting with over 2400 stems·ha^{-1} (Figure 28). Kabzems and Haeussler (2005) reported a similar response for trembling aspen after disturbances such as whole-tree harvesting. Figure 32 shows that there was no harvest treatment response on Site 1 or Site 2, but the whole-tree harvest treatment stimulated aspen root suckering on Site 3.

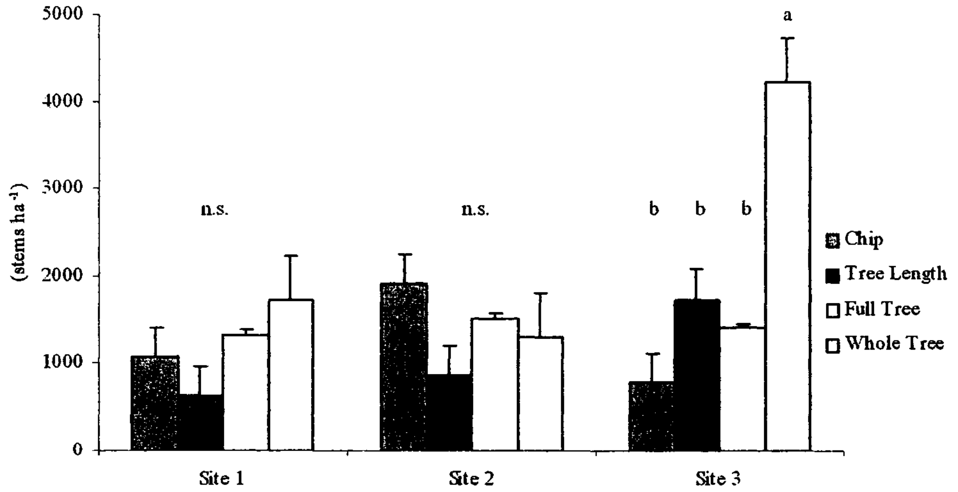


Figure 32. Site and Harvest Treatment differences in trembling aspen densities. Different letters denote significant site differences, based on the SNK tests ($p < 0.05$).

Optimal soil conditions for aspen regeneration are described as being well-drained, loamy soils with high organic matter content. Site 3 was shown (Figure 28) to have greater availability of nutrients compared to the other sites, and is characterized as being moderately well drained, with a finer mineral horizon (silt loam) (Duckert and Morris 2001). Site conditions on Site 3 favour the establishment of trembling aspen and also provided suitable conditions for black spruce establishment, while jack pine responded well on Site 2 (Figure 30).

Whole-tree harvesting has the ability to stimulate regeneration due to the mineral soil exposure that occurs in conjunction with a viable seed source from adjacent stands. Exposed mineral soil provides optimal conditions for seedling establishment (*i.e.*, good moisture conditions for germination), and eliminates slash residues that can reduce light and temperature levels below ideal levels (Rudolph and Laidly 1990). According to Rudolph and Laidly (1990), jack pine regeneration is extremely high under these conditions, especially when competition from other vegetation is not severe (Cayford *et al.* 1967). Trembling aspen suckering is also stimulated under these conditions (Kabzems and Haeussler 2005). Buse and Bell (1992) add that winter harvesting, as was done in this study, can result in four times as many aspen suckers compared to harvest in other seasons.

Harvest treatment was not a significant source of variation for jack pine (Table 11), which had the highest density after full-tree harvesting (~2800 stems·ha^{-1}) (Figure 31), even with the bulk of the crown material/cones being removed during harvesting. Similar results were found in conifer mixedwood sites in southeastern Manitoba by

Waters *et al.* (2004). They reported that pine regenerated best on sites that had been full-tree harvested, due to the increased disturbance of soil and moss, and hypothesized that the decreased slash deposition after full-tree harvesting, compared to tree-length harvesting, was also a positive factor in seedling establishment and regeneration of jack pine. McInnis and Roberts (1995) suggested that the low slash cover created by full-tree harvesting can lead to increased mineral seedbed moisture and soil surface temperatures, which may be a positive factor in jack pine regeneration.

Past research has shown that periodic reductions in organic matter depth, such as those that result after disturbances including whole-tree harvesting or wildfire, are required to enhance decomposition rates and to maintain and restore ecosystem productivity and diversity (Viereck *et al.* 1983, Flanagan and Van Cleve 1983). Bonan (1990) stated that a thick forest floor can result in low thermal conductivity and high water holding capacity, which can reinforce and perpetuate poor soil conditions, while slowing decomposition and restricting nutrient availability (Bonan and Shugart 1989). These conditions can prevent seedling establishment. It might, therefore, be beneficial to utilize silvicultural treatments designed to reduce organic matter accumulation, and mix organic and mineral soils. This mixing, if done without significant soil compaction, can increase tree growth and has the potential to enhance community diversity (Orlander *et al.* 1996, Haeussler *et al.* 1999). Soil horizon mixing can also promote decomposition and enhance tree seedling nutrition by improving soil qualities, such as aeration (Mallik and Hu 1997, Prescott *et al.* 2000).

4.3.2 Standing Crop

Along with tree density differences across the study sites and harvest treatments, there was also a difference in the levels of tree biomass (standing crop), ten years after harvest. Appendix II summarizes the biomass regression equations derived from the destructive sampling used in conjunction with the stand inventory data (Equation [3] - section 3.5.2). For all three species combined together, and jack pine, both site and harvest treatment significantly affected all components, and total biomass (Table 12). The range of total biomass across the three sites varied from ~2 $T \cdot ha^{-1}$ (Site 3) to ~5 $T \cdot ha^{-1}$ (Site 2) (Figure 33 a).

The differences that are shown between site and harvest treatment standing crop estimates are, in all likelihood, largely the result of the differences in regeneration density. For example, Site 2 had greater densities than the other sites (Figure 32), as did the whole-tree harvesting treatment (Figure 31), with both having the highest total biomass (Figure 33). Ruel *et al.* (2004) also reported that after different harvest treatments were employed, regeneration produced trees of the same or similar size, indicating no loss in productivity. Studies by Kabzems and Haeussler (2005) also found little difference between treatment effects of tree-length and full-tree harvesting on the short-term growth rates of boreal species.

Linear contrasts were calculated to find differences between harvest treatments, using the last three of the four contrasts presented in Table 5. The contrasts were calculated using only total biomass (Figure 33), as no significant changes in individual tree biomass components were observed. Even though harvest treatment significantly

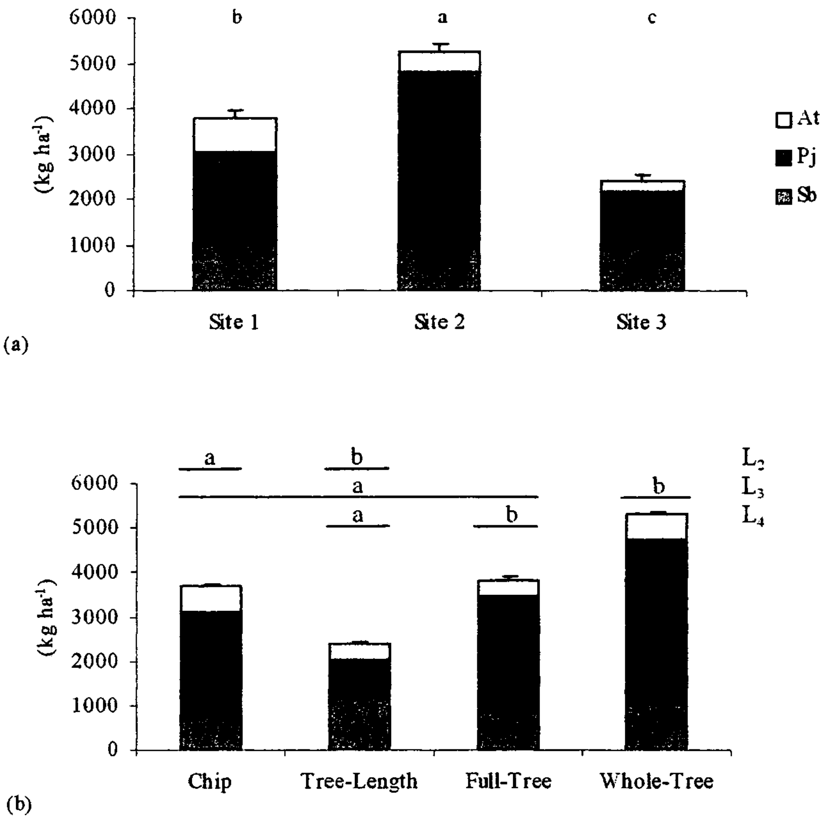


Figure 33. Total biomass distribution amongst species between sites (a), with significant site differences denoted by letters, based on the SNK tests ($p < 0.05$), and significant harvest treatments (b) are illustrated using linear contrast comparisons.

affected all individual components for jack pine, foliage represented 40 % of the total tree biomass of all three species, followed by branchwood (30 %), stemwood and bark (25 %), and current twig growth (5 %). These percentages were consistent across all harvest treatments so only total biomass was considered. Unlike mature forests, a high percentage of the total aboveground biomass was allocated to foliage, which reinforces that the growth pattern of these juvenile trees emphasizes crown development.

Table 12. Species means for the biomass component ANOVA tests with SNK results.

Tree Component	All Species	Black Spruce	Jack Pine	Trembling Aspen
		kg· ha^{-1}		
Foliage:				
Site - 1	1258.0 b	476.3	755.6 b	143.4
2	1882.0 a	443.1	1464.0 a	82.5
3	690.6 c	459.9	457.7 b	57.5
Harvest Treatment - Chip	1236.0 b	382.3	881.8 a	109.3
TL	661.8 c	544.4	319.1 b	64.3
FT	1397.0 b	413.7	982.1 a	79.8
WTH	1813.0 a	499.1	1387.0 a	124.3
Current Twig:				
Site - 1	166.4 b	37.6	114.3 b	28.3
2	260.4 a	35.3	223.1 a	16.7
3	76.5 c	36.8	68.1 b	13.0
Harvest Treatment - Chip	168.7 b	30.8	133.5 a	22.0
TL	67.9 c	42.8	48.4 b	12.8
FT	188.2 b	32.9	149.7 a	16.6
WTH	246.3 a	39.7	209.1 a	25.8
Branchwood:				
Site - 1	1159.0 b	253.7	571.5 b	461.0
2	1451.0 a	226.4	1044.0 a	377.7
3	466.6 c	229.6	401.0 b	70.8
Harvest Treatment - Chip	1058.0 b	183.3	679.0 ab	338.1
TL	553.1 c	294.7	234.5 b	366.8
FT	1024.0 b	212.8	701.6 ab	179.7
WTH	1467.0 a	255.4	1073.0 a	327.9
Stemwood & Bark:				
Site - 1	949.3 b	258.8	515.7 b	287.7
2	1375.0 a	227.9	1083.0 a	164.4
3	430.6 c	229.4	276.3 b	108.0
Harvest Treatment - Chip	914.2 b	179.7	617.0 a	217.5
TL	454.7 c	303.6	222.6 b	129.1
FT	1001.0 b	214.8	741.2 a	156.5
WTH	1303.0 a	256.6	919.7 a	243.6
Total Biomass:				
Site - 1	3452.0 b	1021.0	2002.0 b	775.6
2	4913.0 a	925.3	3883.0 a	445.3
3	1632.0 c	946.2	1211.0 b	224.9
Harvest Treatment - Chip	3299.0 b	768.0	2337.0 a	572.1
TL	1627.0 c	1178.0	845.9 b	364.9
FT	3610.0 b	867.1	2604.0 a	384.4
WTH	4793.0 a	1044.0	3675.0 a	606.3

It would be anticipated that once crown closure is attained and maximum LAI is achieved, a shift in biomass allocation to perennial tissues (*i.e.,* stemwood) would occur (Kimmins 1997).

But, in terms of total biomass, the whole-tree treatment (Figure 33 b) generated significantly higher (L_3) tree biomass after ten years (~ 5 T·ha^{-1}) (Table 12), followed by the chipped and full-tree treatments (~ 3.5 T·ha^{-1}), indicating that the mineral soil exposure facilitated rapid seedling establishment, resulting in increased biomass (Table 12). On the other hand, the tree-length treatment had significantly lower standing crop estimates (~ 2 T·ha^{-1}), resulting from the low densities associated with this treatment (Figure 31). In particular, jack pine recruitment on the tree-length treatment was small compared to the other treatments (Figure 33).

Only jack pine biomass varied across the study sites and harvest treatments. As expected, jack pine biomass was greatest where its density was greatest, on Site 2 and after whole-tree harvesting (L_3) (Figure 34). This positive jack pine response may be related to the fresh moisture regime (Table 1), and seed source availability. Jack pine generally grows best on well drained soils (Rudolph and Laidly 1990), and during early seedling growth is the fastest growing conifer. This is due to a higher photosynthetic rate and NUE than other species such as black spruce (Sullivan *et al.* 1997).

While shade can be beneficial for germination and early survival, it becomes detrimental to jack pine seedlings after the first two years (Buse and Bell 1992). The negative effects of shading could explain why jack pine density, and therefore biomass, are less on tree-length harvested sites (L_4) (Figure 34). Deposited slash can create shade that has the ability generate cooler areas of the microsite, which may, in turn, create unsuitable conditions and limit serotinous cones release of seeds for seedling establishment. Slash also does not provide a suitable seed bed for jack pine, which prefers a mineral soil seedbed with limited competition (Rudolph and Laidly 1990).

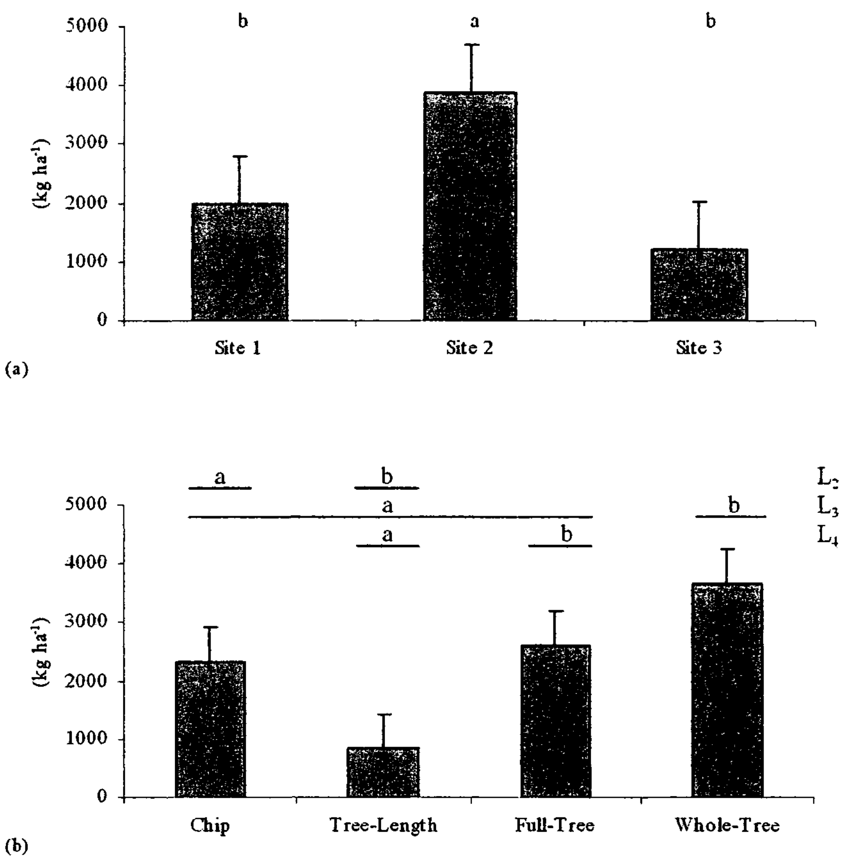


Figure 34. Jack pine total biomass between sites (a) with significant site differences denoted by letters, based on the SNK tests ($p < 0.05$), and significant harvest treatments (b) are illustrated using linear contrast comparisons.

4.3.3 Black Spruce Seedling Growth

The performance (growth and nutrition) of crop trees (*i.e.*, black spruce), serves as a useful means to link changes that occur after harvesting to soil physical and chemical properties to site productivity (*e.g.*, seedling biomass). After harvest, the sites were planted with over-wintered containerized stock from seeds extracted from trees from the experimental sites (Duckert and Morris 2001). The planted black spruce seedlings thus originated from a common starting point (spring 1995), meaning all had an equal chance of success. As such, these seedlings act as a biological integrator of site and treatment-level conditions that might impact productivity (Quoreshi and Timmer 2000).

In terms of both height growth and RCD (based on 10th year measurements), the ANOVA results (Table 13) identified a differential harvest treatment response across the study sites through a significant Site*Harvest Treatment interaction. Linear contrasts were applied to help explain what effect harvest treatment is having on seedling growth parameters. Generally, across the sites seedling growth was greatest for the chip and tree-length treatments, with the poorer growth consistently occurring after whole-tree harvesting (Figure 35 and 36). While the pattern of more intensive treatments producing reduced individual tree growth is evident, there are slight shifts between the chip and tree-length treatment.

Table 13. P-values from the seedling growth parameter tests for black spruce seedlings (significant values are in **bold**, $p < 0.05$).

	Height	Root Collar Diameter
Site (S)	0.3608	**0.0018**
Harvest Treatment (H)	**0**	**0.0001**
S*H	**0.0012**	**0.0161**

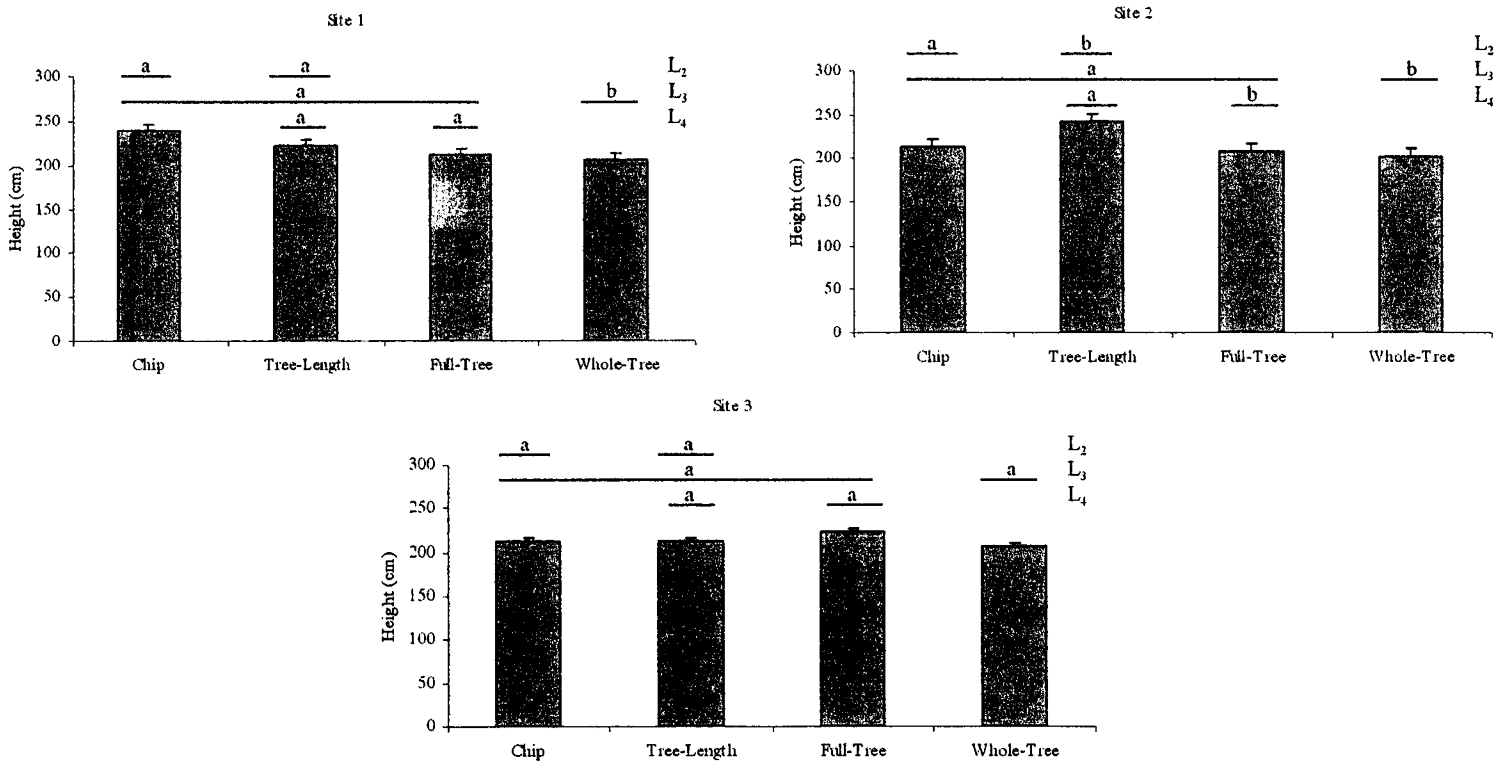


Figure 35. Site*Harvest Treatment interactions for black spruce 10th year height measurements. Significant harvest treatment effects are illustrated using linear contrast comparisons ($p < 0.05$).

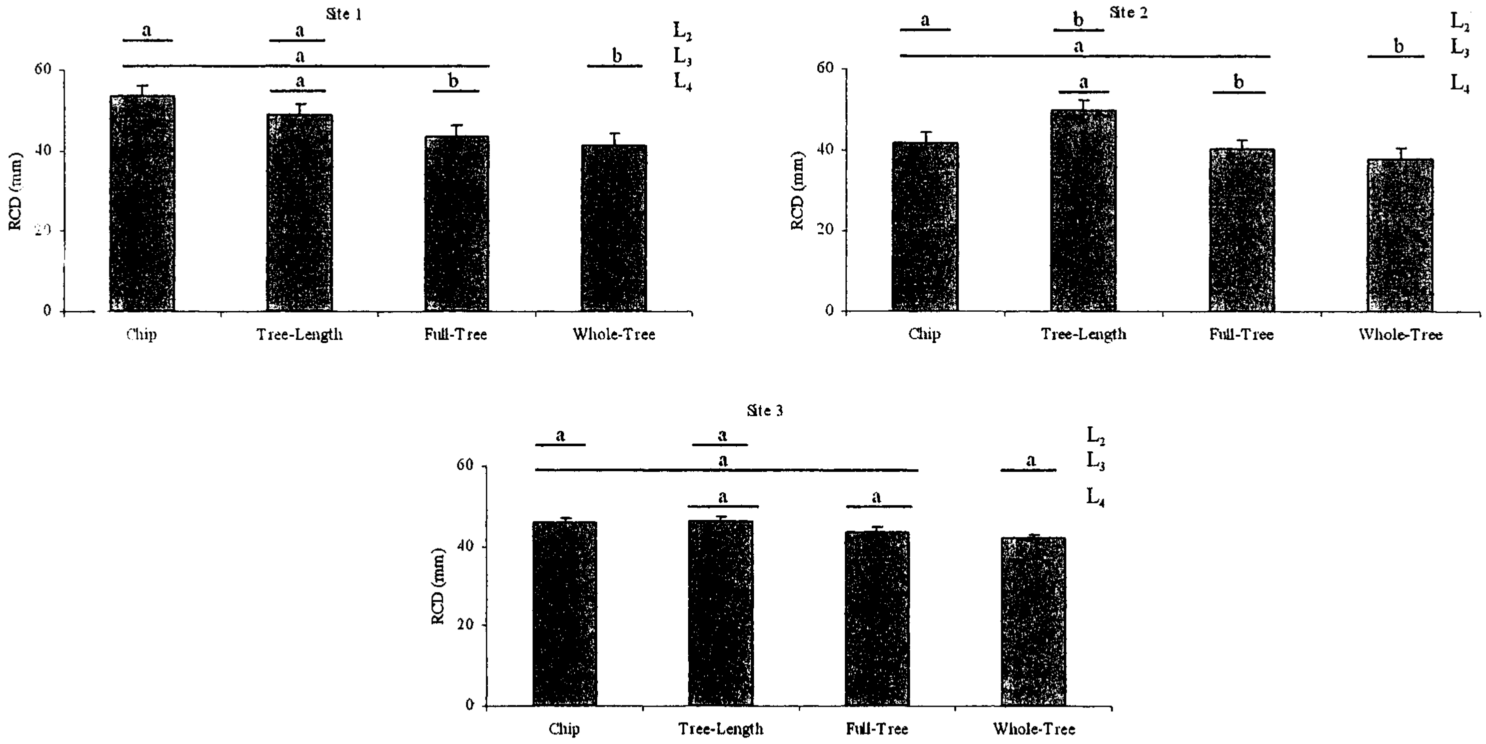


Figure 36. Site*Harvest Treatment interactions for black spruce 10th year RCD measurements. Significant harvest treatment effects are illustrated using linear contrast comparisons ($p < 0.05$).

Site 3 had no significant contrasts for either growth parameter (Figure 35 and 36), while all three contrasts were significant on Site 2, which had significantly higher growth in the tree-length treatment compared to the other treatments. Comparing the whole-tree harvest treatment with all other treatments (L_3), was significant on Site 1 for both height and RCD with the lowest growth. RCD on Site 1 was also significant for L_4 (Figure 36), with the tree-length treatment having greater root collar diameter growth when compared to the full-tree treatment.

Contrasts were also tested for the harvest treatment main effect, which had significant sources of variation (Table 13). Chipping did not significantly affect seedling growth in comparison to tree-length harvesting (L_2) (Figure 37), and where whole-tree harvesting occurred (L_3), black spruce seedlings had significantly less height and root collar growth than did seedlings planted on sites exposed to other harvest treatments.

Black spruce seedlings planted after tree-length harvesting were taller and had greater RCD than trees planted after full-tree harvesting (L_4) (Figure 36). This result is similar to findings by Kabzems and Haeussler (2005) who found tree height greater in tree-length then full-tree harvested sites, but with both being greater then trees growing on whole-tree harvested sites, as was the case here. Pothier (2000) found that height growth was better on upland sites that were less stocked than other sites, and it is well understood that individual tree diameter is strongly correlated with stand density.

In this study, the tree-length treatment had significantly lower densities than the other treatments (Figure 31). The individual tree height and diameter effects, therefore, are somewhat confounded with density, *i.e.,* the tree-length treatment resulted in larger individual trees, but fewer numbers of them. Thus, density and biomass values seem to be interrelated and dependant on each other, high density results in higher biomass, but as seen in these results, not in taller trees.

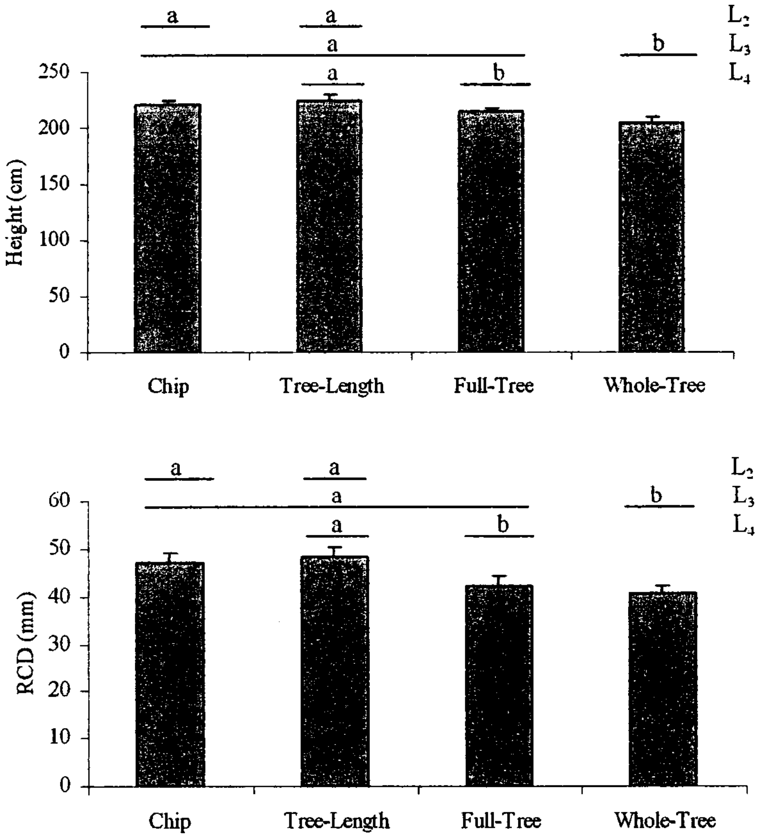


Figure 37. Black spruce height and RCD means across harvest treatments. Significant harvest treatment effects are illustrated using linear contrast comparisons ($p < 0.05$).

4.3.4 Black Spruce Seedling Foliar Nutrition

Foliar analysis is preferred over soil chemical analysis as elemental leaf composition is considered to be a more direct index of nutrient availability to the tree compared to measures of soil nutrient supply (Timmer and Teng 1999). Nutrient status can be an important indicator of both plant quality and overall plant performance (Haase and Rose 1995). Using foliar concentrations and dry weights of a known number of needles (*i.e.*, 100) to calculate foliage nutrient content can provide an easily measured and rapid estimate of tree growth potential (Haase and Rose 1995) and has been linked to long-term stemwood responses (Ebell 1972, Leaf *et al.* 1975, Timmer and Morrow 1984). According to van den Driessche (1974), foliar analysis is a well established method to assist in the diagnosis of tree mineral requirements, and has proven useful where the growth of a stand has been curbed by the deficiency of one or more nutrient elements.

Foliar nutrition differences across sites and treatments are summarized in Table 14. Phosphorus and magnesium foliar concentrations were both significantly affected by the Site*Harvest Treatment interaction (Figure 38 and 39). However, main effects were a significant source of variation for many nutrients for both foliar concentration and content (Table 14).

Table 14. Foliar nutrition p-values (significant values are in **bold**, $p < 0.05$).

Foliar Concentration	N	P	K	Ca	Mg
Site (S)	**0.014**	**0**	**0**	**0.002**	**0**
Harvest Treatment (H)	0.4239	**0**	0.7234	**0.0249**	**0.002**
S*H	0.6665	**0.0175**	0.1632	0.1244	**0.0183**

Foliar Content	N	P	K	Ca	Mg
Site (S)	**0.0123**	**0**	**0.004**	**0.0104**	**0**
Harvest Treatment (H)	**0.009**	**0**	0.1389	0.1583	0.6864
S*H	0.6826	0.1846	0.3057	0.5136	0.1832

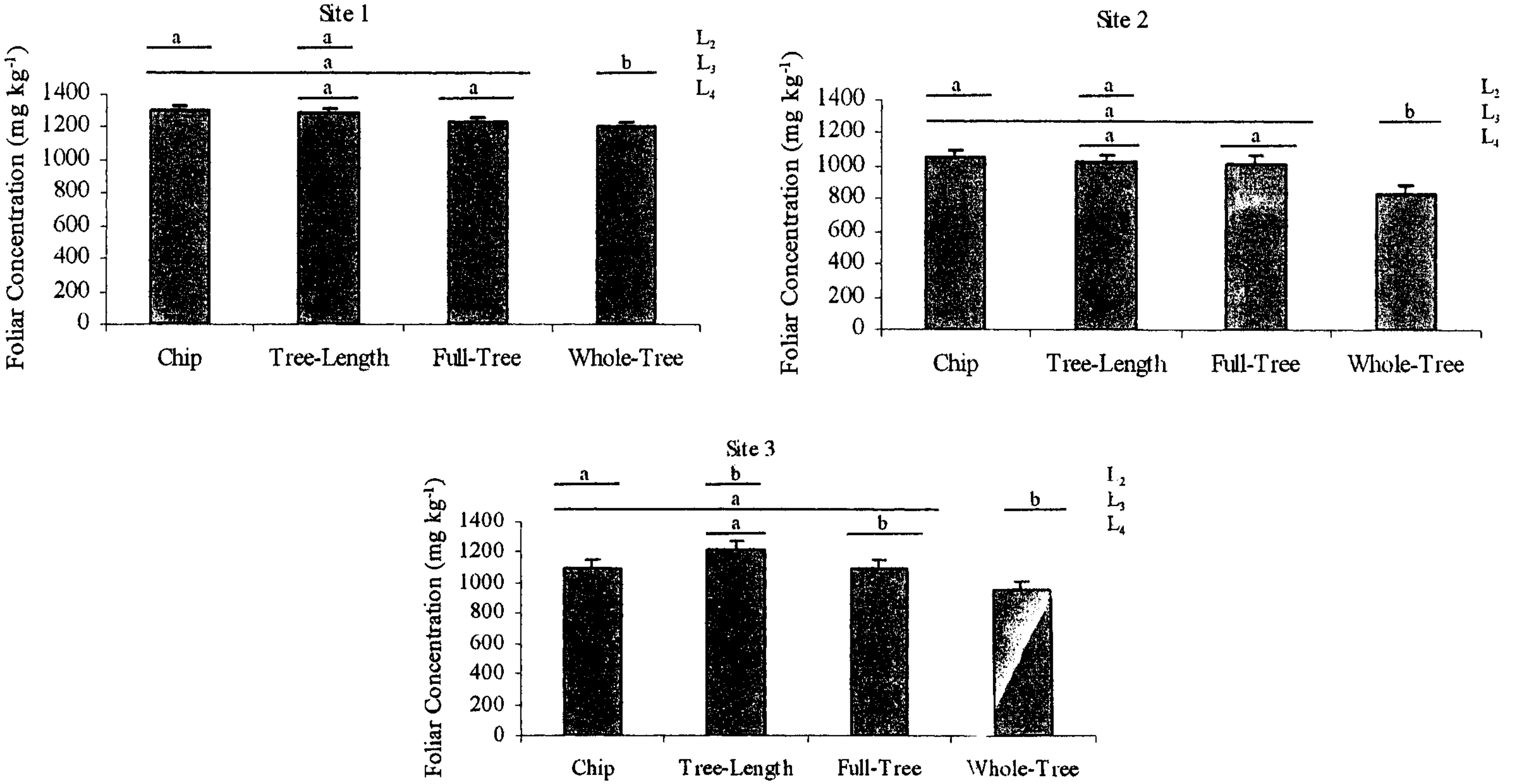


Figure 38. Site*Harvest Treatment interactions for black spruce phosphorus foliar concentrations. Significant harvest treatment effects are illustrated using linear contrast comparisons ($p < 0.05$).

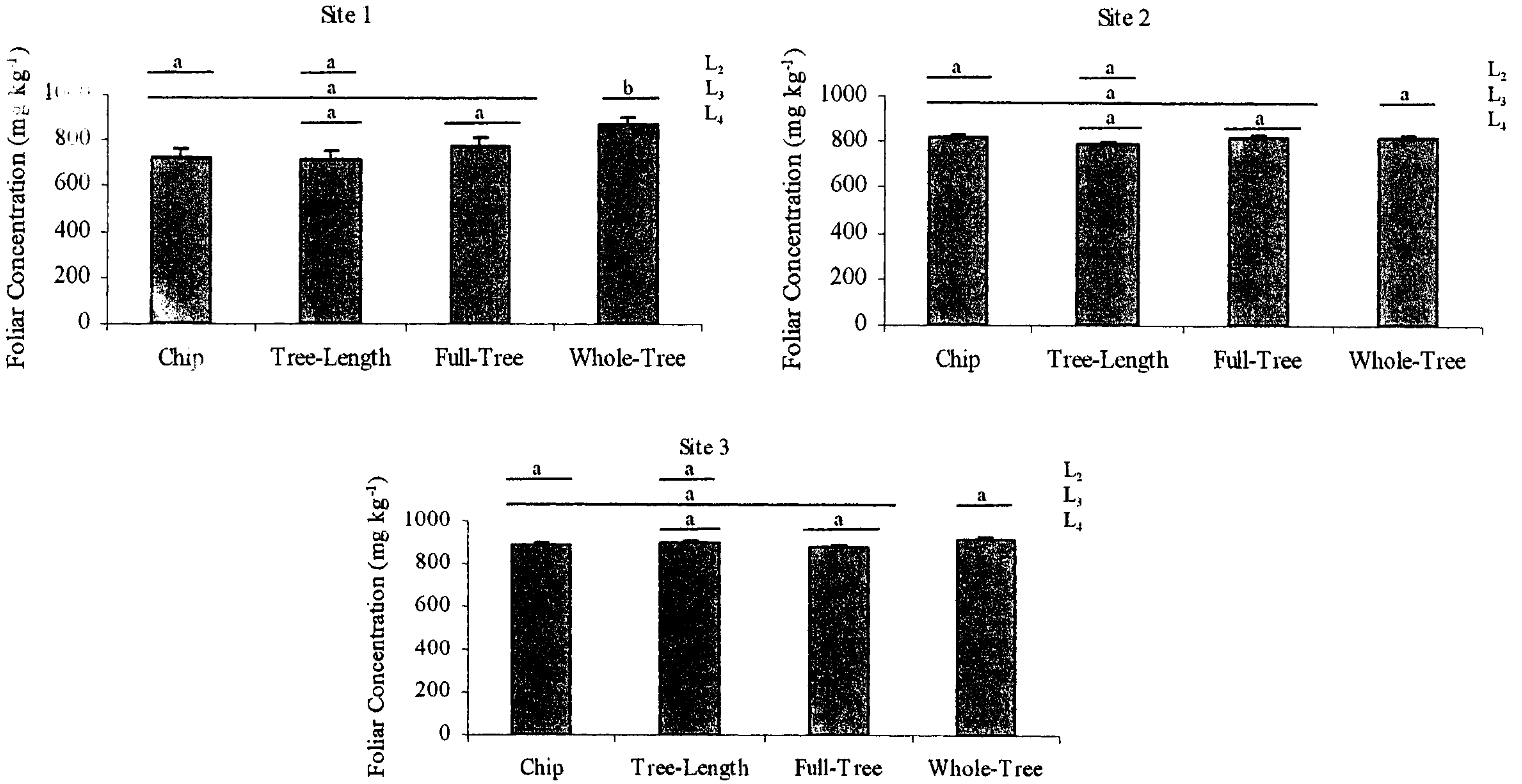


Figure 39. Site*Harvest Treatment interactions for black spruce magnesium foliar concentrations. Significant harvest treatment effects are illustrated using linear contrast comparisons ($p < 0.05$).

The whole-tree treatment (L_3) had significantly lower concentrations of phosphorous when compared to the other treatments on all three of the study sites (Figure 38). All of the contrasts tested were found to be significant on Site 3, and overall, concentration levels of phosphorus were consistently lower in the more intense treatments across all of the sites (Figure 38). Patterns shifted between the chip and tree-length treatments, but generally, as harvest intensity increased, foliar phosphorus concentration decreased. This observation correlates to patterns from the nutrient availability results, with the resins generally collecting less nutrients within the more intensive harvest treatments.

Magnesium foliar concentrations, on the other hand, were an exception to this pattern (Figure 39). For this element, concentration levels increased as harvest intensity increased. L_3, comparing the whole-tree treatment with the other treatments, was found to be significant only on Site 1, and was the only significant contrast across the sites. This result was not unexpected, as when compared to the other treatments, the whole-tree harvesting treatment resulted in large available pools of magnesium, as measured by the resins (Figure 18 c). This increase could be attributed to the characteristics of magnesium, as generally, it is slowly released from slash, and has a low mobility rate, when compared to other nutrient ions (Frey *et al.* 2003). It is also highly available in mineral soils, and although not generating any significant contrasts, had the greatest available pools on Site 3, for both the organic (Figure 21) and mineral horizons (Figure 28). The measured foliar concentrations of magnesium were also slightly higher on Site 3, showing a strong correlation between nutrient availability and plant uptake.

Site was a significant source of variation for all tested nutrients for both foliar concentration (Figure 40) and foliar content (Figure 41). These site differences did vary depending on the element, for example, nitrogen concentrations and contents were highest on Site 2 and lowest on Site 1, while phosphorus and potassium were highest on Site 1, but lowest on Site 2. These differences could be attributed to the differences in organic horizon depths, and parent material that comprises the mineral horizons, but as seen in the interaction analysis, corresponded to site differences in the availability of these elements as measured by the resins.

Generally, sites that had large available nutrient pools also had high levels of foliar nutrient concentration and content. For example, needles from Site 1 had the greatest concentration of potassium (Figure 40 c), which correlates to the large available pools of potassium on that site (Figure 21 b). This was also the case for foliar content of potassium (Figure 41 c). While the connection between foliar uptake and nutrient availability can be correlated, many of the sites that had greater available nutrient pools, were not found to be significantly different from the other sites by the SNK tests. Noticeable trends also included: increased foliar concentration of potassium and calcium on Sites 1 and 3, respectively (Figure 40), and foliar content of potassium on Site 1, and calcium and magnesium on Site 3 (Figure 41).

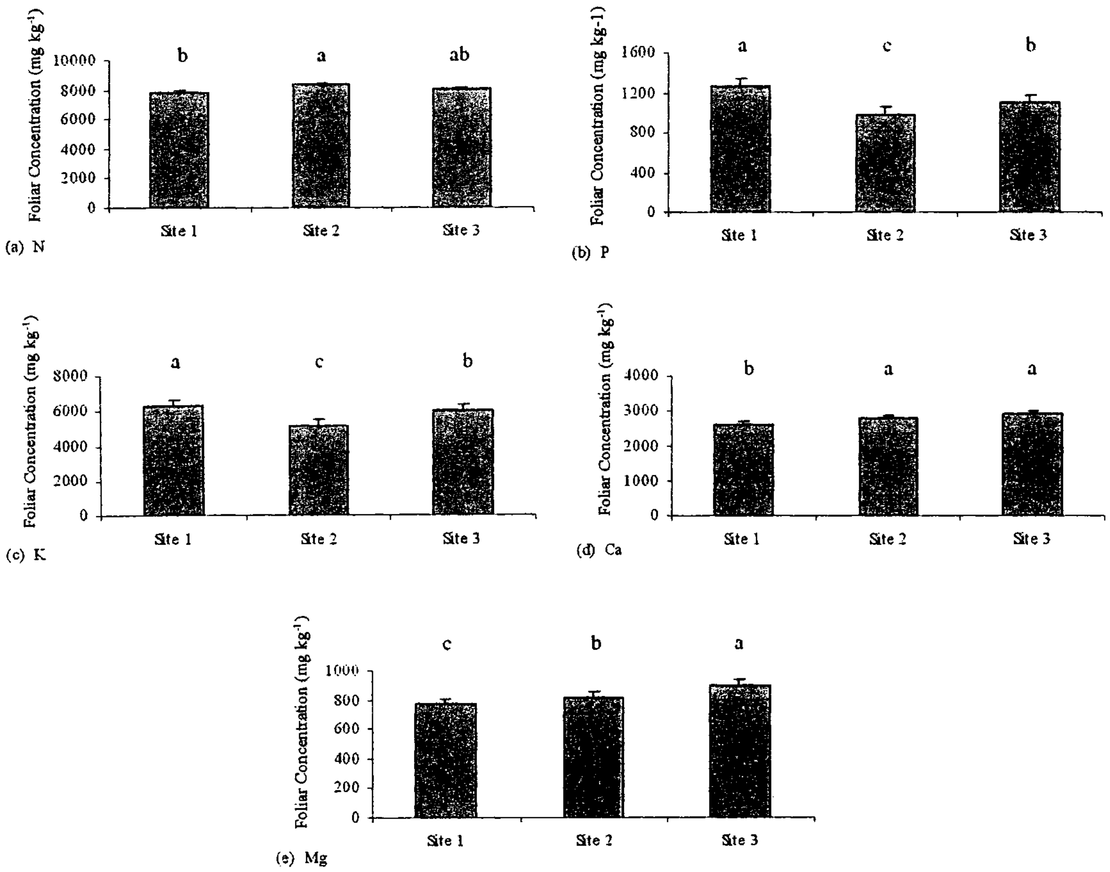


Figure 40. Foliar concentrations across all three sites for nitrogen (a), phosphorus (b), potassium (c), calcium (d), and magnesium (e). Different letters denote significant site differences, based on the SNK tests ($p < 0.05$).

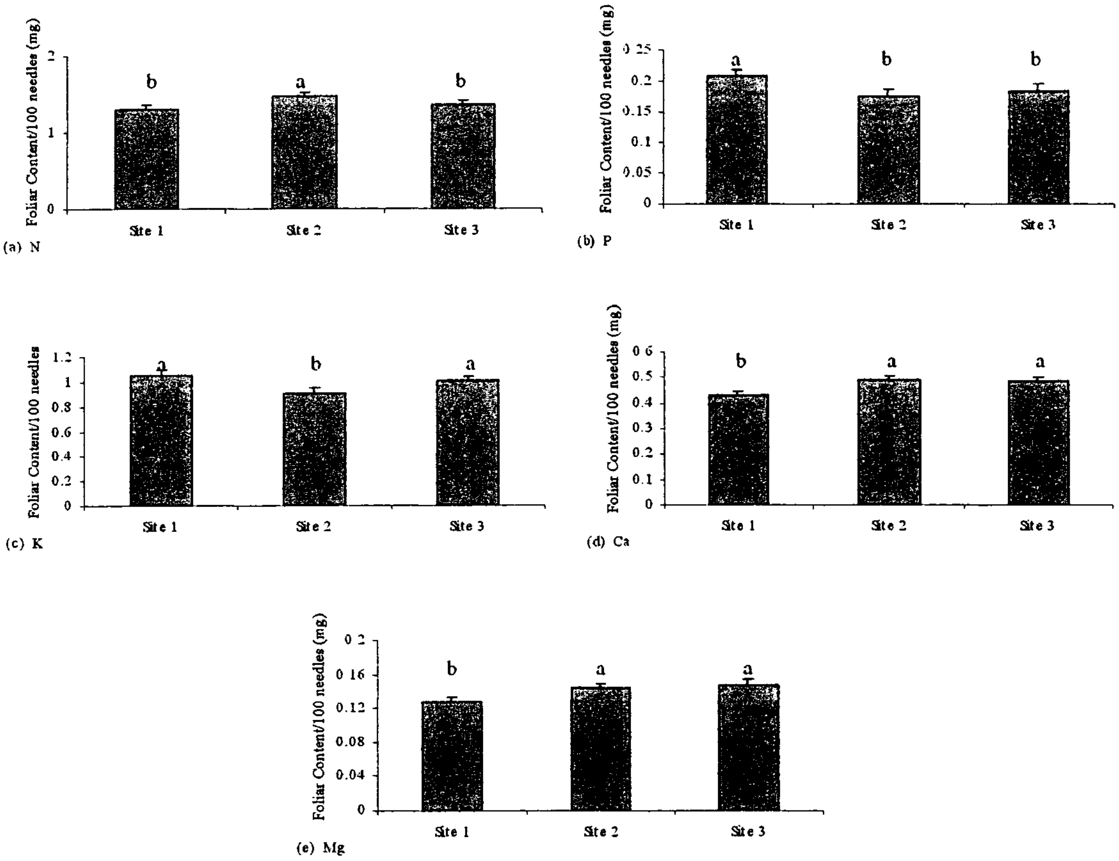


Figure 41. Foliar contents across all three sites for nitrogen (a), phosphorus (b), potassium (c), calcium (d), and magnesium (e). Different letters denote significant site differences, based on the SNK tests ($p < 0.05$).

Harvest treatment was also a significant source of variation for the foliar concentrations of phosphorus, calcium, and magnesium (Figure 42). Phosphorus concentrations generally decreased as harvest treatment intensified, while calcium and magnesium concentrations both increased with harvest intensity, which again, correlated to the size of the available nutrient pools for these elements (Figure 22). Harvest treatment was only a significant source of variation for the foliar content of nitrogen and phosphorus after ANOVA testing, but both potassium and calcium were found to have significant sources of variation after applying the linear contrasts (Figure 43).

Phosphorus, magnesium, and potassium had higher foliar contents after less intense harvest treatments, with calcium (Figure 43 d) only having one significant contrast, comparing the tree-length and chipped treatments (L_2). Unlike the other elements, calcium did not have significant sources of variation between the whole-tree treatment and the other treatments. Whole-tree harvesting has previously been attributed to increased soil nutrient concentrations, such as calcium and magnesium (Frey *et al.* 2003). Linear contrasts results showed significance for several other contrasts for foliar concentration (Figure 42) and foliar content (Figure 43). Only foliar concentration of phosporus, however, was significant for L_4, which compares the tree-length and full-tree harvesting treatment. In this case, concentrations of phosphorus were greate[illegible]er tree-length harvesting (Figure 42), but only for Site 3, as indicated by the significant interaction (Figure 38). This difference is likely due to the fine slash residues left on site after tree-length harvesting occurs. Foliar phosphorus content, however, was not significant for this contrast (Figure 43).

Chipping of slash resulted in significantly lower concentrations and content of calcium when compared to the tree-length treatment (L_2 - Figure 42 and 43). Chipping did not influence soil nutrient pools or availability of calcium, based on earlier contrast calculations, but according to Foster and Morrison (1976), calcium is greatest in stemwood and live branches, not foliage. Thereby, the chipped slash left after this treatment may be a source of calcium quickly accessed by the trees.

Seedlings growing on whole-tree harvested treatments had lower concentrations and contents of phosphorus compared to the other treatments (L_3) (Figure 42 and 43). The whole-tree treatment also had a negative affect on organic horizon phosphorus available pools (Figure 13), suggesting a link between the lower foliar values and the lower nutrient pools estimated for this treatment. Foliar contents of nitrogen and potassium were also significantly lower in seedlings growing after whole-tree treatments (Figure 43). This is consistent with other findings. For example, Pare and Van Cleve (1993) also reported lower amounts of nitrogen, phosphorus and potassium in current biomass on whole-tree harvested (bladed) sites.

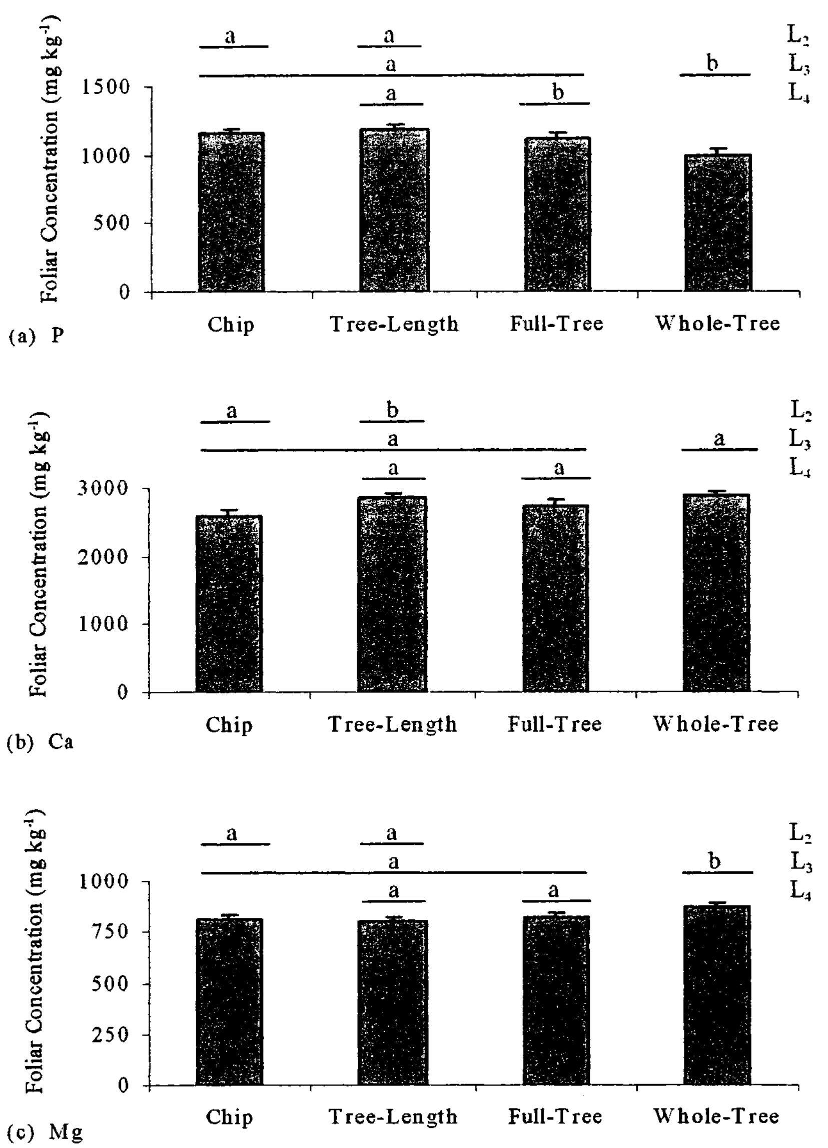


Figure 42. Foliar concentrations across harvest treatments for phosphorus (a), calcium (b), and magnesium (c) with linear contrast results. Different letters over the underlined groupings denote significant differences for the various linear comparisons ($p < 0.05$).

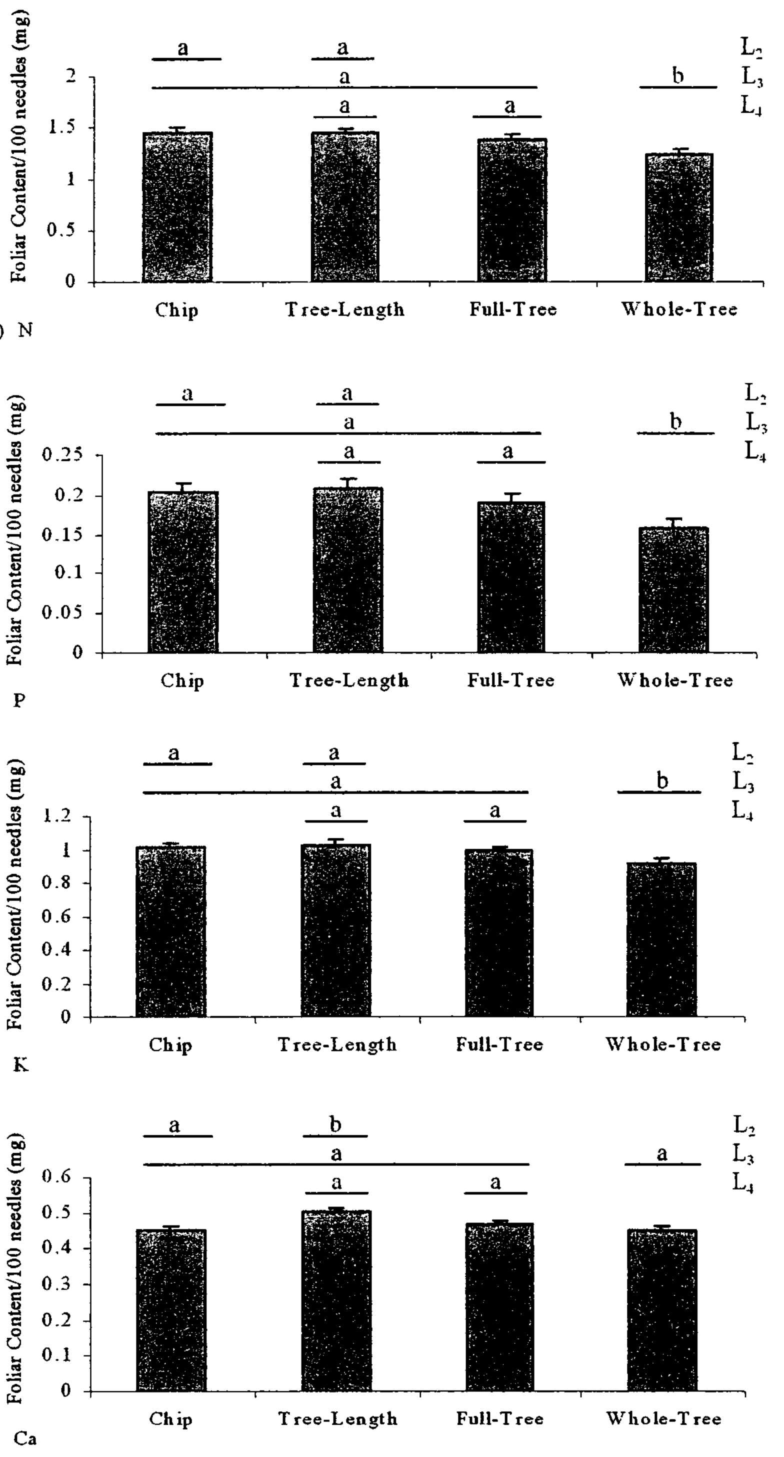


Figure 43. Foliar contents across harvest treatments for nitrogen (a), phosphorus (b), potassium (c), and calcium (d). Different letters over the underlined groupings denote significant differences for the various linear comparisons ($p < 0.05$).

Nitrogen, phosphorus and potassium are among the most important foliar nutrients as they play a role in determining plant leaf area, photosynthetic rate, and net primary productivity of forest ecosystems (Foster and Bhatti 2002). Seedlings growing on whole-tree harvested sites had significantly lower height and RCD growth compared to the other treatments (Figure 37), but this reduction is also confounded by the higher densities found on this treatment (Figure 31). At this stage (10th year), productivity (standing crop) was not shown to be significantly affected by the different treatments, including the whole-tree harvest treatment.

Foliar content tests had fewer significant factors (Table 14), indicating that there might not be as strong an effect as the concentration results suggested. Kimmins (1997) explains that plants can still grow well and have lower concentrations of certain elements than if the plant were only growing moderately well (*i.e.,* dilution effect). It has also been hypothesized that plants should attain a steady nutrient level as their growth adjusts to the nutrient resources that are available in their environment (Ingestad 1982). In this case, the sites are nutrient limited, shallow soil sites. Patterson *et al.* (1997) also reported that black spruce is less sensitive to nitrogen stress than other species, by adapting to nutrient poor conditions and increasing foliage longevity (Bonan and Shugart 1989).

It has also been suggested that the ratios of elements are more important that the absolute levels of elements (Kimmins 1997), and this has been extensively investigated by Ingestad (1967, 1971, 1979, 1981), who reported that the optimum growth of seedlings occurs when the ratios lie in a fairly narrow range. Pine and spruce seedlings need the following ratios of nutrients for optimum nutrition: N:P - 8:1, N:K - 2:1, N:Ca - 17:1, and N:Mg - 12:1 (Kimmins 1997). According to Meyer *et al.* (1997), the macronutrients nitrogen, phosphorus, and potassium, are needed in large amounts, usually greater than 0.05 % or 50 $mg \cdot kg^{-1}$. Expressed as percent of dry weight, the approximate content of healthy foliage is estimated at: N = 1.6 - 2.0, P = 0.15 - 0.35, K = 0.6 -1.2, Ca and Mg = 0.1 - 0.2 (Morrison 1974, Lavender and Walker 1979, Marschner 1986, Rook 1991). Specifically for black spruce, the range of sufficiency for good to very good growth (foliar concentrations expressed as percent dry matter) is estimated at: N = 1.5 - 2.5, P = 0.018 - 0.35, K = 0.35 - 0.7, Ca = 0.11 - 0.4, and Mg = 0.09 - 0.16 (adapted from Swan 1970).

Generally, nitrogen and potassium are required in the largest amounts, with smaller amounts of phosphorus, calcium and magnesium being required. The mean percentages found in this study are within the reported ranges, with nitrogen content averaging 1.5, phosphorus: 0.2, potassium: 1.0, calcium: 0.5, and magnesium: 0.14 (Figure 43). This result, in turn, would suggest that harvest intensity is not affecting nutrient availability in a manner that negatively affects foliar nutrition at this stage of stand development.

4.4 MANAGEMENT IMPLICATIONS

While many studies suggest that harvesting has the potential to reduce nutrient availability through biomass removal (Forge *et al.* 2001), actual findings are mixed. Some results demonstrate nutrient decreases (Schmidt *et al.* 1996), others have reported increases (Vitousek and Matson 1985, Frazer *et al.* 1990), whereas others show stable levels with no differences occurring after harvesting (Maynard and MacIssac 1998). Many factors affect nutrient availability after harvest, including: soil temperature and moisture, soil type, pH, tree species composition, and humus type. Depending on forest type and humus horizon composition, decomposition rates will be affected by the different chemical and physical properties of the forest floor (Chang *et al.* 1995). Most humus horizons in spruce forests are composed of needles containing high lignin levels and exhibit acidic pH levels, both of which promote slower turnover rates (Vitousek 1977, Pastor *et al.* 1987), and have lower nutrient contents compared to deciduous leaf litter (Cote and Fyles 1994).

This study has shown that harvesting does cause lower nutrient pools as harvest intensity increases. However, based on the 10th year results, there is no clear link to reduced tree productivity. For example, higher density and standing crop were found on the more intense harvest treatments, due to the nature of the removals and opportunity for early seedling establishment. Individual black spruce seedling growth, however, was enhanced when removals were lowest. From a forest policy and management perspective, the critical question is: *is there evidence to support the concern regarding nutrient removals that currently exists with respect to full-tree harvesting on shallow-soiled sites?*

Forest disturbances such as harvesting change ecosystem structure and function (Morris 2003), but all ecosystems tend to return to pre-disturbance conditions over time, a process which provides inherent ecosystem stability (Kimmins 1974). Nutrient recovery time will vary depending on the degree and frequency of biomass removals. For example, Morris (2003) estimated nitrogen recovery time on Site 1 and Site 2 at 15 years for tree-length, and 30 years after full-tree harvesting. Calcium, on the other hand, recovery time was estimated at 60 years for tree-length, and nearly 90 years after full-tree harvesting. These increased replacement times associated with full-tree harvesting led policy makers to favour less intense treatments such as tree-length harvesting, especially on very shallow soil sites ($\leq$ 20 cm).

Shallow soils are common in northwestern Ontario, and full-tree harvesting is the most common harvest method used to extract timber. The current results, as well as results by other studies, do not support the hypothesis that full-tree harvesting generally leads to greater reductions in the amounts of soil nutrients when compared to tree-length harvesting (Olsson *et al.* 1996). The whole-tree removal treatment (logging slash and forest floor removal) provides a "worse case scenario" for organic matter removal effects, none of which were shown to significantly affect seedling productivity after 10th year measurements. All harvest treatments will experience some level of nutrient loss, and the effects may be site and stand specific, however these removals can be replaced by nutrient inputs (Alban *et al.* 1978), providing that sufficient time passes before harvesting is conducted again.

5.0 CONCLUSIONS

The objectives of this study were to compare several harvest treatments of differing intensities and their effect on nutrient status and availability, and on seedling growth and productivity. Whole-tree harvesting was found in several cases to reduce nutrient pools and availability, but even as the worst-case scenario, did not affect seedling productivity. If completely removing all biomass and organic matter did not significantly affect seedling productivity, then the effects of less intense treatments will be even less.

Overall, no noticeable differences were found in the seedling growth and nutrient status of the forest floor, and no noticeable differences were found in the foliar contents of the planted black spruce seedlings on the different harvest treatments. More importantly, no noticeable differences were revealed between tree-length and full-tree harvesting, including soil chemistry analysis (total pool size), ion exchange resin analysis (available pool size), standing crop calculations (productivity), and foliar analysis (nutritional status). To better evaluate any possible changes, other methods such as vector analysis could be employed, as well as re-visiting the ion exchange resin procedures. For example, it would be interesting to see the differences in nutrient availability results using different amounts of resin, under differing *in situ* periods.

The regenerating stands evaluated in this study are approaching crown closure, which corresponds to maximal nutrient demand. Therefore, harvest treatment effects, if they occur, may become more pronounced during this stage of stand development. It would be during crown closure that the predictions of longer-term stand growth trajectories (*i.e.,* future forest conditions) can be made with a greater level of confidence. Thus, future research in monitoring the growth and development of the stands on these sites is needed so that more definite conclusions can be drawn on the effects of harvesting on upland shallow soil sites in black spruce forested ecosystems of northwestern Ontario.

Currently in Ontario, full-tree harvesting is not recommended where total soil depth (mineral and surface organic) is less than 20 cm (OMNR 1997b). The results from this study do not support this recommendation with respect to site nutrient sustainability. The sites included in this study had mean depths of 10 - 20 cm of mineral soil with 5 - 10 cm of surface organic (Duckert and Morris 2001). These sites border on the very shallow soil designation noted above, which allow us to evaluate whether harvesting treatments such as full-tree harvesting should be a recommended harvest method.

Forests are diverse and dynamic systems. They are constantly changing through disturbance and succession, and are important to not only the economics of Canada, but are part of its world-renowned landscape. It is the responsibility of forest planners and policy makers to ensure that this resource is here through perpetuity, which comes through the avenues of proper removal techniques, reforestation, and on-going research and policy refinement. It is also important that foresters match sites that are labelled as nutrient poor with less nutrient demanding species, and commit to using a local seed source which will be better able to cope with the poor site conditions (Archibald *et al.* 1997).

6.0 LITERATURE CITED

Abbott, D.T. and D.A. Crossley, Jr. 1982. Woody litter decomposition following clear-cutting. Ecology 63:35-42.

Aber, J.D., D.B. Botkin, and J.M. Mellilo. 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. Can. J. For. Res. 8:306-315.

Aber, J.D., and J.M. Melillo. 1991. Terrestrial Ecosystems. Saunders College Publishing, Philadelphia, Pennsylvania. 368 pp.

Abrams, M.M. and W.M. Jarrell. 1992. Bioavailability index for phosphorus using ion exchange resin impregnated membranes. Soil Sci. Soc. Am. J. 56:1532-1537.

Alban, D.H., D.A. Perala and B.E. Schlaegel. 1978. Biomass and nutrient distribution in aspen, pine and spruce stands on the same soil type in Minnesota. Can. J. For. Res. 8:290-299.

Archibald, D.J., W.B. Wiltshire, D.M. Morris, and B.D. Batchelor. 1997. Forest management guidelines for the protection of the physical environment. Version 1.0. Ont. Min. Nat. Resour., Queen's Printer for Ontario, Toronto. 42pp.

Arnup, R.W., B.J. Dowsley, L.J. Buse, and F.W. Bell. 1995. Field guide to the autoecology of selected crop trees and competitor species in northeastern Ontario. Ont. Min. Nat. Resour., Northeast Sci. Tech. FG-005. 152 pp.

Baskerville, G.L. 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res. 2:49-53.

Belanger, N., D. Pare, and S.H. Yamasaki. 2003. The soil acid-base status of boreal black spruce stands after whole-tree and stem-only harvesting. Can. J. For. Res. 33:1874-1879.

Bernhard-Reverstat, F. 1977. Recherches sur les variations stationelles des cycles biogeochemiques en foret ombrophile de Cote d'Ivoire. Cah. ORSTOM, ser. Pedol. 15:175-189. (Cited in Vitousek 1981)

Beyer, D.M. 1998. The use of ion exchange resins to assess the changes in mineral element availability during the production of the cultivated mushroom *Agaricus bisporus*. Can. J. Bot. 76:2084-2092.

Binkley, D. 1984a. Does forest removal increase rates of decomposition and nitrogen release? For. Ecol. Manage. 8:229-233.

Binkley, D. 1984b. Ion exchange resin bags: factors affecting estimates of nitrogen availability. Soil Soc. Am. J. 48:1181-1189.

Binkley, D. 2002. Ten-year decomposition in a loblolly pine forest. Can. J. For. Res. 32:2231-2235.

Binkley, D. and P. Matson. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. Soil Sci. Soc. Am. J. 47:1050-1052.

Binkley, D., R.F. Powers, J. Pastor, and K.J. Nadelhoffer. 1990. Protocol for testing measures of nitrogen availability in forest soils. pp 111-125 *in* Dyck, W.J. and C.A. Mees (eds.) Impact of Intensive Harvesting on Forest Site Productivity. Proceedings, IEA/BE A3 Workshop, South Island, New Zealand, March 1989. IEA/BE T6/A6 Rep. No. 2. For. Res. Inst., Rotorua, New Zealand, FRI Bulletin No 159. 159 pp.

Birch, H.F. 1958. The effect of drying soil on humus decomposition and nitrogen. Plant Soil. 10:9-31.

Bonan, G.B. 1990. Carbon and nitrogen cycling in North American boreal forests. II. Biogeographic patterns. Can. J. For. Res. 20:1077-1088.

Bonan, G.B. and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annu. Rev. Ecol. Syst. 20:1-28.

Bonan, G.B. and K. Van Cleve. 1992. Soil temperature, nitrogen mineralization, and carbon source-sink relationships in boreal forests. Can. J. For. Res. 22:629-639.

Boone, R.D. 1992. Influence of sampling date and substrate on nitrogen mineralization: comparison of laboratory-incubation and buried-bag methods for two Massachusetts forest soils. Can. J. For. Res. 22:1895-1900.

Bowling, C., G. Niznowski, and M.L. Maley. 1997. Ingress of natural regeneration in plantations after tree-length harvest in northwestern Ontario. Ont. Min. Natur. Resour. Northwest Sci. & Technol. Thunder Bay, Ont. TR-112. 23 pp + append.

Bradley, R.L., B.D. Titus, and K. Hogg. 2001. Does shelterwood harvesting have less impact on forest floor nutrient availability and microbial properties than clearcutting? Biol. Fert. Soils 34:162-169.

Brady, N.C. 1990. The Nature and Properties of Soils. (10th ed.) Macmillan Publishing Company, New York, New York. 621 pp.

Brady, N.C. and R.R. Weil. 1999. The Nature and Properties of Soils. (12th ed.) Prentice-Hall, Inc., Upper Saddle River, New Jersey. 881 pp.

Brumelis, G. and T.J. Carleton. 1988. The vegetation of post-logged black spruce lowlands in central Canada. I. Trees and tall shrubs. Can. J. For. Res. 18:1407-1478.

Buse, L.J. and F.W. Bell. 1992. Critical silvics of selected crop and competitor species in northwestern Ontario. Ont. Min. Nat. Resour., Thunder Bay, Ontario. Northwestern Ont. For. Tech. Devel. Unit. 138 pp.

Cade-Menum, B.J., S.M. Berch, C.M. Preston, and L.M. Lavkulich. 2000. Phosphorus forms and related soil chemistry of Podzolic soils on northern Vancouver Island. II. The effects of clear-cutting and burning. Can. J. For. Res. 30(11):1726-1741.

Carlyle, J.C. and D.C. Malcolm. 1986. The use of ion exchange resin bags to assess N availability beneath pure spruce and larch + spruce stands growing on a deep peat soil. Plant Soil 93:123-127.

Cayford, J.H., Z. Chrosciewicz, and H.P. Sims. 1967. A review of silvicultural research in jack pine. Can. Dept. For. and Rural Devel., For. Branch, Departmental Publication 1173. Can. For. Serv., Ottawa, Ontario. 257 pp.

Chang, S.X., C.M. Preston, and G.F. Weetman. 1995. Soil microbial biomass and microbial and mineralizable N in a clear-cut on northern Vancouver Island, British Columbia. Can. J. For. Res. 25:1595-1607.

Chen, H.Y.H., P.V. Krestov, and K. Klinka. 2002. Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. Can. J. For. Res. 32:112-119.

Cooperband, L.R. and T.J. Logan. 1994. Measuring *in situ* changes in labile soil phosphorus with anion-exchange membranes. Soil Sci. Soc. Am. J. 58:105-114.

Cote, B. and J. Fyles. 1994. Leaf litter disappearance of hardwood species of southern Quebec: interaction between letter quality and stand type. Ecoscience 1:322-328. (Cited in Morris 2003)

Dobermann, A., M.F. Pampolino, and M.A.A. Adviento. 1997. Resin capsules for on-site assessment of soil nutrient supply in lowland rice fields. Soil Sci. Soc. Am. J. 61:1202-1213.

Driscoll, K.G., J.M. Arocena, and H.B. Massicotte. 1999. Post-fire soil nitrogen content and vegetation composition in sub-boreal spruce forests of British Columbia's central interior, Canada. For. Ecol. Manage. 121:227-237.

Duckert, D.R. and D.M. Morris. 2001. Effects of harvest intensity on long-term site productivity in black spruce ecosystems: Establishment report. Ont. Min. Nat. Resour., Centre for Northern Forest Ecosystem Research, Thunder Bay, ON. CNFER TR-008. 24p. + append.

Ebell, L. 1972. Cone production and stem growth response of Douglas-fir to rate and frequency of nitrogen fertilization. Can. J. For. Res. 2:327-338.

Edmonds, R.L. 1987. Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington, U.S.A. Can. J. For. Res. 17:499-509.

Edwards, L.M. 1991. The effect of alternate freezing and thawing on aggregate stability and aggregate size distribution of some Prince Edward Island soils. J. Soil Sci. 42:193-204.

Environment Canada. 1982. Canadian climate normals: temperature and precipitation 1951-1980 for Ontario. Env. Can., Ottawa, Ontario. (Cited in Morris *et al.* 2003)

Environment Canada. 2005. The Atlas of Canada. Her Majesty the Queen in Right of Canada. Nat. Resour. Can. http://atlas.gc.ca/site/english/maps/archives/4thedition/environment/land/043_44. January 31, 2006.

Fahey, T.J., J.W. Hughes, M. Pu, and M.A. Arthur. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. For. Sci. 34:744-768.

Fahey, T.J., P.A. Stevens, M. Hornung, and P. Rowland. 1991. Decomposition and nutrient release from logging residue following conventional harvest of Sitka spruce in North Wales. Forestry 64:271-288.

Farrar, J.L. 1995. Trees in Canada. Fitzhenry and Whiteside Ltd., Markham, Ontario. 502 pp.

Federer, C.A. 1983. Nitrogen mineralization and nitrification: depth variation in four New England forest soils. Soil Sci. Soc. Am. J. 47(5):1008-1014.

Federer, C.A., D.E. Turcotte, and C.T. Smith. 1993. The organic fraction- bulk density relationship and the expression of nutrient content in forest soils. Can. J. For. Res. 23:1026-1032.

Flanagan, J.W. and K. Van Cleve. 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Can. J. For. Res. 13:795-817.

Forge, T.A., A.M. Muehlchen, and S.W. Simard. 2001. Influences of clear-cut harvesting and fertilization on structure and function of the soil food web in ICH Forests of southern interior British Columbia. British Columbia Min. For. Res. Program. Extension Note 59. 8 pp.

Foster, N.W. and J.S. Bhatti. 2002. Nutrient cycling in forest ecosystems. pp 579-582 *in* Lal, R. (ed.) Encyclopedia of Soil Science. Marcel Dekker, Inc., New York, New York. 1450 pp.

Foster, N.W. and I.K. Morrison. 1976. Distribution and cycling of nutrients in a natural *Pinus Banksiana* ecosystem. Ecology 57:110-120.

Frazer, D.W., J.G. McColl, and R.F. Powers. 1990. Soil nitrogen mineralization in a clear cutting chronosequence in a northern California conifer forest. Soil Sci. Soc. Am. J. 54:1146-1152.

Frey, B.R., V.J. Lieffers, A.D. Munson, and P.V. Blenis. 2003. The influence of partial harvesting and forest floor disturbance on nutrient availability and understory vegetation in boreal mixedwoods. Can. J. For. Res. 33:1180-1188.

Gibson, D.J. 1986. Spatial and temporal heterogeneity in soil nutrient supply measured using in-situ ion- exchange resin bags. Plant Soil 96:445-450.

Gordon, A.G. 1983. Nutrient cycling dynamics in differing spruce and mixedwood ecosystems in Ontario and the effects of nutrient removals through harvesting. pp 97-118 *in* Wein, R.W., R.R. Riewe, and I.R. Methven (eds.) Proc. Resour. Dynamics of the Boreal Zone., Thunder Bay, Ontario, Aug. 1982. A.C.U.N.S. 544 pp.

Gordon, A.M., D.M. Morris, and A.G. Gordon. 2001. Ecological considerations in forest regeneration and management. *in* Wagner, R.G. and S.J. Colombo (eds.) Regenerating the Canadian forest: principles and practice for Ontario. Fitzhenry & Whiteside, Markham, Ontario. 650 pp.

Gosz, J.R., G.E. Likens, and F.H. Bormann. 1976. Organic matter and nutrient dynamics of the forest floor in the Hubbard Brook Forest, New Hampshire. Oecologia 22:305-320.

Greenwood, R. 1988. Harvest; Potential environmental effects on the forest estate. pp 205-511 *in* Statement of Evidence Panel 10; Harvest. v.I. Environmental Assessment Hearings. Ont. Min. Nat. Resour., Thunder Bay. 511 pp. (Cited in Wiensczyk 1992)

Grigal, D.F. 2000. Effects of extensive forest management on soil productivity. For. Ecol. Manage. 138:167-185.

Grimshaw, H.M., S.E. Allen, and J.A. Parkinson. 1989. Nutrient elements. pp 81-159 *in* Allen, S.E. (ed.) Chemical analysis of ecological materials. (2nd edition). Blackwell Scientific Publications, Oxford, U.K.. (Cited in Morris *et al.* 2003)

Haase, D.L. and R. Rose. 1995. Vector analysis and its use for interpreting plant nutrient shifts in response to silvicultural treatments. For. Sci. 41(1):54-66.

Haeussler, S., L. Bedford, J.O. Boateng, and A. MacKinnon. 1999. Plant community responses to mechanical site preparation in northern interior British Columbia. Can. J. For. Res. 29:1084-1100.

Hangs, R.D., K.J. Greer, and C.A. Sulewski. 2004. The effect of interspecific competition on conifer seedling growth and nitrogen availability measured using ion-exchange membranes. Can. J. For. Res. 34:754-761.

Harris, M.M. and L.O. Safford. 1996. Effects of season and four tree species on soluble carbon content in fresh and decomposing litter of temperate forests. Soil Sci. 161:130-135.

Hart, S.C., J.M. Stark, E.A. Davidson, and M.K. Firestone. 1994. Nitrogen mineralization, immobilization, and nitrification. pp 985-1010 *in* Methods of Soil Analysis. Part 2. Microbiological and Biochemical Properties. Weaver, R.W., J.S. Angle, and P.S. Bottomley. (eds.) Soil Science Society of America, Madison, Wis. 1121 pp.

Hearnden, K.W., S.V. Millison, and W.C. Wilson. 1993. A report of the status of forest regeneration. Ontario Independent Forest Audit, Ont. Min. Nat. Resour., Toronto.

Hendrickson, O.Q., L. Chatarpaul, and D. Burgess. 1989. Nutrient cycling following whole-tree and conventional harvest in northern mixed forest. Can. J. For. Res. 19:725-735.

Herrmann, A. and E. Witter. 2002. Sources of C and N contributing to the flush in mineralization upon freeze-thaw cycles in soils. Soil Biol. Biochem. 34:1495-1505.

Huang, W.Z. and J.J. Schoenau. 1996. Microsite assessment of forest soil nitrogen, phosphorus, and potassium supply rates in-field using ion exchange membranes. Commun. Soil Sci. Plant Anal. 27(15-17):2895-2908.

Huang, W.Z. and J.J. Schoenau. 1997. Seasonal and spatial variations in soil nitrogen and phosphorus supply rates in a boreal aspen forest. Can. J. Soil Sci. 77:597-612.

Ingestad, T. 1967. Nutrient needs of seedlings and young trees. pp 139-141 *in* Proc. Colloq. For. Fertil., 5th Colloq. Internat., Potash Inst. Jyvaskyla, Finland. (Cited in Kimmins 1997)

Ingestad, T. 1971. A definition of optimum nutrient requirements in birch seedlings. II. Physiol. Plant 24:118-125. (Cited in Kimmins 1997)

Ingestad, T. 1979. Mineral nutrition requirements of *Pinus sylvestris* and *Picea abies* seedlings. Physiol. Plant 45:373-380. (Cited in Kimmins 1997)

Ingestad, T. 1981. Nutrition and growth of coniferous seedlings at varied relative nitrogen addition rates. Physiol. Plant 65 109-116. (Cited in Kimmins 1997)

Ingestad, T. 1982. Relative addition rate and external nutrient concentration: driving variables used in plant nutrition research. Plant Cell Environ. 5:443-453.

Johnson, C.E., A.H. Johnson, T.G. Huntington, and T.G. Siccama. 1991a. Whole-tree clear-cutting effects on soil horizons and organic-matter pools. Soil Sci. Soc. Am. J. 55:497-502.

Johnson, C.E., A.H. Johnson, and T.G. Siccama. 1991b. Whole-tree clear-cutting effects on exchangeable cations and soil acidity. Soil Sci. Soc. Am. J. 55(2):502-508.

Kabzems, R. and S. Haeussler. 2005. Soil properties, aspen, and white spruce responses 5 years after organic matter removal and compaction treatments. Can. J. For. Res. 35:2045-2055.

Keenan, R.J. and J.P. Kimmins. 1993. The ecological effects of clear-cutting. Environ. Rev. 1:121-144.

Keeney, D.R. 1980. Prediction of soil nitrogen availability in forest ecosystems: a literature review. For. Sci. 26:159-171.

Kimmins, J.P. 1974. Sustained yield, timber mining, and the concept of ecological rotation; a British Columbia Coastal Forest. For. Ecol. 54:1008-1019. (Cited in Morris 2003)

Kimmins, J.P. 1977. Evaluation of the consequences for future tree productivity of the loss of nutrients in whole-tree harvesting. For. Ecol. Manage. 1:169-183.

Kimmins, J.P. 1997. Forest Ecology: A Foundation for Sustainable Management. (2nd ed.) Prentice-Hall, Inc., Upper Saddle River, New Jersey. 596 pp.

Kimmins, J.P., D. Binkley, L. Chartarpaul, and J. de Catanza. 1985. Biogeochemistry of temperate forest ecosystems: literature on inventories and dynamics of biomass and nutrients. Can. For. Serv., Petawawa Natl. For. Inst., Inf. Rep. PI-X-47E/F.

Kjonaas, O.J. 1999. Factors affecting stability and efficiency of ion exchange resins in studies of soil nitrogen transformation. Commun. Soil Sci. Plant Anal. 30 (17&18):2377-2397.

Klinka, K., Q. Wang, and G.J. Kayahara. 1994. Quantitative characterization of nutrient regimes in some boreal forest soils. Can. J. Soil Sci. 74(1):29-38.

Knoepp, J.D. and W.T. Swank. 1997. Long-term effects of commercial sawlog harvest on soil cation concentrations. For. Ecol. Manage. 93:1-7.

Knoepp, J.D. and W.T. Swank. 2002. Using soil temperature and moisture to predict forest soil nitrogen mineralization. Biol. Fertil. Soils. 36:177-182.

Krause, H.H. and D. Ramlal. 1987. *In situ* nutrient extraction from forested, clear-cut and site-prepared soil. Can. J. Soil Sci. 67:943-952.

Krause, H.H., G.F. Weetman, and P.A. Arp. 1978. Nutrient cycling in boreal forest ecosystems of North America. pp 287-319 *in* Youngberg, C.T. (ed.) Forest soils and land use. Colorado State University, Fort Collins.

Lajtha, K. 1988. The use of ion-exchange resin bags for measuring nutrient availability in an arid ecosystem. Plant Soil. 105:105-111.

Lane, D. 1999. Hyperstat (2nd ed.) Atomic Dog Publishing, Cincinnati, Ohio. 244 pp.

Lavender, D.P. and R.B. Walker. 1979. Nitrogen and related elements in nutrition of forest trees. pp 15-22 *in* Gessel, S.P., R.M. Kenady, and W.A. Atkinson. (eds.) Proc. For. Fert. Conf., Union, Washington, September 25-27, 1979. (Cited in Meyer *et al.* 1997.)

Lavoie, M., D. Pare, and Y. Bergeron. 2007. Relationships between microsite type and the growth and nutrition of young black spruce on post-disturbed lowland black spruce sites in eastern Canada. Can. J. For. Res. 37: 62-73.

Leaf, A.L., R.F. Wittwer, and D.H. Bickelhaupt. 1975. Four-year growth response of plantation red pine to potash fertilization and irrigation in New York. For. Sci. 21:88-96. (Cited in Haase and Rose 1995)

Leyton, L. 1958. The relationship between the growth and mineral nutrition of conifers. pp 323-345 *in* The Physiology of Forest Trees. Thimann, K.V. (ed.) Ronald Press, New York.

Likens, G.E., F.H. Bormann, N.M. Johnson, D.W. Fisher, and R.S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. Ecol. Monogr. 40:23-47. (Cited in Romanowicz *et al.* 1996)

Lindo, Z. and S. Visser. 2003. Microbial biomass, nitrogen and phosphorus mineralization, and mesofauna in boreal conifer and deciduous forest floors following partial and clear-cut harvesting. Can. J. For. Res. 33:1610-1620.

Lorenzen, T.J. and V.L. Anderson. 1993. Design of Experiments: A No-Name Approach. Marcel Dekker, Inc., New York, New York. 414 pp.

Lundell, Y. 1989. *In situ* ion exchange resin bags to estimate forest site quality. Plant Soil 119:186-190.

Lundell, Y. 2001. Soil nutrient availability assessed by *in situ* ion-exchange resin bags as a predictor of growth of Swedish coniferous forests. Scand. J. For. Res. 16(3):260-268.

Mahendrappa, M.K., N.W Foster, G.F. Weetman, and H.H. Krause. 1986. Nutrient cycling and availability in forest soils. Can. J. Soil Sci. 66:547-572.

Maliondo, S.M., M.K. Mahendrappa, and G.D. van Raalte. 1990. Distribution of biomass and nutrients in some New Brunswick forest stands: Possible implications of whole-tree harvesting. For. Can., Maritimes Inf. Rep. M-X-170E/F. 40pp.

Mallik, A.U. and D. Hu. 1997. Soil respiration following site preparation treatments in boreal mixedwood forests. For. Ecol. Manage. 97:256-275.

Marion, G.M. 1979. Biomass and nutrient removal in long-rotation stands. pp 98-110 *in* Proc. Impact of Intensive Harvesting on Forest Nutrient Cycling. Coll. Environ. Sci. & For., SUNY, Syracuse, New York. (Cited in Kimmins 1997)

Marschner, H. 1986. Mineral Nutrition of Higher Plants. Academic Press Inc., London. 674 pp. (Cited in Meyer *et al.* 1997)

Martin, C.W. 1988. Soil disturbance by logging in New England- Review and management recommendations. North. J. Appl. For. 5:30-34.

Maynard, D.G., and D.A. MacIsaac. 1998. Soil nutrient and vegetation response to patch clear-cutting of an aspen forest near Meadow Lake, Saskatchewan. Can. J. Soil Sci. 78:59-68.

McFarland, J.W., R.W. Ruess, K. Kielland, and A.P. Doyle. 2002. Cycling dynamics of NH_4^+ and amino acid nitrogen in soils of a deciduous boreal forest system. Ecosystems 5:775-788.

McInnis, B.G. and M.R. Roberts. 1995. Seedling microenvironment in full-tree and tree-length logging slash. Can. J. For. Res. 25:128-136.

Meyer, W.L., F.W. Bell, P.J. Bastarache, and C. Bowling. 1997. Concepts of tree mineral nutrition related to fertilizer use in northern Ontario forests. Ont. Min. Natur. Resour. Northwest Sci. & Technol. Thunder Bay, Ont. TR- 114. 34pp.

Meyer, W.L., M. Marsh, and P.A. Arp. 1994. Cation exchange capacities of upland soils in eastern Canada. Can. J. Soil Sci. 74:393-408.

Moore, T.R., J.A. Trofymow, B. Taylor, C. Prescott, C. Camire, L. Duschene, J. Fyles, L. Kozac, M. Kranabetter, I. Morrison, M. Siltanen, S. Smith, B. Titus, S. Visser, R. Wein, and S. Zoltai. 1999. Litter decomposition rates in Canadian forests. Global Change Biol. 5:75-82.

Morris, D.M. 1997. The role of long-term site productivity in maintaining healthy ecosystems: a prerequisite of ecosystem management. For. Chron. 73:731-740.

Morris, D.M. 2000. Biogeochemical cycling of macroelements in black spruce (*Picea mariana* (Mill.) BSP) ecosystems: quantifying precipitation and litterfall fluxes. Ph.D. dissertation, University of Guelph, Guelph, ON. (Cited in Morris *et al.* 2003)

Morris, D.M. 2003. Elemental storage and cycling in boreal mixed woods. Boreal Mixedwood Notes No. 29. Ont. Min. Nat. Resour., Centre for Northern Forest Ecosystem Research, Thunder Bay, ON. Queen's Printer for Ontario. 13 pp.

Morris, D.M., A.G. Gordon, and A.M. Gordon. 2003. Patterns of canopy interception and throughfall along a topographic sequence for black spruce dominated forest ecosystems in northwestern Ontario. Can. J. For. Res. 33:1046-1060.

Morrison, I.K. 1974. Mineral nutrition of conifers with special reference to nutrient status interpretation: a review of literature. Can. For. Serv. Publ.1343. 74 pp. (Cited in Meyer *et al.* 1997)

Morrison, I.K. and N.W. Foster. 1979. Biomass and elemental removal by complete-tree harvesting of medium rotation forest stands. pp 111-129 *in* Leaf, A.L. (ed.) Proceeding of Symposium on Impact of Intensive Harvesting on Forest Nutrient Cycling. State University of New York, Syracuse, New York. 421 pp.

Nadlehoffer, K.J., J.D. Aber, and J.M. Melillo. 1984. Seasonal patterns of ammonium and nitrate uptake in nine temperate forest ecosystems. Plant Soil 80:321-335.

Nicolardot, B., G. Fauvet, and D. Cheneby. 1994. Carbon and nitrogen cycling through soil microbial biomass at various temperature. Soil Biol. Biochem. 26:253-261.

Oades, J.M., G.P. Gillman, G. Uehara, N.V. Hue, M. van Noordwijk, G.P. Robertson, and K. Wada. 1989. Interactions of soil organic matter and variable-charge clays. pp 69-65 *in* Coleman, D.C., J.M. Oades, and G. Uehara (eds.) Dynamics of Soil Organic Matter in Tropical Ecosystems. University of Hawaii Press, Honolulu, HI. (Cited in Oorts *et al.* 2003)

Ohlund, J. and T. Nasholm. 2002. Low nitrogen losses with a new source of nitrogen for cultivation of conifer seedlings. Environ. Sci. Technol. 36:4854-4859.

Olsson, B.J., J. Bengtsson, and H. Lundkvist. 1996. Effects of different forest harvest intensities on the pools of exchangeable cations in coniferous forest soils. For. Ecol. Manage. 84:135-147.

OMNR. 1997a. Silviculture Guide to Managing for Black Spruce, Jack Pine, and Aspen on Boreal Forest Ecosites in Ontario. Book I: Silviculture in Ontario. Version 1.1. Ont. Min. Nat. Resour., Queen's Printer for Ontario, Toronto. 146 pp.

OMNR. 1997b. Silviculture Guide to Managing for Black Spruce, Jack Pine, and Aspen on Boreal Forest Ecosites in Ontario. Book II: Ecological and Management Interpretations for Northwest Ecosites. Version 1.1. Ont. Min. Nat. Resour., Queen's Printer for Ontario, Toronto. 370 pp.

OMNR. 1998. Ontario's Forests: Management for Today and Tomorrow. Ont. Min. Natur. Resour. Queen's Printer for Ontario. 16 pp.

Orlander, G., G. Egnell, and A. Albrekston. 1996. Long-term effects of site preparation on growth in Scots pine. For. Ecol. Manage. 86:27-37.

Pare, D., and K. Van Cleve. 1993. Aboveground biomass production and nutrient accumulation on post-harvested white spruce sites in interior Alaska. Can. J. For. Res. 23:1233-1239.

Pastor, J., R.W. Gardner, V.H. Dale, and W.M. Post. 1987. Successional changes in nitrogen availability as a potential factor contributing to spruce declines in boreal North America. Can. J. For. Res. 17:1394-1400. (Cited in Morris 2003)

Patterson, T.B., R.D. Guy, and Q.L. Dang. 1997. Whole-plant nitrogen- and water-relations traits, and their associated trade-offs, in adjacent muskeg and upland boreal spruce species. Oecologia 110:160-168.

Paul, E.A., and F.E. Clark. 1989. Soil microbiology and biochemistry. Academic Press, Inc., San Diego, Calif. 237 pp. (Cited in Forge *et al.* 2001)

Peltzer, D.A., M.L. Bast, S.D. Wilson, and A.K. Gerry. 2000. Plant diversity and tree responses following contrasting disturbances in boreal forest. For. Ecol. Manage. 127:191-203.

Perala, D.A. 1990. *Populus tremuloides* Michx. -quaking aspen. pp 555-569 *in* Burns, R.M. and B.H. Honkala. (eds.) Silvics of North America. Vol. 2. Hardwoods. U.S. Dep. Agric., Agric. Handb. 654 pp.

Perala, D.A., and D.H. Alban. 1982. Rates of forest floor decomposition and nutrient turnover in aspen, pine and spruce stands on two soils. Res. Pap. NC-227. St. Paul, Minn, USDA, For. Serv., North Central For. Exper. Station. 5 pp.

Persson, T. and A. Wiren. 1995. Nitrogen mineralization and potential nitrification at different depths in acid forest soils. Plant Soil 168-169:55-65.

Pfadenhauer, J. 1979. Die Stickstoffmineralisation in Boden Subtropischer Regenwalder in Sudbrasilien, Oecol. Plant. 14:27-40. (Cited in Vitousek 1981)

Pothier, D. 2000. Ten-year results of strip clear-cutting in Quebec black spruce stands. Can. J. For. Res. 30:59-66.

Prescott, C.E., D.G. Maynard, and R. Laiho. 2000. Humus is northern forests: friend or foe? For. Ecol. Manage. 133:23-36.

Prescott, C.E., B.R. Taylor, W.F.J. Parsons, D.M. Durall, and D. Parkinson. 1993. Nutrient release from decomposing litter in Rocky Mountain coniferous forests: influence of nutrient availability. Can. J. For. Res. 23:1576-1586.

Qian, P. and J.J. Schoenau. 1995. Assessing nitrogen mineralization from soil organic matter using anion exchange membranes. Fert. Res. 40:143-148.

Qian, P. and J.J. Schoenau. 1997. Recent developments in use of ion exchange membranes in agricultural and environmental research. Recent Res. Devel. Soil Sci. 1:43-54.

Qian, P. and J.J. Schoenau. 2002. Practical applications of ion exchange resins in agricultural and environmental soil research. Can. J. Soil Sci. 82:9-21.

Quoreshi, A.M. and V.R. Timmer. 2000. Early outplanting performance of nutrient-loaded containerized black spruce seedlings inoculated with *Laccaria bicolor*: a bioassay study. Can. J. For. Res. 30:744-752.

Racey, G.D., A.G. Harris, J.K. Jeglum, R.F. Foster and G.M. Wickware. 1996. Terrestrial and wetland ecosites of northwestern Ontario. Ont. Min. Nat. Resour., Northwest Sci. & Technol. Field Guide FG-02. 94 pp + Append.

Radwan, M.A. and C.A. Harrington. 1986. Foliar chemical concentrations, growth, and site productivity relations in western red cedar. Can. J. For. Res. 16:1069-1075.

Ralston, M.L. and R.I. Jenrich. 1978. DUD, a derivative free algorithm for nonlinear least squares. Technometrics. 24:7-14.

Raulund-Rasmussen, K. and H. Vejre. 1995. Effect of tree species and soil properties on nutrient immobilization in the forest floor. Plant Soil 168-169:345-352.

Richards, B.N., J.E.N. Smith, G.J. White, and J.L. Charley. 1985. Mineralization of soil nitrogen in three forest communities from the New England region of New South Wales. Aust. J. Ecol. 10:429-441. (Cited in Chang *et al.* 1995)

Roberts, M.R., and H. Dong. 1993. Effects of soil organic layer removal on regeneration after clear-cutting a northern hardwood stand in New Brunswick. Can. J. For. Res. 23: 2093-2100.

Robinson, D.E., R.G. Wagner, F.W. Bell, and C.J. Swanton. 2001. Photosynthesis, nitrogen-use efficiency, and water-use efficiency of jack pine seedlings in competition with four boreal forest plant species. Can. J. For. Res. 31:2014-2025.

Romanowicz, R.B., C.T. Driscoll, T.J. Fahey, C.E. Johnson, G.E. Likens, and T.G. Siccama. 1996. Changes in biogeochemistry of potassium following a whole-tree harvest. Soil Sci. Soc. Am. J. 60(6):1664-1674.

Rook, D.A. 1991. Seedling development and physiology in relation to mineral nutrition. pp. 84-111 *in* R. van den Driessche. Mineral nutrition of conifer seedlings. CRC Press, Boca Raton, Florida. 274 pp. (Cited in Meyer *et al.* 1997)

Rowe, J.S. 1972. Forest Regions of Canada. Dept. Environ., Can. For. Serv., Pub. No. 1300. 172 pp. (Cited in Duckert and Morris 2001)

Rudolph, T.D. and P.R. Laidly. 1990. *Pinus banksiana* Lamb. -jack pine. pp 280-239 *in* Burns, R.M. and B.H. Honkala (eds.) Silvics of North America. Vol. 1. Conifers. USDA, Agric. Handb. 654 pp.

Ruel, J.C., R. Horvath, C.H. Ung, and A. Munson. 2004. Comparing height growth and biomass production of black spruce trees in logged and burned stands. For. Ecol. Manage. 193:371-384.

Safford, L.O., J.C. Bjorkbom, and J.C. Zasada. 1990. *Betula papyrifera* Marsh. - paper birch. pp 158-171 *in* Burns, R.M. and B.H. Honkala (eds.) Silvics of North America. Vol. 2. Hardwoods. USDA, Agric. Handb. 654 pp.

SAS Institute Inc. 1987. SAS/STAT guide for personal computers. (6th ed.) SAS Institute Inc., Cary, North Carolina. 1028 pp.

Schmidt, M.G., S.E. Macdonald, and R.L. Rothwell. 1996. Impacts of harvesting and mechanical site preparation on soil chemical properties of mixed-wood boreal forest sites in Alberta. Can. J. Soil Sci. 76:531-540.

Schoenau, J. and W.Z. Huang. 1991. Anion-exchange membrane, water, and sodium bicarbonate extractions as soil tests for phosphorus. Commun. Soil. Sci. Plant Anal. 22(5&6):465-492.

Schoenau, J., P. Qian, and W.Z. Huang. 1993. Assessing sulphur availability in soil using ion exchange membranes. Sulphur Agric. 17:13-17. (Cited in Sherrod *et al.* 2002)

Sherrod, S.K., J. Belnap, and M.E. Miller. 2002. Comparison of methods for nutrient measurement in calcareous soils: ion-exchange resin bag, capsule, membrane, and chemical extractions. Soil Sci. 167(10):666-679.

Sherrod, S.K., J. Belnap, and M.E. Miller. 2003. Comparison of ion-exchange resin counterions in the nutrient measurement of calcareous soils: Implications for correlative studies of plant-soil relationships. Commun. Soil Sci. Plant Anal. 34(13-14):1981-2001.

Sibbesen, E. 1977. A simple ion-exchange resin procedure for extracting plant-available elements from soil. Plant Soil 46:665-669.

Sibbesen, E. 1978. An investigation of the anion-exchange resin method for soil phosphate extraction. Plant Soil. 50:305-321.

Skogland, T., S. Lomeland, and J. Goksoyr. 1988. Respiratory burst after freezing and thawing of soil: experiments with soil bacteria. Soil Biol. Biochem. 20:851-856.

Skogley, E.O. and A. Dobermann. 1996. Synthetic ion exchange resins: soil and environmental studies. J. Environ. Qual. 25:13-24.

Smith, P.F. 1962. Mineral analysis of plant tissue. Ann. Rev. Plant Physiol. 13:81-108. (Cited in van den Driessche 1974)

Smith, D.M., B.C. Larson, M.J. Kelty, and P.M.S. Ashton. 1997. The Practice of Silviculture: Applied Forest Ecology. (9th ed.) John Wiley and Sons, Inc., New York, New York. 537 pp.

Snedecor, G.W. and W.G. Cochran. 1989. Statistical Methods. (8th ed.) Blackwell Publishing, Ames, Iowa. 503 pp.

Staaf, H., and B.J. Olson. 1994. Effects of slash removal and stump harvesting on soil water chemistry in a clearcutting in SW Sweden. Scand. J. For. Res. 9:305-310.

Stanford, G. and E. Epstein. 1974. Nitrogen mineralization water relations in soils. Soil Sci. Soc. Am. Proc. 38:103-107.

Stark, J.M., and M.K. Firestone. 1996. Kinetic characteristics of ammonium-oxidizer communities in a California oak woodland-annual grassland. Soil Biol. Biochem. 28:1307-1317. (Cited in Knoepp and Swank 2002)

Stark, J.M., and S.C. Hart. 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. Nature 385:61-64.

Stottlemyer, R. and D. Toczydlowski. 1999. Nitrogen mineralization in a mature boreal forest, Isle Royale, Michigan. J. Environ. Qual. 28(2):709-720.

Sullivan, J.H., B.H. Bovard, and E.M. Middleton. 1997. Variability in leaf-level CO_2 and water fluxes in *Pinus banksiana* and *Picea mariana* in Saskatchewan. Tree Physiol. 17:553-561.

Swan, H.S.D. 1970. Relationships between nitrogen supply, growth and nutrient concentrations in the foliage of black spruce and jack pine. Pulp Pap. Res. Inst. Can. Woodland Papers. No. 19. 46 pp. (Cited in Meyer *et al.* 1997)

Tappeiner, J.C. II. 1971. Effect of harvesting methods on the distribution of nutrients in slash and litter. pp. 13-15 *in* Zasada, Z.A. (ed.) Proc. conference on biological and economic considerations in mechanized harvesting. Agric. Exp. Sta. Univ. Minn., Misc. Rep. 116. 51 pp. (Cited in Wiensczyk 1992)

Timmer, V.R. and L.D. Morrow. 1984. Predicting fertilizer growth response and nutrient status of jack pine by foliar diagnosis. pp 335-351 *in* Forest soils and treatment impact. Stone, E.L. (ed.) Proc. 6th N. Am. For. Soils Conf., Dept. For., Wildlife and Fisheries, Univ. of Tennessee, Knoxville. (Cited in Haase and Rose 1995)

Timmer, V.R., H.M. Savinsky, and G.T. Marek. 1983. Impact of intensive harvesting on nutrient budgets of boreal forest stands. pp 131-147 *in* Wein, R.W., R.R. Riewe and I.R. Methren (eds.) Proc. resources and dynamics of the Boreal zone., Thunder Bay, Ont., August 1982, A.C.U.N.S. 544 pp.

Timmer, V.R. and Y. Teng. 1999. Foliar nutrient analysis of sugar maple decline: retrospective vector analysis. pp 69-73 *in* Sugar maple ecology and health: proceedings of an international symposium. Gen. Tech. Rep. NE-26. Radnor, Penn, USDA For. Serv, Northeastern Res. Stn., Warren, Penn., June 2-4 1998.

van den Driessche, R. 1974. Prediction of mineral nutrient status of trees by foliar analysis. Bot. Rev. 40(3): 347-394.

Van Dijk, H. 1971. Colloid chemical properties of humic matter. pp. 16-25 *in* McLaren, A.D., and J. Skujins (eds.) Soil Biochemistry. Vol. 2. Marcel Dekker, New York, New York.

Velleman, P.F. 1997. Data Desk Version 6.0. Data Description, Inc., Ithaca, New York.

Verburg, P.S.J., D. Van Dam, M.M. Hefting, and A. Tietema. 1999. Microbial transformations of C and N in a boreal forest floor as affected by temperature. Plant Soil. 208:187-197.

Vervaet, H., B. Massart, P. Boeckx, O. Van Cleemput, and G. Hofman. 2002. Use of principal component analysis to assess factors controlling net N mineralization in deciduous and coniferous forest soils. Biol. Fertil. Soils 36:93-101.

Viereck, L.A., C.T. Dyrness, K. van Cleve, and M.J. Foote. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Can. J. For. Res. 13:703-720.

Viereck, L.A. and W.F. Johnston. 1990. *Picea mariana* (Mill.) B.S.P. pp 227-237 *in* Burn, R.M. and B.H. Honkala. (eds.) Silvics of North America. Vol. 2. Hardwoods. USDA, Agric. Handb. 654 pp.

Vitousek, P.M. 1977. The regulation of element concentrations in mountain streams in the Northeastern United States. Ecol. Monogr. 47:65-87. (Cited in Morris 2003)

Vitousek, P.M. 1981. Clear-cutting and the nitrogen cycle *in* F.E. Clark. and T. Roswell (eds.) Terrestrial Nitrogen Cycles. Processes, Ecosystem Strategies and Management Impacts. Ecol. Bull. 33:631-642.

Vitousek, P.M., and P.A. Matson. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed Loblolly pine plantation. Ecology 66:1360-1376. (Cited in Lindo and Visser 2003)

Waters, I., S.W. Kembel, J.F. Gingras, and J.M. Shay. 2004. Short-term effects of cut-to-length versus full-tree harvesting on conifer regeneration in jack pine, mixedwood, and black spruce forests in Manitoba. Can. J. For. Res. 34:1938-1945.

Weetman, G.F. and D. Algar. 1983. Low-site class black spruce and jack pine nutrient removals after full-tree and tree-length logging. Can. J. For. Res. 13:1030-1036.

Weetman, G.F. and B. Weber. 1972. The influence of wood harvesting on the nutrient status of two spruce stands. Can. J. For. Res. 2:351-369.

White, E.H. and A.E. Harvey. 1979. Modification of intensive management practises to protect forest nutrient cycles. pp 264-278 *in* Proc. impact of intensive harvesting on forest nutrient cycling. SUNY-ESF, New York, August 13-16 1979, 412 pp.

Wiensczyk, A. 1992. A brief review of the issues surrounding full tree harvesting. Ont. Min. Nat. Resour., N.W. Ont. For. Tech. Dev. Unit, Thunder Bay, Ont., Tech. Note TN-13. 12 pp.

Zar, J.H. 1999. Biostatistical Analysis. (4th ed.) Prentice-Hall, Inc., Upper Saddle River, New Jersey. 663 pp. + append.

APPENDICES

APPENDIX I
UNIT CONVERSION METHODS - PPM to KG·HA^{-1}

The laboratory results obtained were reported in ppm, which is equivalent to mg·L^{-1}. For an example of the calculation, I have used a value of 25.0 mg·L^{-1} of NH_4^+-N. The first step was to calculate the actual amount of NH_4^+ captured by the extraction liquid, which was 50 ml, not 1 L. To do this, multiply the nutrient values by the amount of extract used per sample, and divide by 1000 ml, to yield the value in mg.

Step 1: 25.0 mg · 50 ml/ 1000 ml
= 1.25 mg

Using the value from Step 1, and the surface area of the resin (20 cm^2), the amount of NH_4^+ per hectare can be calculated.

Step 2: 1.25 mg · 100 000 000 cm^2·ha^{-1}/ 20 cm^2
= 6 250 000 mg·ha^{-1}

Step 2 gives the value in mg·ha^{-1} so it is an easy conversion to achieve kg·ha^{-1}. Divide the value from Step 2 by 1 000 000 mg·kg^{-1}.

Step 3: 6 250 000 mg·ha^{-1} / 1 000 000 mg·kg^{-1}
= 6.25 kg·ha^{-1}

The values used in this example are not values representative of NH_4^+-N values typically found within upland, black spruce dominated sites, such as those used as study sites in this experiment. They are merely presented as an example.

APPENDIX II - SMALL TREE BIOMASS REGRESSION EQUATIONS

Table I.1. Model-fitting statistics for biomass-root collar diameter curves for black spruce tree components based on a 2-parameter power function (Equation [3]).

	Model Parameters								
Tree	B_1			B_2					
Component	Value	Std. Error	95% C.I.	Value	Std. Error	95% C.I.	R^2	F-Ratio	MSE
Total Weight	0.3973	0.3118	-0.2437 1.0382	2.2063	0.2001	1.7951 2.6176	0.952	256.7	130627.0
Total Foliage	0.4119	0.3011	-0.2071 1.0308	1.9919	0.1874	1.6066 2.3771	0.952	257.4	26221.7
Current Foliage	0.1265	0.0994	-0.0778 0.3308	2.0156	0.2012	1.6019 2.4292	0.946	226.4	3382.3
Current Twig	0.0415	0.0304	-0.0209 0.1039	1.9254	0.1879	1.5392 2.3116	0.950	246.2	165.9
Branch Wood	0.0577	0.0577	-0.0609 0.1762	2.3489	0.2542	1.8264 2.8714	0.930	173.35	12479.0
Stem Wood	0.0127	0.0174	-0.0232 0.0485	2.6753	0.3475	1.9611 3.3895	0.897	112.93	12120.3
Bark	0.0413	0.0455	-0.0523 0.1348	2.0747	0.2817	1.4956 2.6538	0.902	119.59	1080.6

Table II.2. Model-fitting statistics for biomass-root collar diameter curves for jack pine tree components based on a 2-parameter power function (Equation [3]).

	Model Parameters								
Tree	B_1			B_2					
Component	Value	Std. Error	95% C.I.	Value	Std. Error	95% C.I.	R^2	F-Ratio	MSE
Total Weight	0.0592	0.0453	-0.0339 0.1523	2.6693	0.1869	2.2851 3.0535	0.955	273.3	97017.7
Total Foliage	0.0217	0.0194	-0.0182 0.0616	2.6765	0.2189	2.2266 3.1265	0.939	200.57	18757.0
Current Foliage	0.00946	0.0094	-0.0098 0.0287	2.6479	0.2419	2.1506 3.1452	0.925	159.82	3554.6
Current Twig	0.00454	0.0031	-0.0018 0.0109	2.5960	0.1670	2.2527 2.9394	0.961	319.4	267.6
Branch Wood	0.00109	0.00127	-0.00152 0.00371	3.3410	0.2803	2.7648 3.9173	0.946	229.54	9908.8
Stem Wood	0.1568	0.1400	-0.1309 0.4444	2.0282	0.2229	1.570 2.4865	0.892	107.5	9679.3
Bark	0.1033	0.0603	-0.0206 0.2272	1.7837	0.1475	1.4806 2.0869	0.939	201.5	322.2

Table III.3. Model-fitting statistics for biomass-root collar diameter curves for trembling aspen components based on a 2-parameter power function (Equation [3]).

Tree Component	Model Parameters						R^2	F-Ratio	MSE
	B_1			B_2					
	Value	Std. Error	95% C.I.	Value	Std. Error	95% C.I.			
Total Weight	0.1113	0.0717	-0.0356 0.2582	2.4898	0.1894	2.1018 2.8778	0.965	385.5	6346.0
Total Foliage	0.1121	0.0801	-0.0519 0.2761	2.0589	0.2120	1.6246 2.4931	0.953	286.9	469.0
Current Twig	0.0422	0.0750	-0.1114 0.1958	1.8913	0.5294	0.8069 2.9757	0.762	44.8	138.4
Branch Wood	0.00042	0.00045	-0.00051 0.00135	3.7345	0.3102	3.099 4.370	0.928	179.5	1017.9
Stem Wood	0.1137	0.1048	-0.1011 0.3284	2.1282	0.2733	1.5685 2.6879	0.926	174.71	1264.0
Bark	0.0496	0.0371	-0.0264 1.7149	2.1681	0.2213	1.7149 2.6213	0.950	268.2	205.5