SOIL PROPERTIES FOLLOWING CLEARCUT HARVESTING AND WILDFIRE AND THEIR RELATIONSHIP WITH REGENERATION IN THE QUEBEC BOREAL FOREST

by

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ABSTRACT

SOIL PROPERTIES FOLLOWING CLEARCUT HARVESTING AND WILDFIRE AND THEIR RELATIONSHIP WITH REGENERATION IN THE QUEBEC BOREAL FOREST

A comparison of the soil fertility and relationships between soil fertility and early regenerating vegetation were examined following clearcut harvesting and wildfire in the black spruce-feathermoss zone of west-central Quebec. During the summer of 1997, sampling was conducted in wildfires burnt 2, 14, and 21 years ago, stands clearcut within ±3 years of each fire, and undisturbed control stands. At each site an estimation of vegetative cover of each species present and a volumetric sample of the forest floor (FH), and mineral soil (0-10 cm) were collected from at least 8 fire and cut sites and at least 4 control sites in each study area. The comparison between the soil fertility of stands clreacut and burnt suggested that important differences exist following these two disturbance types in the boreal forest. The forest floor of clearcut sites had greater dry mass, mass of total nutrients and mineralized N than fire or control sites, whereas fire sites generally had higher pH and concentrations of total nutrients than clearcut or control sites. Partitioning of the variance of the vegetation data between soil fertility and general site characteristic variables was carried out to evaluate the direct influence of post-disturbance soil fertility on the composition of regenerating vegetation. All explanatory variables accounted for 53.6% of the variance, of which 23.2% was exclusively attributed to soil fertility variables. Disturbance severity is suggested as an important factor, directly affecting the initial composition of the regenerating vegetation, and indirectly affecting soil fertility and stand productivity in the later stages of regeneration.

RÉSUMÉ

LES PROPRIÉTÉS DU SOL APRÈS COUPE À BLANC ET FEU, ET LEUR RELATION AVEC LA RÉGÉNÉRATION DANS LA FORÊT BORÉALE DU QUÉBEC

La fertilité du sol a été comparée dans des peuplements après la coupe à blanc et des feux de forêt dans la pessière noire à mousses du centre et de l'ouest du Québec. Les relations existant entre la végétation du début de la régénération et la fertilité du sol ont aussi été examinées. Des sites brûlés par des feux naturels il y a 2, 14 et 21 ans, des sites qui ont été coupés à blanc à ± trois ans de chaque feu et des sites témoins non-pertubés ont tous été échantillonnés pendant l'été 1997. Pour chaque site étudié, une évaluation du couvert végétal par espèce et une échantillonnage volumétrique de la couverture morte (horizons F et H) et le sol minéral (0-10 cm) ont été récoltés sur au moins huit sites de feu de forêt et de coupe à blanc, et au moins quatre sites témoins. La comparaison entre des peuplements coupés à blanc et brûlés illustre que, suite à ces deux types de perturbations de la forêt boréale, il existe des différences importantes au niveau de la fertilité du sol. La masse des éléments nutritifs totaux et le N disponible (minéralisation) du couvert mort des sites coupés à blanc étaient plus élevés que pour les sites de feu de forêt et les sites témoins. Les sites incendiés avaient, cependant, des concentrations d'éléments nutritifs disponibles et totaux généralement plus élevées que les sites de coupe à blanc et les sites témoins. La variance observée dans les données de végétation a été partitionée entre des variables reflétant la fertilité du sol et les caractéristiques générales des sites afin d'évaluer l'influence directe de la fertilité du sol sur la composition de la régénération végétale. L'ensemble des variables environnementales mesurées représente 53.6% de la variance, dont 23.2% étaient exclusivement attribuables à la fertilité des sols. La sévérité de la perturbation semble être un facteur important, affectant directement la composition initiale de la régénération végétale et indirectement la fertilité du sol et la productivité d'un peuplement forestier à long terme.

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INTRODUCTION

0.1 Boreal Ecology and Natural Disturbances

Relative to southern temperate forests, net annual production is low in the boreal forest, but is not surprising given the short growing season and low availability of nutrients (Bonan, 1992; Barbour et al., 1987; Pritchett and Fisher, 1987). Tree species, such as white spruce (*Picea glauca*) and black spruce (*Picea mariana*) dominate mature boreal stands in a mix of other conifers and a few deciduous species (Barbour et al., 1987). The understory of mature stands is characterized by a thick continuous mat of feathermoss (e.g. *Pleurozium schreberi*) and lichens (Larsen, 1980). Increased productivity in the feathermoss layer and a build-up of organic matter in the forest floor during boreal succession represents: 1) an increasing nutrient sink (Paré et al., 1993), due to lower temperatures at the forest floor and resulting slower rates of decomposition (Pritchett and Fisher, 1987), 2) decreased nutrient availability, and 3) decreased tree productivity (Larsen, 1980).

Natural disturbances play a vital role in function and structure of most forest ecosystems (Attiwill, 1994). The Canadian Boreal forest is no exception. Small and large scale disturbances occur often, generating a mosaic of uneven aged stands across the landscape. Fire (Foster, 1983), spruce budworm outbreaks (Morin, 1994; Blais, 1983) and windthrow all occur relatively frequently in the Canadian boreal forest (Kimmins, 1996) and serve to promote successional processes and species diversity (Attiwill, 1994).

Stand destroying crown fires occur frequently in the boreal forest (Kimmins, 1996; Payette, 1992). Adaptations in the dominant tree species of the boreal forest illustrate the dependance and co-evolution of the vegetation and the natural disturbance regime. Through thousands of years of natural selection (MacDonald, 1995), reproductive strategies, such as the widespread dispersal of small, light seeds, suckering from roots, and serotinous cones that open with intense heat, have helped tree species in the boreal forest adapt to disturbances like wildfire (Johnson, 1992; Perry, 1994).

0.2 Clearcut Harvesting and Sustainable Forest Management

'Nature provides a blueprint, but one that we must use carefully.'

(Perry, 1994)

Clearcutting is one of the major anthropogenic disturbances in the boreal forest, representing almost 90% of all logging practices in Canada (BSAT, 1994). Recent emphasis in sustainable forestry has focused on management practices that mimic (as closely as possible) the effects of natural disturbances (Bergeron and Harvey, 1997; Hansen et al., 1991). For clearcutting as a forest management practice to mimic the effects of wildfire, it must preserve inherent ecosystem processes while maintaining the natural configuration of late successional uneven aged stands across the boreal landscape (Bondrup-Neilsen, 1995; Perry, 1994)

Working knowledge of the natural disturbance regime is necessary to maintain the diversity and productivity of managed forests (Attiwill, 1994). Both the periodicity and spatial pattern of natural disturbances must be respected, ensuring the mosaic of uneven aged stands is maintained, and therefore providing different ecosystem niches in stands of different successional seres (BSAT, 1994; Perry, 1994). At the smaller stand scale it is important for forest management to preserve key ecosystem processes, maintaining the biotic and abiotic dynamics that occur between natural disturbances, in order to guarantee long-term productivity of boreal ecosystems (Perry and Amaranthus, 1997; Perry, 1994).

0.3 Effect of Fire on Forest Ecosystems

Wildfire consumes organic matter, generating a pulse of mineralized nutrients and preparing the seedbed for secondary succession (Kelsall et al., 1977). The impact of fire on ecosystem biological, chemical and physical soil processes is directly related to disturbance severity (Pritchett and Fisher, 1987). Nutrient losses are common during and following fire and occur mostly through the pathways of volatilization and ash convection, but also through surface runoff, wind and water erosion, and leaching (Schoch and

Binkley, 1986).

Volatilization primarily effects the loss of carbon, sulphur and nitrogen. Nitrogen volatilatilizes at 200°C (Pritchett and Fisher, 1987) and is therefore easily lost during wildfires which achieve temperatures of 300-700°C (Knight, 1966). It is estimated that organic nitrogen losses can be as high as 15-30% of the total nitrogen in burned biomass (Kutiel and Shaviv, 1992; Kutiel and Naveh, 1987). Base cations (Ca, K, Mg) and other less volatile nutrients. such as P can be lost by ash convection during wildfire (Woodmansee and Wallach, 1981).

The remaining nutrients (most importantly NH_4^+, Ca^{2+}, K^+, Mg^{2+} and P) are deposited as ash on the forest floor in their mineral form. The concentrated supply of available nutrients in ash are vulnerable to erosion and runoff, as a result of lower infiltration rates and a decrease in the soil's absorption capability (Kelsall, et al., 1977; Ahlgren and Ahlgren, 1960). Solubilized nutrients that percolate through the soil profile are available for plant and microorganism utilization, fixed on exchange sites, or lost through leaching (Woodmansee and Wallach, 1981).

Wildfire often results in the combustion of organic matter in the forest floor. In sandy soils, the humus layer may be responsible for the majority of the cation exchange capacity (CEC) and therefore the ability of the soil to retain plant nutrients against the effects of leaching (Kelsall, 1977). During a severe fire, 20% of the CEC can be lost due to its dependance on the humus layer (Pritchett and Fisher, 1987).

A common effect of fire is a substantial increase in soil pH (Kutiel and Shaviv, 1992). The magnitude of the increase is directly related to the increased concentration of base cations at the soil surface, as well as the texture and organic matter content of the soil (Pritchett and Fisher, 1987). The flush of base cations through the soil profile removes Al^{3+} and H^+ from exchange sites and places them into solution where they can be easily leached, increasing base saturation and consequently soil pH.

Soil microbes live in direct contact with the soil and are therefore very sensitive to changes in the soil microenvironment. The majority of microbial activity occurs near the soil surface (Paul and Clark, 1989) and is negatively effected by large increases in soil temperature and reduced soil moisture occurring in the first 2.5 to 5 cm during fire (Ahlgren, 1974). Soil temperatures as low as 100° C (buffered by soil moisture) have been known to kill the majority of microbial populations (Barbour et al., 1987).

Immediately following fire, ecosystem physical and chemical components are greatly changed. The newly acquired charcoal and darkened forest floor act in concert with increased incident radiation to produce higher soil temperatures (Ulrey and Graham, 1993). Soil water is made more available as a result of reduced interception and evapotranspiration by the vegetative community (Adams and Boyle, 1980). Organic matter consumed by fire decreases the CEC (Wright and Bailey, 1982), and solubilized ash percolating through the soil profile increases pH and nutrient availability (Ahlgren, 1974).

Little net nitrification or denitrification occurs in most ecosystems that contain viable root systems, living aerial portions of plants, and an active microbial community (Killham, 1990). This phenomenon is mainly caused by the 'tightness' of the nitrogen cycle in most forest ecosystems. Normally, NH_4^+ is rapidly taken up by plants and microorganisms (Larsen, 1980). Reduced immobilization of nutrients by plants, combined with the rapid mineralization of nutrients by fire, elevates the availability of nutrients to abnormally high levels. Excess nitrogen produced by either ash deposition or mineralization by microbes is available for other microbial process like nitrification. An increase in nitrogen availability accompanied by an increase in soil pH and the availability of other nutrients results in a growth of the nitrifying bacteria population (Wright and Bailey, 1982; Ahlgren, 1974; Ahlgren and Ahlgren, 1960). Nitrification and possibly dentrification alter the form of available nitrogen, making nitrogen susceptible to loss by either leaching of mobile nitrates or by the volatilization of nitrous oxides (Paul and Clark, 1989).

The influence of fire on soil biota is highly variable and not well understood (Ahlgren, 1974; Barbour et al., 1987). In most cases the effects of the nutrient pulse and other changes following fire are short lived (within the first 4 years) (Adams and Boyle, 1982; 1980), but some studies have demonstrated that it can take the microbial population up to 12 years following disturbance to become reestablish (Fritze et al., 1993). As the vegetation continues to regenerate, the forest floor recovers, causing the soil environment to stabilize and the microbial population to return to prefire levels (Woodmansee and Wallach, 1981). Until such time, the soil physical environment will remain in a state of flux, subjected to the vagaries of the ambient environment, reduced rates of water infiltration and increased rates of erosion (Wright and Bailey, 1982).

0.4 Effect of Clear-cut Harvesting on Forest Ecosystems

Clear-cut harvesting has been scrutinized by an informed public, and defended by the forest industry, which argues that clear-cut harvesting is the safest, most economically efficient and environmentally sustainable management practice currently available (Keenan and Kimmins, 1993). The five main effects of clear-cut harvesting on forest soil fertility are: 1) nutrient removal in the harvested material, 2) increased rates of erosion and runoff accompanied by leaching of nutrients, 3) accelerated biological mineralization of organic matter, 4) acidification of forest soil (Mroz et al., 1985), and 5) soil compaction (Keenan and Kimmins, 1993; Greacen and Sands, 1980). The degree to which nutrients are lost from an ecosystem following clear-cut harvesting varies with ecosystem conditions, such as vegetation type and physical site characteristics (slope, drainage,...), as well as the severity of the clearcut and scarification, but will decrease in proportion to the rate of regenerating vegetation (from Marks and Bormann, 1972).

Any biomass harvested or removed from a forest represents a nutrient loss and net acidification of the ecosystem (Edmonds et al., 1989). Base cation absorption by trees is an active process in which base cations in soil solution are exchanged for H^+ ions. Immobilized base cations in harvested timber are not returned to the soil resulting in nutrient loss and ecosystem acidification (Nykvist and Rosen, 1985).

Changes in forest hydrology are common following harvesting and cause increased rates of erosion and leaching (Armson, 1977). A reduction in the rate of transpiration in harvested ecosystems can result in a significant rise in the water table and increase nutrient loss due to leaching (Burger and Prichett, 1988). Increased potential for erosion is associated with the improper construction of logging roads; excessive disturbance of the understory vegetation, and soil; soil compaction; and intensive site preparation (Prichett, 1979), reducing the rates of infiltration and increasing surface runoff. Nutrient loss from erosion and leaching is expected to decline following disturbance at a rate inversely proportional to the extent of regeneration (Marks and Bormann, 1972).

Factors influencing the rate of decomposition in natural ecosystems include temperature, the availability of moisture, and the quality of available organic matter (Swift et al., 1979). There is usually a substantial increase in decomposition of litter and logging residues following harvesting (Kimmins, 1997; Mroz et al., 1985). Decomposition rates are increased as a result of the mechanical repositioning of soil organic matter, input of fresh carbon from logging residues, increased incident radiation (increased soil temperature) and greater availability of soil water (Keenan and Kimmins, 1993; Burger and Pritchett, 1988; McColl and Powers, 1984).

Increased mineralization produces a gradual nutrient pulse after logging. The recovery of the ecosystem and therefore the return of decomposition and mineralization rates to predisturbance levels is likely to occur within a period greater than 5 years following clear-cut harvesting in the boreal forest (Keenan and Kimmins, 1993). The duration of the pulse is dependent on the rate of microclimate restoration (Marks and Bormann, 1972), which is proportionate to the rate of regeneration of trees and understory vegetation following disturbance (Keenan and Kimmins, 1993).

Increased concentration of available nitrogen following clear-cut harvesting represents a break in the nitrogen cycle (Hart et al., 1981). Nitrogen uptake by plants is decreased following harvesting, during which soil inorganic nitrogen levels are expected to increase (Vitousek and Matson, 1985). Without trees to assimilate available nitrogen, excess nitrogen is available to nitrifiers and therefore possible oxidized to nitrate (Lawrence et al., 1987; Adams and Boyle, 1982; Hart et al., 1981; Vitousek et al., 1979). During the process of nitrification either NH_4^+ or NH_3 is oxidized to nitrate or nitrite, releasing H^+ into soil solution. The abundance of H^+ removes base cations from exchange sites where they become vulnerable to leaching (Likens et al., 1970). Nitrate is considered a very mobile nutrient and is consequently easily lost through leaching (Paul and Clark, 1989). Nitrification therefore results in the possible compounded loss of nutrients through the production of mobile nitrates and the removal of base cations from exchange sites.

Soil compaction in many cases is considered one of the most severe consequences of timber harvesting (Keenan and Kimmins, 1993). Compaction, principally caused by vehicles used for a range of mechanized forestry operations, results in increased soil strength and decreased total porosity and infiltration rates (Greacen and Sands, 1980). Serious compaction decreases the water supply, soil aeration, and restricts root space, reducing the rate of regeneration and tree growth (Pritchett and Fisher, 1987). However, frost heaving in cooler climates has been reported to reduce the effect of compaction within a couple of years following harvesting (Keenan and Kimmins, 1993)

0.5 Effect of Scarification and Ground Vegetation on Soil Fertility

Most mid successional black spruce stands in the boreal forest are relatively open, with a scattering of ericaceous dwarf shrubs and a continuous mat of feathermoss (Larsen, 1980). As the canopy closes in mid succession, primary production of the understory vegetation has been observed to exceed that of the tree species present (Oechel and Van Cleve, 1986). Feathermoss such as *Pleurozium schreberi* is an effective competitor, intercepting nutrients from precipitation, throughfall and decomposing litter, reducing the availability of nutrients for tree growth (Weber and Van Cleve, 1984).

Following harvesting a large portion of the Ericaceae-feathermoss community is left undisturbed, effectively sequestering nutrients from decomposing roots and slash (Kimmins, 1997; Norberg et al., 1997). Increased productivity in the understory during boreal succession reduces the availability of nutrients and light for planted seedlings (Jäderlund et al., 1997; Zachrission et al., 1997), and is capable of inhibiting the germination of some seedlings (Steijlen et al., 1995). For planted seedlings to regenerate successfully, site preparation is needed to reduce the competitive ability of the understory.

Scarification exposes the mineral soil, prepares the soil for planting and reduces the competition from the established Ericaceae-Feathermoss community (Jäderlund et al., 1997; Norberg et al., 1997). However, with increased ecosystem disturbance, there is often an associated increase in nutrient loss (Munson et al., 1993; Burger and Pritchett, 1988). Prévost (1997) found scarification to effect only the loss of K and Mg, but not N, which is often considered the nutrient most limiting growth in boreal ecosystems (Larsen, 1980).

0.6 Variance Partitioning and Canonical Correspondence Analysis in Ecology

Borcard et al., (1992) developed a statistical model in which multivariate statistics (e.g. canonical correspondence analysis-CCA and redundancy analysis-RDA) are used to partition the variance of independent (environmental) variables in describing a biological community. Explanatory variables can be divided into subsets using a partial CCA (or partial RDA), where variables and their confounded effects are eliminated as covariables, isolating the suite of environmental variables of interest so they can be examined greater depth, and their importance in explaining the variation of the biological community determined.

Ordination techniques are increasing in popularity with ecologists analyzing complex natural systems. Canonical correspondence analysis (CCA) is a direct gradient ordination technique in which the biological community under study is assumed to have a unimodal response to explanatory environmental variables (ter Braak, 1995). In a CCA biplot, site or species scores are usually represented in a scattergram of two or more dimensions where species (or sites) of similar distribution and abundance are grouped closer than dissimilar species (or sites) (Barbour et al., 1987). Environmental variables are drawn as arrows from the origin, where their length and direction describes their importance and area of influence in relation to the variation of the biological community. In the same way species located on one side of the origin are negatively associated with species located on the other side, arrows pointed in opposite directions represent environmental variables that are negatively associated, and species located in the opposite direction of an arrow are negatively associated (ter Braak, 1995).

Fire plays an important role in maintaining successional processes and species diversity in the boreal forest (Payette, 1992). Wildfire and more recently clearcut havesting have become the principal agents of stand initiation in the boreal forest and consequentally, changes in forest productivity and biodiversity may occur in the future if processes that control soil fertility and plant succession differ between clearcut and burned sites. Chapter 1 compares the soil fertility of stands clearcut and burnt 2, 14 and 21 years ago in the Quebec boreal forest; and Chapter 2 examines the relationships between soil fertility and the abundance and distribution of regenerating vegetation in the Quebec boreal forest.

CHAPTER 1

Effect of Clearcut Harvesting and Wildfire on Soil Fertility in the Quebec Boreal Forest

1.1 Introduction

Stand replacing wildfires occur frequently in the boreal forest, shaping species diversity, ecosystem and successional processes (Kimmins, 1996). Over thousands of years, natural selection has refined successional processes (MacDonald, 1997), making wildfire and other natural disturbances an integral part of boreal ecosystem functioning (Attiwill, 1994). As the canopy closes in late boreal succession, decomposition decreases and nutrient sequestering by the forest floor increases (Paré et al., 1993). Wildfire consumes the forest floor and aboveground biomass, generating a pulse of available nutrients (Kelsall et al., 1977). Boreal vegetation has adapted to wildfire with serotinus cones that require a period of intense heat for germination, suckering from roots and through the dispersal of small, light seeds (Johnson, 1992).

Few studies have compared the effects of wildfire and clearcutting on soil fertility in the boreal forest but research examining these disturbances independently suggest similarities and differences between them. Clearcutting is generally similar to wildfire in that it initiates stand regeneration over large areas and hence has the potential to influence succession and ecosystem processes to a significant degree. At the landscape level, clearcutting can alter the periodicity and the spatial pattern from that of natural disturbances but the natural disturbance regime can be mimicked by the adoption of appropriate cutting patterns (Attiwill, 1994; BSAT, 1994). At the stand level, however, it is unclear whether clearcutting will have the same affect on ecosystem processes as wildfire. Fire releases nutrients from vegetation and forest floor biomass, generating a pulse of nutrients that are available to regenerating vegetation, and most often reduces forest floor depth, resulting in a seed bed appropriate to the establishment of early successional boreal species (Kelsall et al., 1977). Clearcutting, in contrast, leaves a large portion of the forest floor undisturbed and thus may not generate the same nutrient pulse observed with wildfire and may impair the establishment of tree species by creating a seed bed to which indigenous species are not adapted (Margolis and Brand, 1990). Fire can cause substantial losses of N, C, and S through volatilization (Alhgren and Alhgren, 1960; Kelsall et al., 1977; Woodmansee and Wallach, 1981), whereas clearcutting may increase soil acidity and the loss of base cations (Likens et al., 1970; Mann et al., 1988; Keenan and Kimmins, 1993).

Clearcut harvesting annually disturbs an area of productive forest similar in size to that disturbed by wildfire (Canadian Council of Forest Ministers, 1997) and hence is becoming the dominant form of disturbance in the boreal forest. Changes in forest productivity and biodiversity may occur in the future if processes that control soil fertility and plant succession differ significantly between clearcut and burned sites. It is important, therefore, to understand how forest sites differ following clearcutting and wildfire in order to evaluate the possibility of long-term changes in productivity. The objective of this study is to compare the effects of wildfire and clearcutting on the mass and dynamics of carbon and nutrients in the forest floor and mineral soil of stands of three different ages following disturbance in the boreal forest of northwestern Quebec.

1.2 Materials & Methods

1.2.1 Study Areas

During the summer of 1997, three study areas were located within the black spruce zone of the Quebec boreal forest. Each study area contained sites regenerating after a natural wildfire, sites clearcut within ±3 years of the wildfire and undisturbed controls. All sites were located on till and were dominated by black spruce (*Picea mariana*) that were at least 90 years old at the time of disturbance or 90 years old at the time of sampling in control sites. The 21 year old study area, located in the northern clay belt consisted of a clay till and was much finer deposit than the tills in the other two study areas. Study areas of different ages represent in some respects a chronosequence, due to inherent differences between study areas the chronosequence is only loosely established and used when only strong trends are evident.

Timber in the 21 and 14 year old study areas was harvested by clearcutting (whole tree harvesting) and by coupe avec protection de la régénération et des sols (CPRS) in the 2 year old study area. CPRS (careful logging) resembles clearcutting in that it removes the boles and branches from the harvested area, but places emphases on protecting natural regeneration and limiting the impact of mechanical harvesting on soils (Chevalier, 1993). Due to insufficient densities of natural regeneration, scarification (disk) and tree planting were included as part of the cut treatment in the 2 year old study area.

The number of samples collected in each study area varied due to field logistics and site accessibility. High levels of harvesting in all areas particularly constrained the number of control sites sampled. Additional study area characteristics, including treatment replication are provided in Table 1.

1.2.2 Sampling

In each site, eight random points were sampled within a 25 x 25m plot. Forest floor depth was measured, and a volumetric sample of both the forest floor (FH), and the mineral soil (0-10 cm) were taken at each sampling point. Forest floor samples were passed through a 1.5 cm sieve to remove coarse fragments and homogenize the sample. Samples were bulked to produce a composite sample of the forest floor and mineral soil in each plot. All samples were air dried prior to analysis.

1.2.3 Laboratory Analysis

Forest floor and mineral soil samples were analyzed for organic carbon using a modification of the Mebius procedure (Yeomans and Bremner, 1988), pH in 0.01M $CaCl_2$ (Hendershot et al., 1993), extractable base cations using 0.1N $BaCl_2$ (Hendershot and Duquette, 1986) and Mehlich III available P (Tran and Simard, 1993). Particle size analysis was performed on mineral samples pretreated for organic matter using the hydrometer method (McKeague, 1976). Forest floor samples were digested for measurements of total N, P, K, Ca and Mg (Parkinson and Allen, 1975). Concentrations of extractable and total Ca, K and Mg were measured using a Perkin-Elmer atomic absorption spectrometer. Total P and N and Mehlich III P, were determined colorimetrically using a Lachat Quickchem automated chemical analysis system.

Net nitrogen mineralization and nitrification was measured on 5g of forest floor and 10g of mineral soil, brought up and regulated to 60% of field capacity during a 45 day aerobic incubation period in the dark at 24°C. Samples were then extracted with 1N KCl for mineralized N and determined colorimetrically as for total N above. Mineralized N was determined as the concentration of NH_4^+ and NO_3^- in the incubated samples minus the concentration of NH_4^+ and NO_3^- in non-incubated samples. Net nitrification was calculated as the concentration of NO_3^- in the incubated samples minus the concentration of NO_3^- in non-incubated samples.

1.2.4 Statistical Analysis

Outliers were detected and removed at $\alpha=0.05$ using the Dixon test (Dixon, 1950). One-way ANOVAs were used to detect treatment effects between fire, cut and controls within each study area. Comparison of means were performed using a protected significant difference LSD (t) test at $\alpha<0.05$ (Anon, 1996). Correlations were performed using Pearson's correlation.

1.3 Results

1.3.1 Physical Properties

The depth of the forest floor in the 21 and 2 year old fire sites was significantly less than clearcut sites and less than control sites in all study areas. Cut sites were also found to have significantly shallower forest floors than control sites in the 14 and 2 year old study areas. Forest floor mass in clearcut sites was consistently greater than in control sites and at least 33% higher than in fire sites with significant differences occurring in the 21 and 2 year old study areas.

1.3.2 Chemical Properties

Organic Carbon

Fire sites had significantly less total mass of organic carbon in the forest floor than in cut sites of both the 21 and 2 year old study areas (Table 2). Levels of organic carbon in the mineral soil showed no treatment effect in any of the study areas.

Concentrations of Extractable Nutrients and pH

In general concentrations of extractable nutrients in the forest floor and mineral soil were highest in fire sites followed by clearcut and control sites (Table 3). Extractable Ca in the forest floor of fire and cut sites was significantly greater than that in control sites in all study areas, with the 14 and 2 year old fire sites also having significantly higher concentrations than clearcut sites of the same year. Extractable Ca in the mineral soil of fire sites was significantly greater than control sites in the 14 and 2 year old study areas and cut sites in the 14 year old study area. The mineral soil of the 2 year old cut sites had concentrations of extractable Ca that were significantly greater than control sites of the same age. Mehlich III extractable P was at least four times higher in the forest floor, and almost twice as high in the mineral soil of the 2 year old fire sites, than that in any other treatment. Extractable Ca, K and P in the forest floor were all positively correlated (p<0.002) with concentrations in the mineral soil.

Forest floor pH of the 14 and 2 year old fire sites was significantly higher than that in both clearcut and control sites of the same year, but no significant treatment effects were observed in the pH of the mineral soil. Forest floor pH was found to be highly correlated (p<0.001) with extractable Ca.

Total Nutrients in the Forest Floor

Concentrations of total nutrients in the forest floor were generally higher in the 14 and 2 year old fire sites than in control or cut sites, with cut sites often having significantly higher concentrations than control sites (Table 4). In the 21 year old study area, there were no differences between fire and cut sites although total N and Ca were higher in the disturbed sites than in control sites. Cut sites have a greater total mass of nutrients than either fire or control sites in all study areas although these differences were not always significant. Mass of N and K in the 2 year old fire sites were significantly less than in control sites of the same year.

1.3.3 Biological Properties

Net Mineralized N and Nitrification

Concentration and mass of mineralized N in the forest floor were significantly greater in the 21 and 2 year old clearcut sites than in fire and control sites of the same year (Figure 1). Mass of mineralized N in the mineral soil was significantly greater in cut sites than in control sites in the 21 and 14 year old study areas and in the 2 year old study area at $\alpha=0.1$. Concentration of mineralized N in the mineral soil was significantly higher in cut sites than in control and fire sites in all study areas. No significant differences in N mineralization was detected between fire and control sites in any study area. Mass (not shown) and concentration of net mineralization in both the forest floor and mineral soil show similar trends and a high positive correlation ($p \leq 0.001$).

Nitrification levels were consistently low relative to net N mineralization levels and near the detection limit for all treatments and study areas. Forest floor mass and concentration of nitrate in incubated samples shows a high positive correlation with pH ($p < 0.001$).

1.4 Discussion

The forest floor plays an important role in the nutrient dynamics of the boreal forest. It may contain up to 72% of the available soil nutrients (Foster and Morrison, 1987), the largest percentage of fine roots (Persson, 1983) and greatest amount of biological activity (Pritchett and Fisher, 1987) in the soil profile. Our data shows that wildfire and clearcutting alter the physical, chemical and biological properties of the forest floor for a period of at least 21 years following disturbance in the Quebec boreal forest.

1.4.1 Physical Effects of Disturbance on the Forest Floor

The forest floors of all clearcut sites had higher forest floor dry weight and organic carbon content, relative to the control sites suggesting increased biomass inputs following clearcutting. Logging residues deposited during clearcutting and the evolution of dead tree roots through decomposition to humic and fibric material, increased the mass of the forest floor. Control sites contain trees with viable root systems that do not experience the same degree of dieback and decomposition as cuts and are therefore removed during sampling. The 21 and 14 year old clearcut sites had significantly heavier forest floors than control sites, suggesting that clearcutting can effect the physical properties of the forest floor for a period greater than 21 years.

Where clearcutting increases the biomass in the forest floor, wildfire reduces it. Forest floor dry weight, organic carbon content, and humus depth all illustrate the capacity of wildfire to consume organic matter. Humus depth in fire sites is significantly less than control sites in all study areas, suggesting that it can take the forest floor over 21 years to recover from wildfire.

1.4.2 Nutrient Pulse & pH

The 14 and 2 year old fire sites have greater concentrations of extractable nutrients than cut and control sites, in both the mineral soil and forest floor. Extractable Ca, K and P in the mineral soil are all positively correlated (p<0.002) with concentrations in the forest floor, suggesting that the pulse of nutrients in the forest floor is carried through to the mineral soil and is connected by either ameliorated environmental conditions and associated higher biological activity, or leached from the forest floor. The pulse of exchangeable Ca that occurs in the forest floor of the 2 year old disturbed sites, and to a lesser extent in the mineral soil, is still significant after 21 years although the differences between cut and fire sites has disappeared. Extractable P also shows a dramatic pulse in the forest floor and mineral soil of the 2 year old fire, but P levels return to those of the control in 14 years. Our results demonstrate that fire consumes biomass, generating a pulse of available nutrient of greater intensity than following clearcutting.

Forest floor pH following wildfire is significantly higher than in both clearcut and control sites for a period greater than 14 years following disturbance. Exchangeable Ca is highly correlated with pH (p<0.001), suggesting that base cations mineralized during fire are leached through the soil column, decreasing forest floor acidity. Other studies have also reported a rise in pH following fire (Kutiel and Naveh, 1987) and a correlation between exchangeable base cation concentration and pH (Paré et al., 1993).

Although in most cases clearcutting has been shown to reduce base saturation and consequentially soil pH (Mroz, 1985; Johnson et al., 1991) the pH in the forest floor of the 14 year old cut is significantly greater than control sites of the same year. Increased rates of nitrification and associated production of H^+ during the conversion of NH_4^+ to NO_3^- has been connected with increased forest soil acidity following clearcutting (Likens et al., 1970). However, low levels of nitrification, coupled with increased base cation availability (Ca) in this study are presumed responsible for an increase in pH following clearcutting.

Our results suggest that N mineralization in forest floor and mineral soil can be significantly greater in clearcut sites than in either fire or control sites for at least 21 years. Enhanced ability in the forest floor and mineral soil to supply mineralized N following clearcutting has often been attributed to fresh organic matter inputs from root decay, logging debris and the intermixing of the forest floor and mineral soil, accompanied by improved environmental conditions, such as soil moisture and temperature (Keenan and Kimmins, 1993), and reduced N uptake (Vitousek and Matson, 1985).

Increased N mineralization has also been reported following wildfire, due to bacterial populations taking advantage of high pH, carbon and nutrient availability (Woodmansee and Wallach, 1981). This study however, did not find significant differences between the rates of net mineralization in wildfire and control sites in either the forest floor or mineral soil. Fritze et al. (1993) found that the microbial community could require up to 12 years to recover from fire. Pietikainen and Fritze (1995) associated the decline in microbial activity with either the direct effect of fire on the microbial community or as a result of modifications to soil properties associated with wildfire.

Increased rates of nitrification have been observed following both clearcutting and wildfire (Ahlgren and Ahlgren, 1960; Vitousek et al., 1979; Vitousek and Matson, 1985; Pietikäinen and Fritze, 1995). Relative to mineralization levels, nitrification levels in this study were insignificant. Net nitrogen mineralization produces an abundant supply of available nitrogen in the 21 and 2 year old clearcuts, assuring an adequate source of available N for nitrifying organisms. Low pH values measured in this study (<4.0) and a high positive correlation between forest floor net nitrification and pH (p<0.001) suggests that nitrification was restricted due to high concentrations of available NH_4^+ at low pH inhibiting the conversion of NO_2^- to NO_3^- (Paul and Clark, 1989).

1.4.3 Total Nutrient Capital

Mass of total N and K in the 2 year old fire were significantly less than control sites in the same area. Nitrogen, which volatilizes at 200°C (Pritchett and Fisher, 1987), is easily lost during wildfires achieving temperatures of 300-700°C (Knight, 1966). Kutiel and Naveh (1987) estimated that up to 25% of total nitrogen can be lost during wildfire. Other less volatile nutrients, such as base cations and phosphorus are subject to loss through ash convection (Edmonds et al., 1989), wind and water erosion and especially more mobile ions, such as K^+, are lost through leaching (Woodmansee and Wallach, 1981).

The 2 year old study area was the only area in which scarification and planting were included as part of the cut treatment. The literature suggests that site preparation commonly increases the loss of nutrients from disturbed ecosystems (Burger and Pritchett, 1988). However, mass and concentration of total nutrients in the forest floor following clearcutting and scarification in the 2 year old study area did not drop significantly below levels in control sites, suggesting that scarification did not cause significant nutrient loss.

This study suggests that wildfire supplies a greater concentration of total nutrients in the rooting zone of regenerating vegetation than in either clearcut or control sites, whereas clearcutting has a greater mass of total nutrients in the forest floor, suggesting a greater capacity to supply nitrogen to benefit long-term productivity than either fire or control sites. However, secondary succession in clearcuts occurs on sites with a relatively intact forest floor and communities of understory vegetation, competing with or inhibiting the growth of emerging saplings (Zackrisson et al., 1997). Clearcut sites may therefore contain higher nutrient reserves in the forest floor than fire sites, but the availability of those nutrients to developing saplings maybe restricted by established vegetation.

1.4.4 Ecosystem Recovery

It is recognized that the chronosequence in this study is only loosely established, but some basic trends can be drawn over time. The effect of the nutrient pulse and other related effects decline with time. The rate of vegetative regeneration in disturbed ecosystems determines the length and the magnitude of the nutrient loss (Paré and Van Cleve, 1993). Reestablishing vegetation serves to assimilate excess nutrients, regulate soil temperature and moisture levels (Marks and Bormann, 1972; Woodmansee and Wallach, 1981), returning decomposition, nutrient cycling and availability to predisturbance levels (Woodmansee and Wallach, 1981; Keenan and Kimmins, 1993).

1.5 Conclusion

This study has shown that both clearcutting and wildfire produce a pulse of mineralized nutrients, and that the duration and magnitude of the pulse is dependant on the type of disturbance and nutrient.. Fire oxidized organic matter, decreasing the biomass within the forest floor, generating a pulse of mineralized nutrients and caused a significant loss of N and K in the youngest study area. In contrast, clearcutting increased the amount of biomass in the forest floor, produced a nutrient pulse of lower intensity through the biological mineralization of nutrients, resulted in a higher total mass of forest floor nutrients than either control or fire sites, and did not result in significant nutrient loss. This suggests that clearcut harvesting and wildfire may have significantly different effects on ecosystem processes. More research is necessary to determine whether the forest floor and mineral soil conditions produced by clearcutting will lead to levels of long-term productivity or biodiversity that differ significantly from those produced by wildfire.

Table 1.1. Site characteristics.

Study Area	Replication	Forestry Region[a]	Location	Fire Area (ha)	Cut Years	Average Soil Texture (0-10cm)	Average Annual Temperature (°C)[b]	Average Annual Precipitation (mm)[b]
2	10 Fire 10 Cut 8 Control	Gouin	48°44'-59' N 76°08'-38' W	47 709	1992-94	Loamy Sand	1.2	840
14	8 Fire 8 Cut 5 Control	Gouin	48°44'-57' N 74°31'-54' W	14 535	1981-86	Loamy Sand	0.8	948.4
21	10 Fire 10 Cut 4 Control	Northern Clay	49°17'-51' N 79°00'-19' W	31 054	1975-80	Sandy Clay Loam	0.6	822

[a]Forestry regions as proposed by Rowe (1972).
[b]Meteorological data provided by the nearest weather station (Anon, 1982).

Table 1.2. Humus depth (cm) dry mass (kg/m^2) and organic carbon content (kg/m^2) in the forest floor and organic carbon content (kg/m^2) in the mineral horizon.

Study Area	2			14			21		
Treatment	Fire	Cut	Control	Fire	Cut	Control	Fire	Cut	Control
				Forest Floor (FH)					
Humus Depth	6.4c	13.7b	21.0a	8.2c	13.5b	20.3a	11.6b	15.8a	18.4a
Dry Mass	10.2b	24.4a	22.3a	12.1b	18.0a	15.6b	14.7b	21.7a	15.3b
Organic C	1.93b	4.78a	4.34a	2.32a	3.52a	3.11a	3.01b	4.38a	3.39ab
				Mineral Soil					
Organic C	1.23a	1.71a	1.37a	0.790a	1.13a	1.10a	2.09a	2.44a	2.44a

Note: Different letters refer to significant differences between treatments within each study area using a protected LSD (t) test (α=0.05).

Table 1.3. Extractable Ca, K, Mg (cmol/kg), P (ug/g) and pH in the forest floor and mineral horizon.

Study Area	2			14			21		
Treatment	Fire	Cut	Control	Fire	Cut	Control	Fire	Cut	Control
				Forest Floor (FH)					
Ca	12.2a	9.26b	6.76c	16.0a	11.0b	7.27c	13.6a	13.4a	7.33b
K	1.10a	0.88b	1.07ab	1.40a	1.07b	0.980b	1.07b	1.12b	1.73a
Mg	2.56a	2.27ab	1.91b	2.73a	2.69a	1.68b	3.03a	3.06a	2.36a
MIII P	231a	30.5b	24.5b	33.7a	25.0a	42.7a	34.1a	29.9a	39.3a
pH	3.50a	3.29b	3.27b	3.61a	3.37b	3.19c	3.46a	3.50a	3.30a
				Mineral Soil					
Ca	0.492a	0.358a	0.178b	0.462a	0.275b	0.168b	0.834a	0.759a	0.338a
K	0.0726a	0.0722a	0.0411b	0.0633a	0.0474b	0.0529b	0.165a	0.159a	0.121a
Mg	0.105a	0.0859a	0.0413b	0.0668a	0.0596a	0.0363b	0.214a	0.267a	0.359a
MIII P	19.8a	10.5b	3.54b	7.39a	2.62b	6.01ab	7.14a	4.00a	6.51a
pH	3.91a	3.87a	3.93a	3.98a	3.90a	3.97a	3.71a	3.70a	3.82a

Note: Different letters refer to significant differences between treatments within each study area using a protected LSD (t) test (α=0.05).

Table 1.4. Concentration (mg/g) and mass (kg/ha) of total nutrients in the forest floor.

Study Area	2			14			21		
Treatment	Fire	Cut	Control	Fire	Cut	Control	Fire	Cut	Control
				Concentration					
N	10.2a	8.26b	9.25ab	11.1a	9.72b	8.80b	8.43a	8.44a	7.01b
P	0.857a	0.520b	0.535b	0.839a	0.657b	0.559b	0.666a	0.673a	0.631a
K	1.00a	0.868a	0.844a	1.25a	0.959b	0.790b	1.33a	1.75a	1.63a
Ca	3.47a	2.70b	1.68c	4.52a	3.14b	1.84c	3.64a	3.41a	1.64b
Mg	0.398a	0.372a	0.252b	0.492a	0.417a	0.297b	0.534a	0.766a	0.288a
				Mass					
N	471b	832a	946a	586a	800a	600a	547b	849a	476b
P	36.2a	55.1a	51.8a	44.2ab	56.9a	33.7b	42.7b	63.3a	42.8b
K	46.5b	94.3a	80.8a	65.0a	72.9a	54.4a	84.4a	191.8a	110.0a
Ca	146b	297a	179b	235ab	256a	133b	210b	324a	111b
Mg	19.7b	40.7a	25.5b	25.7a	33.2a	15.9a	33.6a	62.1a	19.9a

Note: Different letters refer to significant differences between treatments within each study area using a protected LSD (t) test (α=0.05).

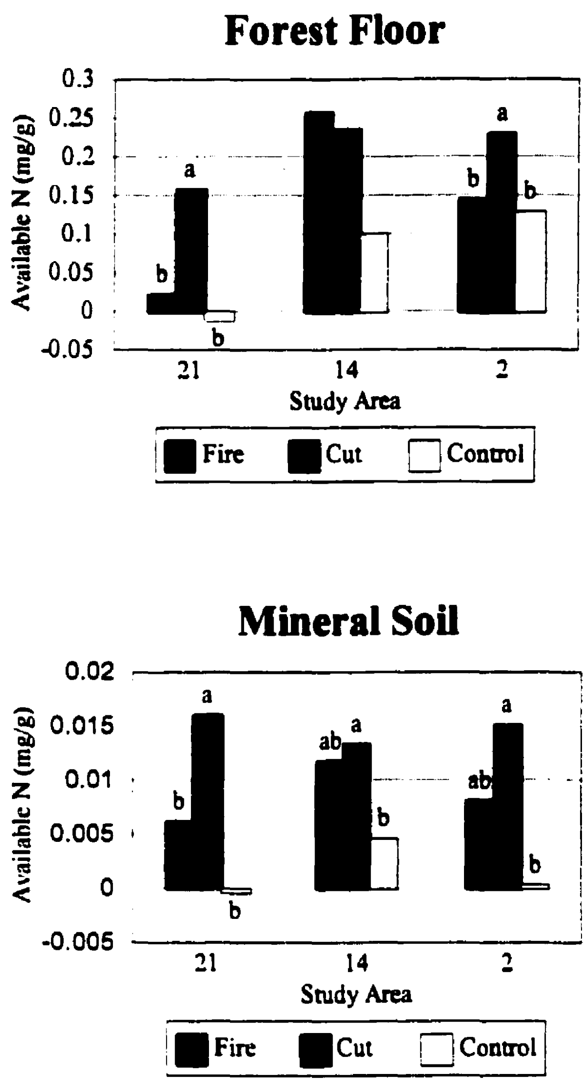

Figure 1.1. Concentration of net nitrogen mineralization in the forest floor and mineral soil. Different letters indicate significant differences between treatments within each study area using a protected LSD (t) test (α=0.05)

CONNECTING PARAGRAPH

Chapter 1 compares the effect of wildfire and clearcutting on soil fertility. Chapter 2 uses multivariate statistics and variance partitioning to explore the relationship between soil fertility and regenerating vegetation following clearcut harvesting and wildfire in the Quebec boreal forest.

CHAPTER 2

Soil and Plant Interactions Following Clearcut Harvesting and Wildfire in the Quebec Black Spruce-Feathermoss Forest

2.1 Introduction

Mature black spruce-feathermoss stands are characterized by a closed coniferous canopy, sparse understory vegetation and a continuous mat of feathermoss (Larsen 1980). As crown closure increases, light and temperature at the forest floor decreases, slowing decomposition and increasing productivity of the feathermoss layer (Larsen 1980; Van Cleve and Viereck 1981; Bonan 1992). Weber and Van Cleve (1984) observed the primary productivity of feathermoss to exceed that of the tree species present in late boreal succession. The build-up of organic matter in the forest floor represents an increasing nutrient sink whereby large amounts of nutrients are removed from circulation and nutrient supply may limit plant growth (MacLean et al. 1983).

In Canada, clear-cut harvesting annually affects an area of productive forest proportional to that of wildfire (Canadian Council of Forest Ministers 1996). Both these disturbances are major agents of stand initiation in the boreal forest as they generate favorable establishment conditions for pioneer species by removing the forest canopy and modifying forest floor structure (Kelsall et al. 1977, Payette 1992; Keenan and Kimmins 1993). In addition, growth of regenerating vegetation is facilitated by the release of nutrients immobilized in the forest floor during wildfire (Viereck 1983). Similarly, altered environmental conditions at the level of the forest floor following clear-cutting increase nutrient mineralization (Keenan and Kimmins 1993). However, many comparative studies have found differences in the composition of regenerating vegetation following wildfire and clear-cutting in the boreal forest (Noble et al. 1977; Abrams and Dickmann 1982; Carleton and MacLellan 1994; Johnston and Elliott 1996; Ehnes 1998; Nguyen-Xuan 1999). This suggests that these two disturbance types may exert different influences on the dynamics of stand regeneration.

Ecosystem processes such as the bioregulation and feedback mechanisms between soil and plants are an important part of successional dynamics in the boreal forest. Brumelis and Carleton (1988, 1989) observed that differences in post-disturbance vegetation composition could be associated to different soil nutritional dynamics. Chapin (1995) demonstrated that different colonizing species exhibited differences in their capacity to exploit soil nutrients following a major disturbance. Rintoul (1997) showed that differences in disturbance severity affected the plant tissue nutrient content of the regenerating vegetation. Differences in plant-soil relationships observed following different disturbance types and severity levels may have profound implications in the maintenance of soil processes (Perry 1994).

Many studies have focused on the nutritional dynamics and/or vegetation composition following clear-cutting (Brumelis and Carleton 1988; Brumelis and Carleton 1989; Keenan and Kimmins 1993; Brais et al. 1995a) or following wildfire (Alhgren and Alhgren 1960; Kelsall et al. 1977; Paré et al. 1993; Brais *et al.*, 1995b). However there have been few comparative studies that have examined the possible influence of disturbance type and severity on the interaction between soil fertility and regenerating vegetation in the boreal forest (Johnston and Elliott 1998). The objective of this chapter is to examine the interactions between soil fertility and early regenerating vegetation after clear-cut harvesting and wildfire in the Quebec boreal forest. Previous parts of this study have shown that: 1) differences in the severity of forest floor disturbance can explain some of the compositional differences observed in early post-fire and post-logging vegetation (Nguyen-Xuan 1999), and 2) important differences in soil fertility exist following these two disturbance types (Chapter 1). The present chapter attempts to illustrate how differences in soil fertility following wildfire and clear-cut harvesting are also reflected in the post-disturbance vegetation composition.

2.2 Materials and methods

2.2.1 Study Areas

During the summer of 1997, three study areas were located within the black spruce zone of the Quebec boreal forest. Each study area contained sites regenerating after a natural wildfire and sites clearcut within ±3 years of the wildfire (the same data set was used in both chapters, minus the control sites in Chapter 2). At the time of disturbance, all stands were mature, dominated by black spruce (*Picea mariana* (Mill.) BSP), and underlain by glacial till. The 21 year old study area was located in the northern clay belt and its surficial deposit was much finer than the glacial tills found in the other two study areas located on the boreal shield.

Timber was harvested by clear-cut harvesting (whole tree harvesting) in the 21 and 14 year old study areas and by clear-cut harvesting with protection of regeneration and soils (CPRS-careful logging) in the 2 year old study area. CPRS resembles clear-cutting with emphasis put on protecting natural tree regeneration and limiting the impact of mechanical harvesting on soils (Chevalier 1993). Due to insufficient densities of natural regeneration, scarification (disk) and tree planting were performed following harvesting in the 2 year old study area. Study area characteristics are provided in Table 2.1.

2.2.2 Sampling

In each stand a 25m x 25m plot was set up, within which the vegetation was sampled in 15 randomly located 1m x 1m quadrats. An estimation of the percent coverage of invascular and vascular plant species was performed for the vegetation on the ground, below 1m, and from 1-3m. The forest floor and mineral horizon were sampled at 8 of the 15 sampling points. Forest floor depth was measured, and a volumetric sample of both the forest floor (FH), and the mineral soil (0-10 cm) were taken at each sampling point. Forest floor samples were passed through a 1.5 cm sieve to remove coarse fragments and homogenize the sample. Samples were bulked to produce a composite sample of the forest floor and mineral soil in each plot. All samples were air dried prior to analysis. Aspect, slope, slope position, and moisture regime were recorded and the age of each stand at the time of disturbance was estimated by a count of the annual growth rings of five trees killed during the disturbance (burned snags or logging stumps).

2.2.3 Lab Analysis

Ahlgren and Ahlgren (1960) and Keenan and Kimmins (1993) provide reviews on the effects of wildfire and clear-cut harvesting on hydrological, vegetational, and nutritional dynamics. In general, both reviews suggest that significant changes to the organic matter content, total and available nutrients, microbial activity, and pH in the soil can be observed following disturbance. Forest floor and mineral soil samples were analyzed for organic carbon content using a modification of the Mebius procedure (Yeomans & Bemner 1988), pH in 0.01M $CaCl_2$ (Hendershot et al. 1993), extractable base cations using 0.1N $BaCl_2$ (Hendershot & Duquette 1986) and Mehlich III Available P (Tran & Simard 1993). Particle size analysis was performed on mineral samples pretreated for organic matter using the hydrometer method (McKeague 1976). Organic matter content of the forest floor was determined by loss on ignition using 2g of sample brought up to 550°C for two hours in a muffle furnace (Kalra and Maynard 1991). Forest floor samples were digested for measurements of total N, P, K, Ca and Mg (Parkinson & Allen, 1975). Concentrations of extractable and total Ca, K and Mg were measured using a Perkin-Elmer atomic absorption spectrometer. Total P and N and Mehlich III P, were determined colorimetrically using a Lachat Quickchem automated chemical analysis system.

Net nitrogen mineralization (available N) and nitrification was measured on 5g of forest floor and 10g of mineral soil, brought up and regulated to 60% of field capacity during a 45 day aerobic incubation period in the dark at 24°C. Samples were then extracted with 1N KCl for available N and determined colormetrically as for total N above. Available N was determined as the concentration of NH_4^+ and NO_3^- in the incubated samples minus the concentration of NH_4^+ and NO_3^- in non-incubated samples. Net nitrification was calculated as the concentration of NO_3^- in the incubated samples minus the concentration of NO_3^- in non-incubated samples.

Microbial basal respiration was measured on 7g of forest floor and 15g of mineral soil, brought up to 60% of field capacity and incubated for 10 days at room temperature in 30 ml plastic jars. Prior to sampling the jars were flushed with ambient air and sealed for 1 hour. The accumulation of CO_2 in the plastic jars during the incubation period was determined using gas chromatography.

2.2.4 Data Analysis

The average cover of each species was determined for each stand. Species only occurring in more than 10% and less than 90% of disturbed stands were selected for data analysis. A species list with the species codes used in graphical representations is provided in Appendix A. Canonical correspondence analysis (CCA) (ter Braak 1986) was used to see if differences in species composition following wildfire and clear-cutting could be related to differences in soil fertility following these two disturbance types. CCA allows the simultaneous analysis of the overall species composition in relation to numerous environmental variables (ter Braak 1987). In addition to, and in interaction with soil fertility, many other site-related factors can influence post-disturbance vegetation composition. These include light, temperature, and moisture regimes, disturbance history, and ecophysiographic region. Thus the environmental variables used in the CCA included soil fertility variables as well as site characteristics variables. Since CCA is a multivariate method closely related to multiple linear regressions (ter Braak, 1986), the number of environmental variables used and the amount of colinearity between them had to be minimized. Thus, subsets of soil fertility and site characteristic variables were separately chosen through forward selection at a level of significance of 0.1. The final soil fertility subset consisted of the following variables: concentrations of extractable Ca, organic C, and mineralized N, pH, and basal respiration in the mineral soil, and concentrations of extractable Ca, P, and total N, mass of organic matter and mineralized N in the forest floor. The description and abbreviation of each soil variable is provided in Table 2.2. The final site characteristics subset consisted of: average duff depth, percent sand (0-10cm), aspect, moisture regime, stand age at the time of disturbance, time since most recent disturbance, and longitude.

The relationships between early post-disturbance vegetation composition and soil fertility were examined using three different CCAs. The first CCA (Global) included both explanatory subsets as environmental variables. The second CCA (Soil Fertility) only included the soil fertility subset as environmental variables, while the third CCA (Partial Soil Fertility) used the soil fertility subset as environmental variables and the site characteristics subset as covariables. These different CCAs enabled a better evaluation of the effects of soil fertility on post-disturbance vegetation with and without the consideration of the influence of site characteristics. The importance of this influence was evaluated through the partitioning of the variance (Borcard et al. 1992) observed in the vegetation between the subsets of soil fertility and site characteristic variables. Levels of correlation (Spearman) between fertility variables and descriptive vegetation variables were also examined. Except for Spearman's and Pearson's correlation performed using the SPSS analytical software package (SPSS 1997), statistical analysis were performed using the CANOCO statistical package (ter Braak 1987-1992).

2.3 Results

2.3.1 Variance Partitioning and the Global Perspective

All explanatory variables (Global CCA) accounted for 63.6% of the variance in the vegetation data set (Figure 2.1). Soil fertility and site characteristics exclusively accounted for 23.2% and 14.7%, respectively, of the variance in the vegetation data set with the remaining 25.7% of the variance explained by the confounded effect of both sets of explanatory variables. The first axis in the Global CCA accounted for nearly 17% of the total variance in the vegetation data set and separated out the 2 year old burned stands from the other disturbed stands (Figure 2.2). Associated with the 2 year old burned stands was a nutrient pulse represented by extractable P (FCExtP). The environmental variables with the highest level of association to the first axis were: extractable P, time since most recent disturbance, and duff depth (Table 2.3). The second axis represented about 14% of the total variance and separated out the 14 and 21 year old burned stands from the cluster of cut stands around the origin (Figure 2.2). Longitude and total N in the forest floor were the environmental variables that showed the greatest association to this axis ($r > 0.50$), and mineralized N in the mineral soil, percent sand, mineralized N in the forest floor, and pH of the mineral soil also showed some degree of association to it (Table 2.3).

The Soil Fertility CCA (not shown) was very similar to the Global CCA. For the first three axes of the two ordinations, correlation coefficients (Pearson's r) between the site scores were 1.00, 0.93 and 0.92. The correlation coefficients were 0.97, 0.94 and

0.89 between species scores. Both ordinations were therefore very similar, having similar patterns of stand and species differentiation. Furthermore, even though the soil fertility variables were the only variables used to constrain the ordination axes of the Soil Fertility CCA, little change was seen in the correlation coefficients of most environmental variables in comparison to the ones obtained in the Global CCA (Table 2.3). Thus, the Soil Fertility CCA represented the influence of soil fertility with the confounded influence of site characteristics. The Soil Fertility CCA explained 48.9% of the total variance in the vegetation data set (Figure 2.1).

2.3.2 The Soil Fertility Perspective

About 52% of the variation explained by the Partial Soil Fertility CCA can be represented on the first two ordination axes. Two main directions of stand differentiation could be observed in the ordination space of the two first CCA axes (Figure 2.3). The cut and burned stands of the 2 year old study area were separated from disturbed sites of the two other study areas along the first direction of differentiation. Associated with the fire sites of the 2 year old study area is a pulse of available nutrients represented by extractable P in the forest floor (FCExtP). The average concentration of extractable P in the cluster of fire sites of this area is 2.5 times greater than any site outside the association. This first gradient was more strongly associated with the second ordination axis (Table 2.3). Also associated with the early fire and nutrient pulse was a high presence and abundance of *Marchantia polymorpha* (bmp), *Ceratodon purpureus* (bcp), and *Epilobium angustifolium* (cea) (Figure 2.4). The cut sites of the 2 year old study area were located at the opposite end of the first differentiating gradient in respect to the fire sites of the same area, and were characterized by a high presence and abundance of *Aralia hispida* (cah), *Carex deflexa* (ccxd), and *Betula papyrifera* (cbp).

The second differentiating direction corresponded to a soil fertility gradient represented by extractable Ca (FCExtCa), total N (FCTotN), and (FMMin) in the forest floor and extractable Ca (MCExtCa), mineralized N (MCMin), pH (MpH), and basal respiration (MCBasal) in the mineral soil (Figure 2.3). The following vascular plants were associated with increasing fertility (Figure 2.4): *Aralia nudicaulis* (can), *Clintonia borealis* (ccb), *Deschampsia flexuosa* (cdf), *Pinus banksiana* (cpb, dpb), *Prunus pensylvanica* (cpp, dpp), *Pteridium aquilinum* (cpa), *Rubus idaeus* (cri), *Solidago macrophylla* (csm), *Sorbus americana* (csa, dsa), *Trientalis borealis* (ctb) *Viburnum cassinoides* (cvbc, dvbc). Associated with decreasing fertility were *Abies balsamea* (cab, dab) and many cryptograms: *Cladina mitis* (acm), *Cladonia cenotea* (accn), *Cladonia crispata* (accp), *Hylocomnium splendens* (bhs), *Pleurozium shreberi* (bps), *Ptilidium ciliare* (bpcl), *Ptilium crista-castrense* (bpcr), *Trapeliopsis granulosa* (atg). Associated with the fertility gradient was the differentiation of the majority of 14 year old burned and 21 year old cuts stands with increasing fertility, and the majority of 14 year old cut and 21 year old burned stands with decreasing fertility (Figure 2.3). This second differentiating gradient is generally more pronounced along the first ordination axis (Table 2.3). The position of the stands on the second and third CCA axes (not shown) indicated that increased extractable Ca (FCExtCa) and total N (FCTotN) in the forest floor greatly contributed to the differentiation of the 14 year old fires from the 14 year old cuts, while increased mineralized N in the forest floor and mineral soil (FCMin, MCMin) greatly contributed to the differentiation of the 21 year old cuts from the 21 year old fires.

The concentration of total N in the forest floor showed a significant positive correlation (Spearman's r, $p<0.01$) with the concentration of mineralized N in the forest floor ($r = 0.38$), the total cover of deciduous shrubs and trees ($r = 0.38$), and the total cover of herbaceous plants ($r = 0.67$). Total N was also significantly negative correlated with the C:N in the forest floor ($r = -0.64$) and total cover of lichens ($r = -0.32$, $p = 0.015$). Herbaceous vegetation was also significantly positively correlated with the concentration of mineralized N in the forest floor ($r = 0.42$) while lichens were negatively correlated to it ($r = -0.43$). Cover of deciduous shrubs and trees and total cover of vascular plants (herbs and deciduous) were positively correlated to extractable Ca in the forest floor ($r = 0.44$ and 0.47 respectively). Increasing humus depth was associated with decreasing herbaceous cover ($r = -0.32$, $p = 0.016$), decreasing total N in forest floor ($r = -0.29$, $p = 0.029$). Many of these relationships are illustrated in Fig. 2.5.

2.4 Discussion

2.4.1 Importance of the influence of soil fertility on post-disturbance vegetation composition

The series of canonical correspondence analyses (CCA) using different sets of explanatory variables provides insight into the respective influence of physical site characteristics and site fertility variables on post-disturbance vegetation composition. Variance partitioning and the high correlation between the scores in the Global and Soil Fertility CCAs demonstrate the importance of the interaction between nutritional dynamics and the physical environment in describing the variation in the composition of vegetation in the boreal forest. It has long been recognized that physical environmental variables, such as moisture and temperature regimes effect nutrient dynamics in forest ecosystems (Perry 1994).

Although a large part of the changes observed in soil nutritional dynamics following wildfire and clear-cut harvesting indirectly result from changes in the physical properties of the forest floor (Woodmansee and Wallach 1981; Keenan and Kimmins 1993), an important portion of the nutrient changes can also be directly attributed to disturbance itself as illustrated by the significant amount of variance accounted for by the third CCA (Partial Soil Fertility). This is especially true for wildfire which is capable of generating a pulse of available nutrients through the oxidization of carbon, mineralizing nutrients in the forest floor and aboveground biomass (Chapter 1).

2.4.2 Interactions between post-disturbance soil fertility and vegetation composition

Soil-plant interactions are an integral part of the regeneration dynamics of forest ecosystems. Plant growth is directly linked to the availability of soil nutrients. The life histories of many boreal plant species greatly reflects their ability to exploit the available nutrient resources at different times during forest succession (Chapin and Van Cleve 1981). Thus, in many instances the vegetation composition of boreal stands can be determined by soil fertility (Carleton and Maycock 1980; Carleton and Maycock 1981; Carleton et al. 1985). However, plants can equally influence soil fertility as they play a major role in soil nutrient cycling during all stages of succession through nutrient absorption, storage and release in the different compartments of the boreal forest (Van Cleve and Viereck 1981). Therefore, vegetation composition can have an important influence on soil fertility (Paré et al. 1993; Brais et al. 1995b). These soil-plant interactions are reflected in the 2 main differential directions observed in the Global and Partial Soil Fertility CCAs. The almost orthogonal nature of these two directions of stand differentiation suggests that they represent two distinct dynamics in the regeneration of forest stands following disturbance. Hence, they provide some insight on soil-plant interactions during the regeneration of burned and clear-cut stands and their possible evolution with time.

The differential direction involving the sites of the 2 year old study area illustrates some of the soil-plant interactions observed immediately after disturbance. Many of the species strongly associated with clear-cut and burned sites of this area (*Betula papyrifera*, *Carex deflexa*, *Ceratodon purpureus*, *Epilobium angustifolium* and *Marchantia polymorpha*) have often been reported as successful colonizers of exposed mineral soil after disturbance (Rowe 1983; Oswald and Brown 1993; Prévost 1997). *Betula papyrifera*, *Carex spp.*, and *Epilobium angustifolium* are often the predominant species in the seed rain shortly after wildfire and clear-cut harvesting (Johnson 1975; Archibold 1980; Qi and Scarrett 1998), and their association with recently disturbed sites reflects the favourable establishment conditions often encountered following severe wildfires and scarified clear-cuts (Nguyen-Xuan 1999). Given that the ground and understorey vegetation cover did not exceed 15% in either burned or clear-cut sites, the influence of plants on soil fertility in the 2 year old study area was probably minimal. However, significant differences were observed for many soil fertility variables between the fire and cut sites (Chapter 1). Thus, the differential direction observed illustrates the influence of soil fertility differences on the vegetation composition of early regeneration following wildfire and clear-cutting. The positioning of the phosphorus vector in the direction of the 2 year old burned stands illustrates the importance of the nutritional pulse generated during fire. Phosphorus is an element that is highly available following fire, but whose availability quickly decreases afterwards (Viereck 1983). This nutrient pulse greatly favours the growth of post-fire thrivers such as *Marchantia polymorpha* and *Epilobium angustifolium* and their abundance soon decreases as the pulse subsides (Ahlgren 1960; Stark and Steele 1977).

The differential gradient involving the sites of the 14 and 21 year old study areas illustrates some of the soil-plant interactions observed once most of the regenerating vegetation has become established, before tree dominance is attained in the canopy. The species that are located at the opposing ends of this gradient define two contrasting compositional types. The species associated with increased soil fertility characterize a vegetation composition that is mostly dense, tall, and dominated by herbaceous vascular plants and deciduous shrubs and trees. Many of them are shade intolerant species whose establishment and/or germination has been facilitated by the disturbance of the forest floor (Nguyen-Xuan 1999). The species that are associated with lower soil fertility represent a vegetation composition that is dominated by conifers and high bryophyte or lichen ground cover. This compositional type often reflects lower levels of forest floor disturbance (Nguyen-Xuan 1999). Given the greater cover of ground and understorey vegetation (28 to 66% and 36 to 70% respectively) in the disturbed stands of these two areas, the influence of plant composition on soil fertility is certainly more important than in the 2 year old study area. The litter produced by deciduous shrubs and trees, broadleaf herbs, grasses, and ferns associated with the direction of greater N mineralization is easier to degrade and therefore has a higher turnover rate than coniferous or invascular litter (Moore 1984). Furthermore, the lower ground cover of invascular vegetation amongst sites associated with increased mineralization is beneficial to nutrient turnover. Reindeer lichens and feather mosses, such as *Pleurozium schreberi* and *Hylocomnium splendens*, contain low concentrations of nutrients (Moore 1981), decreasing litter quality (Larsen 1980; Van Cleve 1974). However, cool soil temperatures due to the insulating effect of the feather moss layer is often the most severe effect of the dominance of invascular plants on nutrient cycling in the boreal forest (Moore 1981; Weber and Van Cleve 1984). The nutritional gradient observed in the second differentiating direction thus corresponds to increased litter quality and rates of nutrient cycling associated with increased dominance of vascular plants as suggested by the positive correlation between total N, cover of vascular plants and N mineralization in the forest floor.

2.4.3 Severity of forest floor disturbance and post-disturbance soil fertility

This study suggests that there is a dichotomy between stands regenerating with greater cover of lichens and mosses and those predominantly regenerating with vascular plants. Feathermosses are considered effective competitors for nutritional resources, intercepting nutrients from precipitation, throughfall and decomposing litter, reducing the availability of nutrients for vascular plant growth (Weber and Van Cleve 1984). If disturbance is not severe enough to disrupt the competitive ability of the feather moss community present in late boreal succession, their dominance is likely to continue during stand initiation, suppressing seedling establishment and slowing rates of nutrient turnover (Fisher 1979; Steijlen et al. 1995).

In the present study, clear-cut harvesting often left a large portion of the forest floor untouched, whereas wildfire consumed at least a portion of the forest floor, and the ground and aboveground vegetation. It would seem that wildfire has greater potential to improve stand fertility as it disrupts the competitive ability of the understory and ground plant communities, and favors the establishment of vascular species that generate more labile litter. For clear-cut harvesting to maintain the productivity of boreal ecosystems, it must sufficiently disturb the competitive advantage of the nonvascular ground community. However, the location of the 21 year old fires at the lower end of the soil fertility gradient suggests that wildfires that only partially burn the forest floor do not necessarily improve stand fertility. In this area revegetation of burnt humus is often dominated by lichen communities, while vascular plant regeneration occurred mainly from the resprouting of underground parts and was predominated by ericaceous shrubs (Nguyen-Xuan 1999). The resistance to decomposition of such vegetation types was demonstrated by greater N cycling following logging than burning nearly 20 years after disturbance (Chapter 1).

2.5 Conclusion

Thus, it can be seen that disturbance type and severity of forest floor disturbance can affect post-disturbance regeneration dynamics in two ways. First, disturbance type and severity determine the composition of the vegetation that will establish itself immediately following disturbance. Second, once the immediate and direct effects of disturbance on vegetation establishment and soil nutrients have subsided, the indirect effects of disturbance type and severity on the regenerating stand can be observed through the increasing influence exerted by the established vegetation on soil nutritional dynamics. This has implications for sustainable forestry in the following ways: 1) the choice of harvesting method and post-harvest silvicultural treatments has to be made in function of the regeneration dynamics desired, with an important consideration for their effects on soil fertility, 2) concerns for the composition of the regenerating vegetation should not be exclusively in terms of commercial tree species, but should include other pioneer species that have beneficial effects on soil fertility.

Table 2.1. Site characteristics.

Study Area	Location	Replication	Fire Year	Fire Area (ha)	Cut Years	Forestry Region[a]	Avg. Soil Texture (0-10cm)	Avg. Annual Temp. (C)[b]	Avg. Annual Precip. (mm)[b]
2	48 44'-59' 00 N 76 08'-38' 00 W	10 Fire 10 Cut	1995	47 709	1992-94	Gouin	Loamy Sand	1.2	840
14	48 44'-57' 00 N 74 31'-54' 00 W	8 Fire 8 Cut	1983	14 535	1981-86	Gouin	Loamy Sand	0.8	948.4
21	49 17'-51' 00 N 79 00'-19' 00 W	10 Fire 10 Cut	1976	31 054	1975-80	Northern Clay	Sandy Clay Loam	0.6	822

[a]Forestry regions as proposed by Rowe (1972).
[b]Meteorological data provided by the nearest weather station (Anon, 1982).

Table 2.2. Environmental variables used in variance partitioning and canonical correspondence analysis.

Subset	Environmental Variable	Description
Site Characteristics	Duff	Average duff depth in each site
	Sand	Percent sand of the first 10cm
	Aspect	Aspect of stand - between 0 (N) and 180 (S)
	Moist.	Moisture regime
	Time	Time since most recent disturbance
	Age	Stand age at time of disturbance
	Long.	Longitude of each site
Soil Fertility	MCExtCa	Concentration of extractable Ca in the mineral soil
	MCOrgC	Concentration of organic C in the mineral soil
	MCMin	Concentration of mineralized N (available N) in the mineral soil
	MpH	Mineral soil pH
	Mbasal	Basal respiration in the mineral soil
	FCExtCa	Concentration of extractable Ca in the forest floor
	FCExtP	Concentration of Mehlich III extractable P in the forest floor
	FCTotN	Concentration of total N in the forest floor
	FMIgn	Mass of organic matter in the forest floor determined by loss on ignition
	FMMin	Mass of N mineralization (available N) in the forest floor

Table 2.3. Interset correlation coefficients of environmental variables with the first and second axes of the Global CCA, Soil CCA, and Partial Soil CCA. Passive analysis of site characteristics variables was used to determine their interset correlation coefficients for the Soil CCA. There are no interset correlation coefficients given for the site characteristics variables in the Partial Soil CCA since these variables are used as covariables in this analysis.

	Global CCA		Soil CCA		Partial Soil CCA	
	axis 1	axis 2	axis 1	axis 2	axis 1	axis 2
Soil fertility variables						
MCExtCa	-0.07	-0.03	-0.08	-0.08	0.23	0.25
MCOrgC	-0.13	-0.34	-0.15	-0.43	0.05	0.02
MCMin	-0.12	0.49	-0.10	0.41	0.26	0.15
MpH	0.21	0.43	0.23	0.53	0.37	0.09
Mbasal	-0.28	0.14	-0.27	0.16	0.23	-0.09
FCExtCa	0.05	0.18	0.06	0.34	0.63	0.38
FCExtP	0.82	-0.04	0.84	-0.12	-0.38	0.69
FCTotN	0.21	0.59	0.25	0.73	0.49	0.48
FMIgn	-0.38	-0.11	-0.41	-0.21	0.05	0.03
FMMin	-0.16	0.45	-0.14	0.36	0.33	-0.05
Site characteristics variables						
Duff depth	-0.54	-0.01	-0.56	-0.17	-	-
Percent sand	0.28	0.46	0.32	0.54	-	-
Aspect	0.22	-0.07	0.23	0.03	-	-
Moisture regime	-0.11	-0.28	-0.12	-0.40	-	-
Time since most recent disturbance	-0.69	-0.35	-0.69	-0.29	-	-
Stand age at time of disturbance	-0.12	0.22	-0.09	0.29	-	-
Longitude	-0.14	-0.63	-0.19	-0.69	-	-

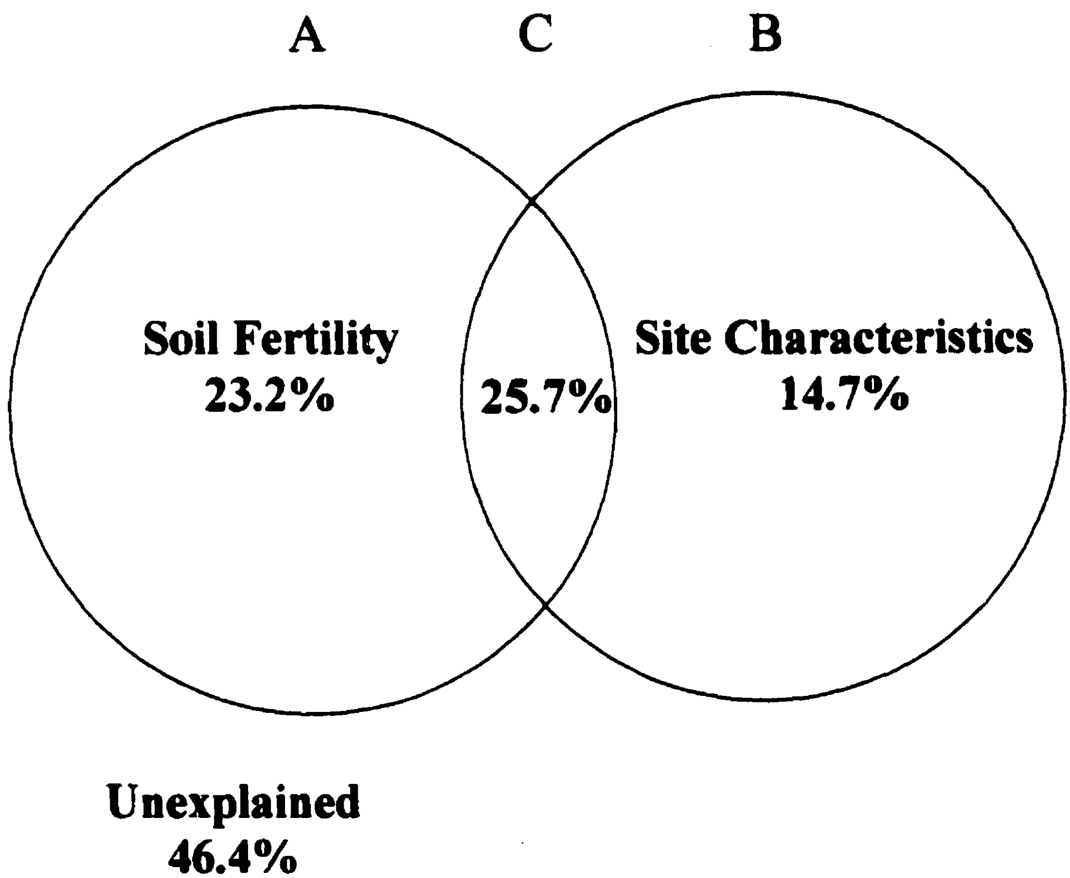

Figure 2.1. Partitioning of the vegetation data set variance using soil fertility and site characteristics as subsets of explanatory variables. Global CCA = A + B + C. Soil Fertility CCA = A + B. Partial Soil Fertility = A.

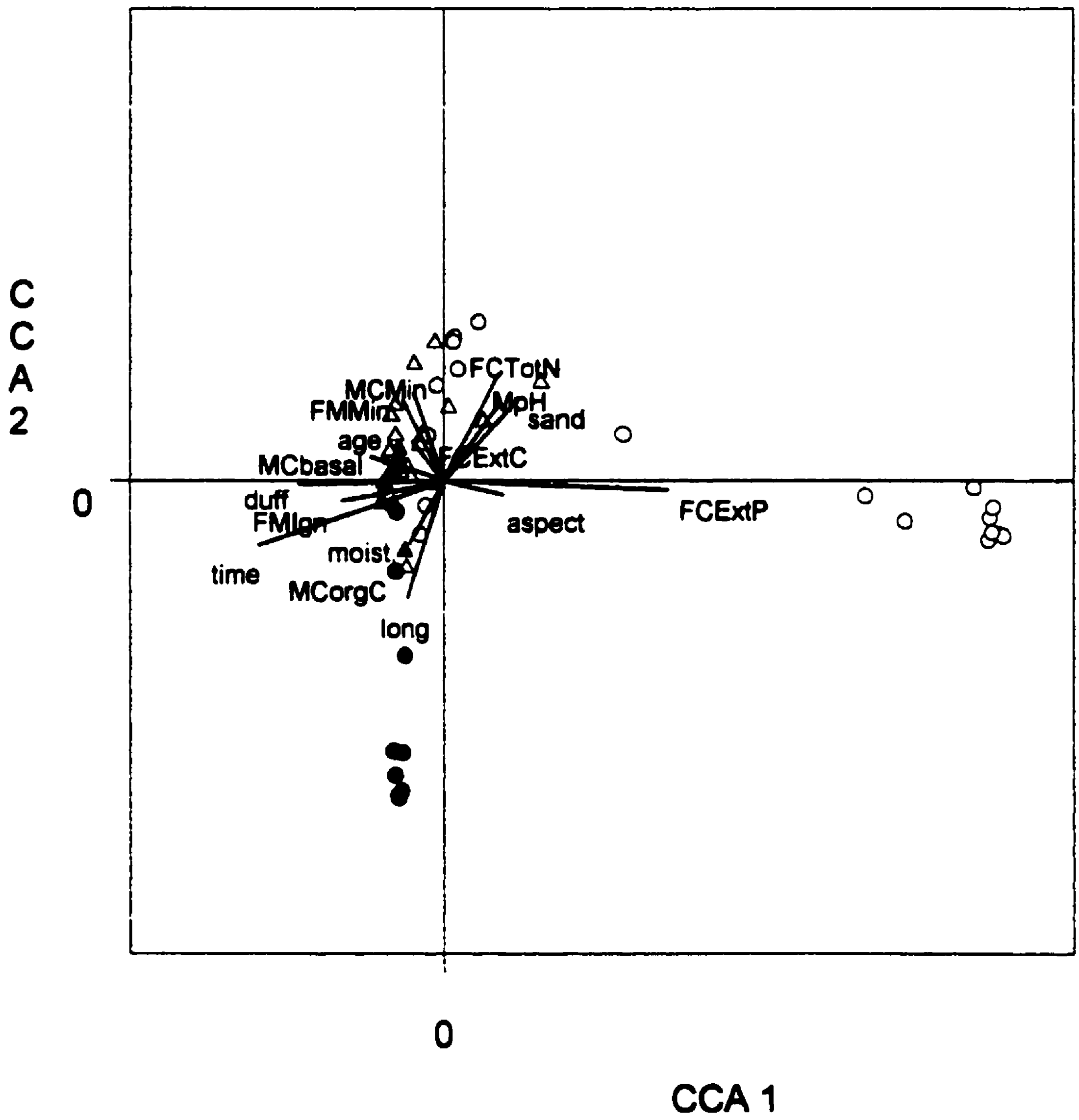

Figure 2.2. Global CCA ordination of disturbed sites along two first CCA axes. Fire (○) and clear-cut (△) sites of the 2 year old study area (○) and clear-cut (△) sites of the 14 year old study area. Fire (●) and clear-cut (▲) sites of the 21 year old study area.

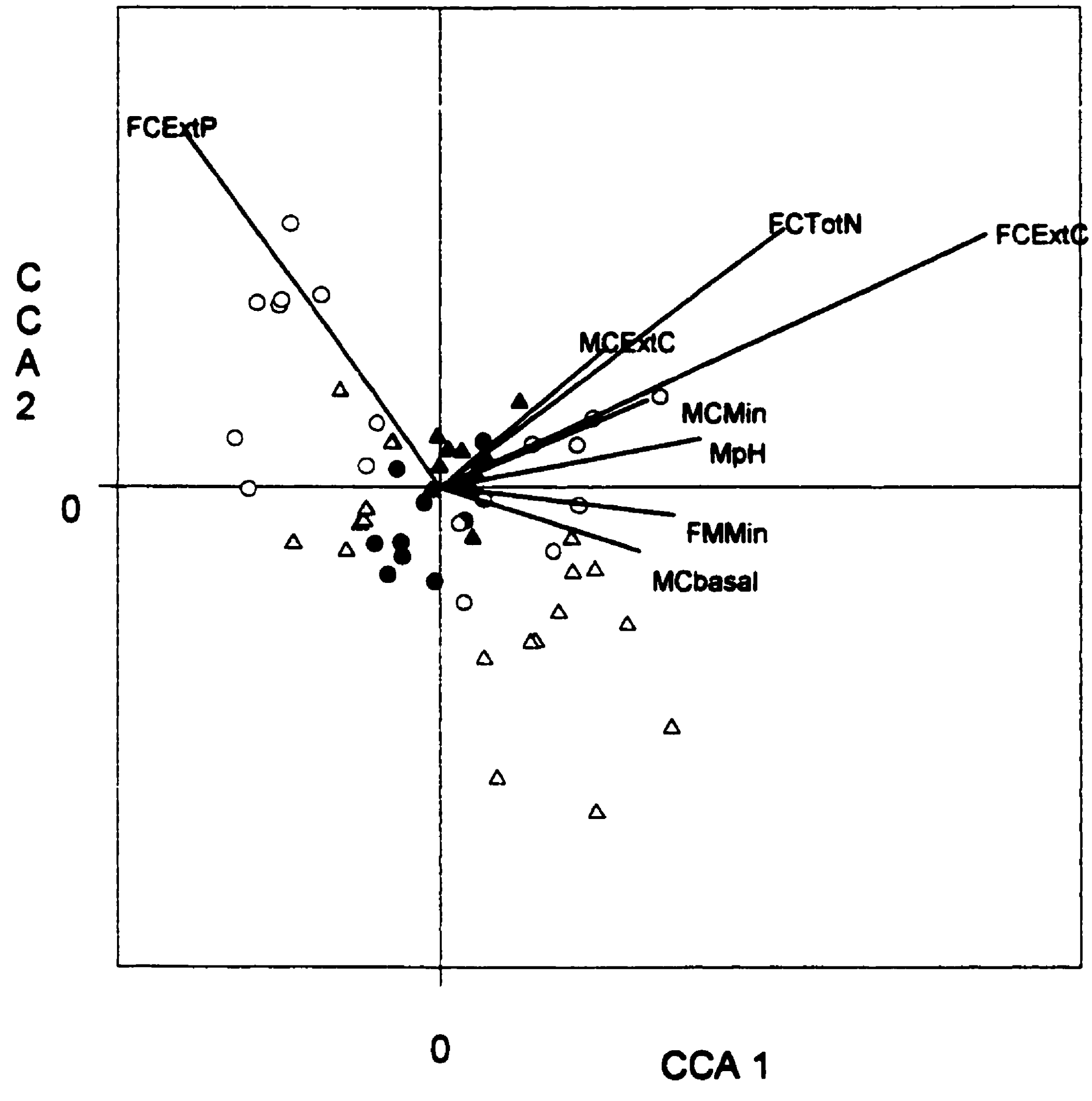

Figure 2.3. Partial Soil Fertility CCA ordination of disturbed along two first CCA axes. Symbols are the same as in previous figure.

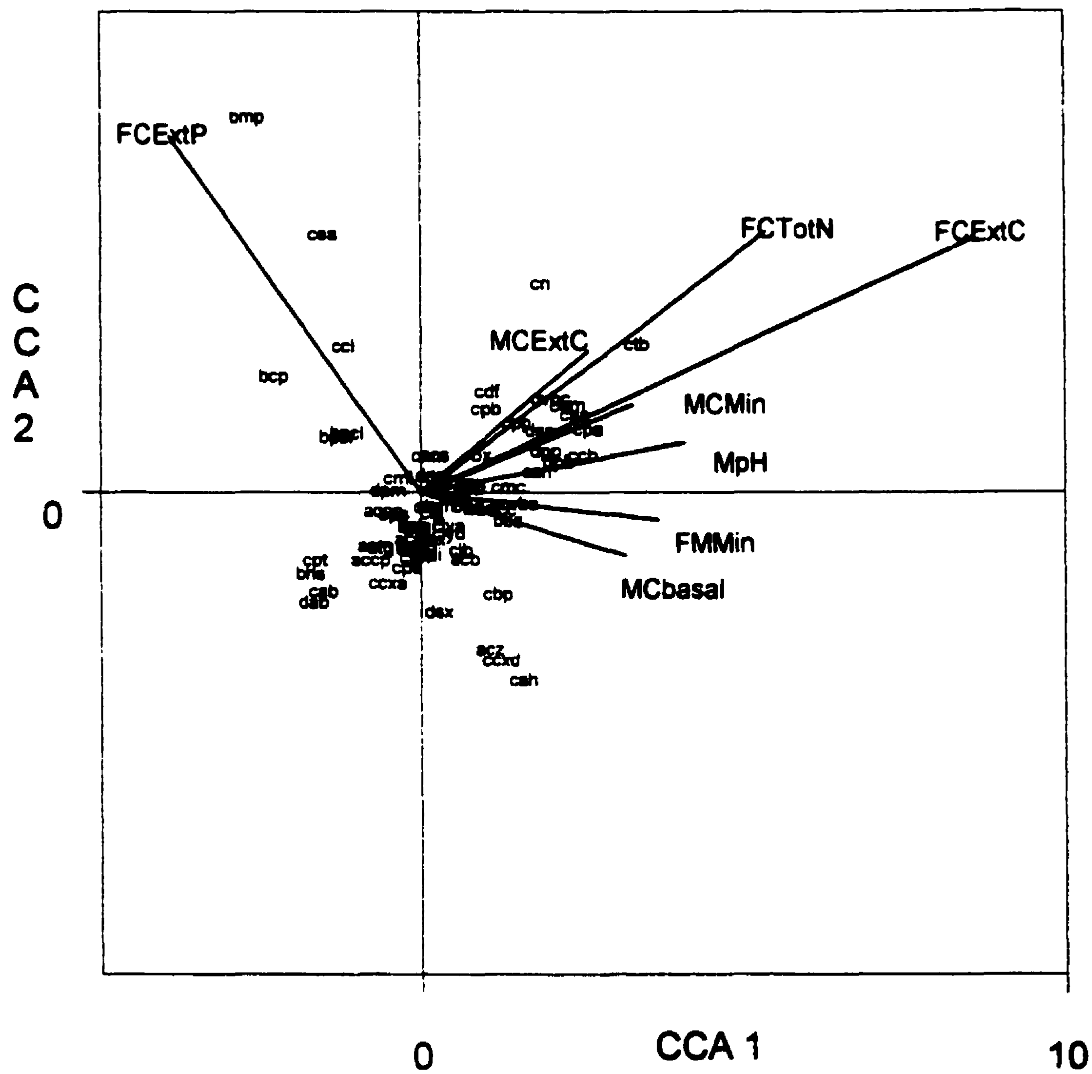

Figure 2.4. Partial Soil Fertility CCA ordination of species along two first ordination axes. Species full name provided in appendix 1. Prefixes describe plant form : lichens (a), bryophytes (b), vascular plants below 1 m (c), vascular plants between 1 and 3 m (d).

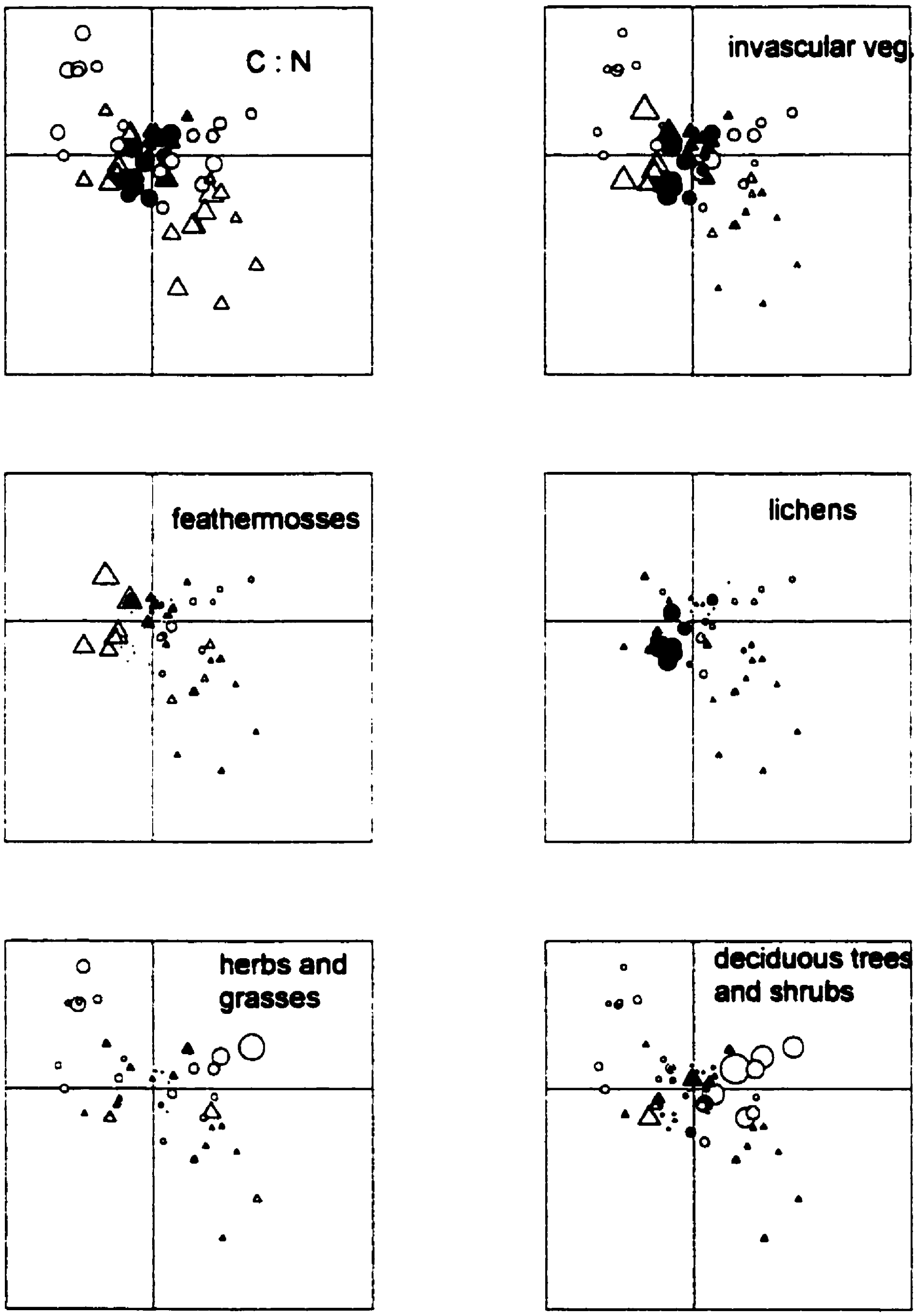

Figure 2.5. Partial Soil Fertility CCA ordination of disturbed stands. Size of symbol is proportional to value of descriptor observed at a given site. Descriptors illustrated are : forest floor C : N, % cover of groung vegetation, % cover of feathermosses, % cover of lichens, % cover of herbs and grasses, % cover of deciduous shrubs and trees. Symbol legend same as in previous figures.

CONCLUSION

This study suggests that wildfire consumes the forest floor, increasing the availability of nutrients in the rooting zone of regenerating vegetation; whereas clearcut harvesting increases the rate of nitrogen mineralization and contains a greater mass of total nutrients in the forest floor, suggesting that clearcutting may benefit long-term productivity by maintaining greater nutrient reserves and higher rates of nutrient cycling.

Further study of the relationship between soil fertility and regenerating vegetation suggested that disturbance type and severity of forest floor disturbance can affect post-disturbance regeneration dynamics in two ways. First, disturbance type and severity determine the composition of the vegetation that will establish itself immediately following disturbance. Second, once the immediate and direct effects of disturbance on vegetation establishment and soil nutrients has passed, the established vegetation plays an increasingly important role in the nutritional dynamics of the disturbed ecosystem.

Sustainable forestry practices should recognize the importance of the effects of disturbance type and severity on soil fertility and regenerating vegetation and their implication in the long-term productivity and biodiversity of the boreal forest. Furthermore, the choice of the desired composition of regenerating vegetation should not be exclusively made in terms of commercial tree species, but should include other pioneer species that have the ability to enhance litter quality and consequently nutrient cycling.

5.1 Direction of Further Research

The scope of this study was very focussed, examining the effects of clearcut harvesting and wildfire on soil fertility and the relationships between regenerating vegetation and soil fertility in black spruce stands on glacial till in the Quebec boreal forest. Additionally, the sampling criteria used in stand selection attempt to isolate similar levels of disturbance severity in both wildfires and clearcuts. Further research should be more open to address issues of the effects of disturbance in a variety of ecosystems, such as those with different deposits and tree species as well as different levels of disturbance severity.

During the course of this study it was noted that there is a lack of information concerning the mechanisms involved in the dominance of the ericaceae-feathermoss community in the understory of mature boreal stands. More research is needed to examine the effects of the competitive ability of the ericaceae-feathermoss community and the dynamics of their litter decomposition following clearcut harvesting on emerging early successional boreal vegetation.

REFERENCES

Abrams, M . D. and Dickman, D. I. 1982. Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan. Can. J. Bot. 60:946-954.

Adams, P. W. and Boyle, J. R. 1980. Effects of fire on soil nutrient in clear-cut and whole-tree harvest sites in central Michigan. Soil Sci. Soc. Am. J. 44:847-850.

Adams, P. W. and Boyle, J. R. 1982. Soil fertility changes following clear-cut and whole-tree harvesting and burning in central Michigan. Soil Sci. Soc. Am. J. 46:638-640.

Ahlgren, C.E. 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. Ecology 41 : 431-445.

Ahlgren, I. F. 1974. The effect of fire on soil microbes. *In* Fire and Ecosystems. *Edited by* T. T. Kozlowski and C. E. Ahlgren. Academic Press. New York. 195-224 pp.

Ahlgren, I. F. and Ahlgren, C. E. 1960. Ecological effects of forest fire. Bot. Rev. 26: 483-517.

Anonymous. 1982. Normales climatiques au Canada, 1951-1980: Québec. Environnement Canada, Service de l'environnement atmosphérique, Downsview, Ontario.

Anonymous. 1996. Statistix® for Windows: User's Manual. Tallahassee, Florida.

Archibold, O.W. 1980. Seed input into a postfire forest site in northern Saskatchewan. Can. J. For. Res. 10: 129-134.

Armson, K. A. 1977. Forest Soils: properties and processes. University of Toronto Press, Toronto.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. For. Ecol. Manag. 63:247-300.

Barbour, M. G., Burk, J. H. and Pitts, W. D. 1987. Terrestrial Plant Ecology. 2nd ed. Benjamin/Cummings Publishing Company. Don Mills, Ontario. 634 pp.

Beaton, J. D. 1959. The influence of burning on the soil in the timber range of Lac Le Jeune, British Columbia. I. Physical properties. Can J. Soil Sci. 39:1-11.

Bergeron, Y. and Harvey, B. 1997. Basing silviculture on natural ecosystems dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manag. 92: 235-242.

Biodiversity Science Assessment Team (BSAT). 1994. Biodiversity in Canada: a science assessment for environment Canada. Environment Canada. Ottawa.

Blais, J. R. 1983. Trends in the frequency, extent and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13:539-547.

Bonan, G. B. 1992. Processes in boreal forests. *In* A Systems Analysis of the Global Boreal Forest *Edited by* H. H. Shugart, R. Leemans and G. B. Bonan. Cambridge University Press, New York. 126-143 pp.

Bondrup-Nielsen, S. 1995. Forestry and the boreal forest: maintaining inherent landscape patterns. Water, Air Soil Pollut. 82: 71-76.

Borcard, D., Legendre, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology. 73: 1045-1055.

Brais, S., Camiré, C. and Paré, D. 1995a. Impacts of whole-tree harvesting and winter windrowing on soil pH and base status of clayey sites of northwestern Quebec. Can. J. For. Res. 25 : 997-1007.

Brais, S., Camiré, C., Bergeron, Y. and Paré, D. 1995b. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. For. Ecol. Manage. 76 : 181-189.

Brumelis, G. and Carleton, T. J. 1988. The vegetation of postlogged black spruce lowlands in central Canada. I. Trees and tall shrubs. Can. J. For. Res. 18:1470-1478.

Brumelis, G. and Carleton, T. J. 1989. The vegetation of postlogged black spruce lowlands in central Canada. II. Understory vegetation. J. Appl. Ecology 26:321-339.

Burger, J. A. and Pritchett, W. L. 1988. Site preparation effects on soil moisture and available nutrients in a pine plantation in the Florida Flatwoods. For. Sci. 34:77-87.

Canadian Council of Forest Minsters. 1997. Compendium of Canadian Forestry Statistics: 1996, national forestry database. Natural Resources Canada, Ottawa.

Carleton, T.J, Jones, P.K. and Pierpoint, G. 1985. The prediction of understorey vegetation by environmental factors for the purpose of site classification in forestry : an example from northern Ontario using residual ordination analysis. Can. J. For. Res. : 1099-1108.

Carleton, T.J. and MacLellan, P. 1994. Woody vegetation responses to fire versus clear-cutting : a comparative survey in the central Canadian boreal forest. Écoscience 1(2) : 141-152.

Carleton, T.J. and Maycock, P. F. 1980. Vegetation of the boreal forests south of James Bay. Ecology 61(5) : 1199-1212.

Carleton, T.J. and Maycock, P. F. 1981. Understorey-canopy affinities in the boreal forest vegetation. Can. J. Bot. 59 : 1709-1716.

Chapin, D. M. 1995. Physiological and morphological characteristics of two colonizing plant species on Mount St. Helens. Am. Midl. Nat. 133:76-87.

Chapin, F.S. and Van Cleve, K. 1981. Plant nutrient absorption and retention under differing fire regimes. *in* : Proceedings from the conference : Fire regimes and Ecosystem Properties. Honolulu, Hawaii, 11-15 December, 1978. USDA, report # WO-26. Pp. 379-400.

Chevalier, P. 1993. Gestion des Ressources Renouvelables: Secteurs Agricole et Forestier. Presses de l' Université du Québec, Sainte Foy, Canada.

Dixon, W. J. 1950. Analysis of extreme values. Ann. Math. Stat. 21:488-506.

Dyrness, C. T. and Youngberg, C. T. 1957. The effect of logging and slash burning on soil structure. Soil Sci. Soc. Amer. Proc. 21:444-447.

Edmonds, R. L., Binkley, D., Feller, M. C., Sollins, P., Abee, P., and Myrold, D. D. 1989. Nutrient cycling: effects of productivity of Northwest forests. *In* Maintaining the long-term productivity in the Pacific Northwest forest ecosystems. *Edited by* D. A. Perry, R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C. R. Perry and R. F. Powers. Timber Press, Portland, Oreg. pp. 17-35.

Ehnes, J. W. and Shay, J. M. 1995. Natural recovery of logged and burned plant communities in the Lake Winnipeg East Forest Section, Manitoba. University of Manitoba.

Fisher, P. F. 1979. Possible allopathic effects of reindeer-moss (Cladonia) on jack pine and white spruce. For. Sci. 25:256-260.

Foster, D. R. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. Can. J. Bot. 61:2459-2471.

Fritze, H., Pennanen, T. and Pietikainen, J. 1993. Recovery of soil biomass and activity from prescribed burning. Can. J. For. Res. 23:1286-1290.

Furuberg Gjeddtjernet, A. M. 1995. Forest operations and environmental protection. Water, Air Soil Pollut. 82:35-41.

Greacen, E. L. and Sands, R. 1980. Compaction of forest soils: a review. Aust. J. Soil Res. 18:163-189.

Hansen, A. J., Spies, T. A. Swanson, F. J. and Ohmann, J. L. 1991. Conserving biodiversity in managed forests: lessons form natural forests. Bioscience. 41:382-392.

Hart, G. E., DeByle, N. V. and Hennes, R. W. 1981. Slash treatment after clear-cutting lodgepole pine affects in soil water. J. For. 79:446-450.

Hendershot, W. H. and Duquette, M. 1986. A simple barium chloride method for determining cation exchange capacity and exchangeable cations. Soil Sci. Soc. Am. J. 50:605-608.

Hendershot, W. H., Lalande, H. and Duquette, M. 1993. Soil reaction and exchangeable acidity. *In* Soil Sampling and Methods of Analysis. *Edited by* M. R. Carter. Lewis Publishers, London. pp. 141-146.

Jäderlund, A., Zachrisson, O., Dahlberg, A. and Nilsson, M-C. 1997. Interference of Vaccinium myrtillus on the establishment growth, and nutrition of Picea abies seedlings in a northern boreal site. Can. J. For. Res. 27: 2017-2025.

Johnson, E.A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. Can. J. Bot. 53: 2933-2941.

Johnson, E. A. 1992. Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. Cambridge University Press, New York.

Johnston, M.H. and Elliott, J. A. 1996. Impacts of logging and wildfire on an upland black spruce community in northwestern Ontario. Environmental Monitoring and Assessment 39 : 283-297.

Johnston, M.H. and Elliott, J. A. 1998. The effects of fire severity on ash, and plant and soil nutrient levels following experimental burning in a boreal mixedwood stand. Can. J. Soil Sci. 78: 35-44.

Kalra, Y. P. and Maynard, D. G. 1991. Methods manual for forest soil and plant analysis. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-319.

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

Kelsall, J. P., Telfer, E. S. and Wright, T. D. 1977. The effects of fire on the ecology of the Boreal Forest with particular reference to the Canadian North and selected bibliography. Occasional Paper Number 32. Canadian Wildlife Service, Ottawa.

Killham, K. 1990. Nitrification in coniferous forest soils. Plant and Soil. 128: 31-44.

Kimmins, J. P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. Soil Sci. Soc. Am. J. 60:1643-1654.

Kimmins, J. P. 1997. Forest Ecology: A foundation for sustainable management. Prentice-Hall, Upper Saddle River, New Jersey.

Knight, H. 1966. Loss of nitrogen from the forest floor by burning. For. Chron. 42:149-152.

Kutiel, P. and Naveh, Z. 1987. The effects of fire on nutrients in a pine forest soil. Plant and Soil. 104:269-274.

Kutiel, P. and Shaviv, A. 1992. Effects of soil type, plant composition and leaching on soil nutrients following a simulated forest fire. For. Ecol. Manag. 53:329-343.

Larsen, J. A. 1980. The Boreal Ecosystem. Academic Press, Toronto.

Lawrence, G. B., Fuller, R. D. and Driscoll, C. T. 1987. Release of aluminum and loss of nutrients following whole-tree harvesting at the Hubbard Brook experimental forest, New Hampshire. J. Environ. Qual. 17:418-424.

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

MacDonald, G. B. 1995. The case for boreal mixedwood management: an Ontario perspective. For. Chron. 71:725-734.

MacLean, D. A., Woddley, S. J., Weber, M. G. and Wein, R. W. 1983. Fire and nutrient cycling. *In* The role of fire in Northern Circumpolar Ecosystems. *Edited by* R. W. Wein and D. A. MacLean. John Wiley and Sons, New York. 111-132pp.

Mann, L. K., Johnson, D. W., West, D. C., Cole, D. W., Hornbeck, J. W., Martin, C. W., Riekerk, H., Smith, C. T., Swank, W. T., Tritton, L. M. and Van Lear, D. H. 1988. Effects of whole-tree and stem-only clearcutting on postharvest hydrologic losses, nutrient capital and regrowth. For. Sci. 34:412-428.

Margolis, H. A. and Brand, D. G. 1990. An ecophysiological basis for understanding plantation establishment. Can. J. For. Res. 20: 375-390.

Marks, P. L. and Bormann, F. H. 1972. Revegetation following forest cutting: mechanism for return to steady-state nutrient cycling. Science. 176:914-915.

McColl, J. G. and Powers, R. F. 1984. Consequences of forest management on soil-tree relationships. *In*. Nutrition of Plantation Forests. *Edited by* G. D. Bowen and E. K. S. Nambiar. Academic Press, Montreal. 379-412 pp.

McKeague, J. A. (*Editor*). 1976. Manual on Soil Sampling and Methods of Analysis. Can. Soc. Soil Sci. Ottawa, Ontario.

Moore, T. R. 1981. Controls on the decomposition of organic matter in subarctic spruce-lichen woodland soils. Soil Science. 131:107-113.

Moore, T. R. 1984. Litter decomposition in subarctic spruce-lichen woodland, eastern Canada. Ecology. 65:299-308.

Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the Boreal Zone of Quebec. Can. J. For. Res. 24:730-741.

Mroz, G. D., Jurgensen, M. F. and Frederick, D. J. 1985. Soil nutrient changes following whole-tree harvesting on three northern hardwood sites. Soil Sci. Soc. Am. J. 49:1552-1557.

Munson, A. D., Margolis, H. A. and Brand, D. G. 1993. Intensive silvicultural treatment: impacts on soil fertility and planted conifer response. Soil Sci. Soc. Am. J. 57:246-255.

Nguyen-Xuan, T. 1999. The importance of forest floor disturbance in early regeneration patterns of the boreal forest of western and central Quebec: a wildfire vs. logging comparison. To be submitted.

Noble, M. G., DeBoer, L. K., Johnson, K. L., Coffin, B. A., Fellows, L. G. and Christensen, N.A. 1977. Quantitative relationships among some *Pinus banksiana – Picea mariana* forests subjected to wildfire and postlogging treatments. Can. J. For. Res. 7 : 368-377.

Norberg, G., Jäderlund, A., Zachrisson, O., Nordfjell, T. Wardle, D. A., Nilsson, M-C, and Dolling, A. 1997. Vegetation control by stem treatment in boreal forests: a comparison with burning and soil scarification. Can. J. For. Res. 27:2026-2033.

Nykvist, N. and Rosen, K. 1985. Effect of clear-felling and slash removal on the acidity of northern coniferous soils. For. Ecol. Manag. 11:157-169.

Oechel, W. C. and Van Cleve, K. 1986. Role of bryophytes in nutrient cycling in the taiga. *In* Forest Ecosystems in the Alaska Taiga: A Synthesis of Structure and Function. *Edited by* K. VanCleve, F. S. III. Chapin, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, Springer-Verlag. New York. pp. 121-137.

Oswald, E. T. and Brown, B. N. 1993. Vegetation development on skid trials and burned sites in southeastern British Columbia. For. Chron. 69:75-80.

Paré, D., Bergeron, Y. and Camire, C. 1993. Changes in the forest floor of Canadian southern boreal forest after disturbance. J. Veg. Sci. 4:811-818.

Paré, D. and Van Cleve, K. 1992. Aboveground biomass production and nutrient accumulation on post-harvested white spruce sites on the interior Alaska. Can. J. For. Res. 23:1223-1238.

Parkinson, J. A. and Allen, S. E. 1975. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. Commun. Soil Sci. Plant Anal. 6(1):1-11

Paul, E. A. and Clark, F. E. 1989. Soil Microbiology and Biochemistry. Academic Press, Toronto.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. *In* A Systems Analysis of the Global Boreal Forest. *Edited by* H. H. Shugart, R. Leemans, and G. B. Bonan. Cambridge University Press, New York. 144-169 pp.

Perry, D. A. 1994. Forest Ecosystems. Johns Hopkins University Press, Baltimore.

Perry, D. A. and Amaranthus, M. P. 1997. Disturbance, Recovery, and Stability. *In* Creating a forestry for the 21st century: the science of ecosystem management. *Edited by* K. A. Kohm and J. F. Franklin. Island Press. Wahington, D. C. pp. 31-57.

Persson, H. Å. 1993. The distribution and productivity of fine roots in boreal forest. Plant and Soil. **71**: 87-101.

Pietikäinen, J. and Fritze, H. 1995. Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. Soil Boil. Biochem. 27:101-109.

Prescott, C. E. 1997. Effects of clearcutting and alternative silvicultural systems on rates of decomposition and nitrogen mineralization in a coastal montane coniferous forest. For. Eco. Manag. 95:253-260.

Prévost, M. 1997. Effets du scarifiage sur les propiétés du sol et l'ensemencement naturel dans une pessière noire à mousses de la forêt boréale québécois. Can. J. For. Res. 26:72-86.

Prichett, W. L. 1979. Properties and Management of Forest Soils. John Wiley and Sons, Toronto.

Pritchett, W. L. and R. F. Fisher. 1987. Properties and Management of Forest Soils. 2nd ed. John Wiley and Sons, Toronto.

Qi, M. and Scarrett, J. B. 1998. Effects of harvesting method on seed bank dynamics in a boreal mixedwood forest in northwestern Ontario. Can. J. Bot. 76: 872-883.

Rintoul, T. and Johnston, M. 1996. Vegetation response to harvesting, harvesting and prescribed burning and wildfire in northwestern Ontario. *In* Proc. Of the 2nd Workshop on Disturbance Dynamics in Boreal Forests. *Edited by* Y. Bergeron and G. Frisque. Rouyn-Noranda, Quebec, August 26-30, 1994. 212-213 pp.

Rowe, J. S. 1972. Forest Regions in Canada. Canadian Forest Service, Publication No. 1300.

Rowe, J.S. 1983. Concepts of fire effects on plant individual and species. *in* : Wein, R.W. and D.A. MacLean (eds.), The Role of Fire in Northern Circumpolar Ecosystems. John Wiley and Sons Ltd, New-York. pp. 134-154.

Schoch, P. and Binkley, D. 1986. Prescribed burning increased nitrogen availability in a mature Loblolly pine stand. For. Ecol. Manag. 14:13-22.

SPSS. 1997. SPSS for Windows. Release 8.0. SPSS Inc., Chicago.

Stark, N. and Steele, R. 1977. Nutrient content of boreal forest shrubs following burning. Amer. J. Bot. 64 (10) : 1218-1224.

Steijlen, I., Nilsson, M-C. and Zackrisson, O. 1995. Seed regeneration of Scots pine in boreal forest stands dominated by lichen and feathermoss. Can. J. For. Res. 25:713-733.

Swift, M. J., Heal, O. W. and Anderson, J. M. 1979. Decomposition in Terrestrial Ecosystems. University of California Press, Los Angeles.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: A new eigenvector technique for direct gradient analysis. Ecology 67: 1167-1179.

ter Braak, C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69: 69-77.

ter Braak, C. J. F. 1987-1992. CANOCO - a FORTRAN program for Canonical Community Ordination. Microcomputer Power, Ithaca, New-York.

ter Braak, C. J. F. 1995. Ordination. *In* Data Analysis in Community and Landscape Ecology. *Edited by* R. H. G. Jongman, C. J. F. ter Braak and O. F. R. Van Tongeren. Cambridge University Press, New York.

Tran, T. S. and Simard, R. R.. 1993. Mehlick III-extractable nutrients. *in* Soil Sampling and Methods of Analysis. *Edited by* M. R. Carter. Lewis Publishers, London. pp. 43-50.

Ulrey, R. A. and Graham, R. C. 1993. Forest fire effects on soil colour and texture. Soil Sci. Soc. Am. J. 57:135-140.

Van Cleve, K. 1974. Organic matter quality in relation to decomposition. *In* Soil Organisms and decomposition in Tundra: proceedings of the microbiology, decomposition and invertebrate working groups meeting, University of Alaska, Fairbanks, Alaska, USA, August 1973. *Edited by* A. J. Holding, O. W. Heal, S. F. MacLean, and P. W. Flanagan. Tundra Biome Steering Committee, Stockholm, pp. 311-324.

Van Cleve, K. and Viereck, L. A. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. *in* : West, D.C., Shugart, H.H. and D.B. Botkin (eds.), Forest Succession : Concepts and Applications. Springer-Verlag, New-York. pp. 185-211.

Viereck, L. A. 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. *In* The role of fire in Northern Circumpolar Ecosystems. *Edited by* R. W. Wein and D. A. MacLean. John Wiley and Sons, New York. 201-220pp.

Vitousek, P. M., Gosz, J. R., Grier, C. C., Melillo, J. M., Reiners, W. A. and Todd, R. L. 1979. Nitrate losses from disturbed ecosystems. Science. 204:469-474.

Vitousek, P. M. and Matson, P. A. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed lobolly pine plantation. Ecology. 66:1360-1376.

Weber, M. G. and Van Cleve, K. 1984. Nitrogen transformations in feathermoss and forest floor layers of interior Alaska black spruce ecosystems. Can J. For. Res. 14:278-290.

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

Woodmansee, R. G. and Wallach. L. S. 1981. Effects of fire regime on biogeochemical cycles. *In* Proceedings from the conference: Fire Regimes and Ecosystem Properties, Honolulu, Hawaii, 11-15 December 1978. USDA, report # WO-26. p. 379-400.

Wright, H. A. and Bailey, A. W. 1982. Fire Ecology, United States and Southern Canada. John Wiley and Sons, Toronto. 501 pp.

Yeomans, J. C. and J. M Bremner. 1988. A rapid and precise method for routine determination of organic carbon in soil. Commun. Soil Sci. Plant Anal. 19(13): 1467-1476.

Zachrission, O., Nilsson, M-C., Dahlberg, A. and Jäderlund, A. 1997. Interference mechanisms in conifer-Ericaceae-feathermoss comminutes. OIKOS. 78: 209-220.

APPENDIX A

List of species used in ordinations. Ordination codes and litter quality producing types. Lichens (L), feathermosses (F), herbaceous (H), deciduous (D).

Lichens

Trapeliosis granulosa	atg	L
Cladonia botrytes (Hag.) Willd.	acb	L
Cladonia cenotea (Ach.) Schaer.	accn	L
Cladonia cornuta (L.) Hoffm.	acco	L
Cladonia crispata (Ach) Flot.	accp	L
Cladonia cristatella Tuck./*coccifera* (L.) Willd.	acct	L
Cladonia deformis (L.) Hoffm.	acd	L
Cladonia gracilis (L.) Willd	acg	L
Cladonia spp.	acz	L
Cladina mitis (Sandst.) Hale and Culb	acm	L
Cladina rangiferina (L.) Harm.	acr	L
Cladina stellaris (Opiz) Brodo	acs	L

Bryophytes

Brachythecium spp.	bbz	
Ceratodon purpureus	bcp	
Dicranum spp.	bdi	F
Hylocomnium splendens (Hedw.) BSG	bhs	F
Marchantia polymorpha	bmp	
Pleurozium shreberi (BSG) Mitt.	bps	F
Pohlia spp.	bph	
Polytrichum spp.	bpo	
Ptilidium ciliare	bpcl	F
Ptilium crista-castrensis (Hedw.) De Not	bpcr	F
Sphagnum spp.	bs	F
Unknown moss	bx	

Vascular Plants (below 1 m)

Abies balsamea (L.) Mill.	cab	
Aralia hispida Vent.	cah	H
Amelanchier spp.	cam	D
Aralia nudicaulis L.	can	H
Betula papyrifera Marsh.	cbp	D
Clintonia borealis (Ait.) Raf.	ccb	
Cornus canadensis L.	ccc	
Coptis groenlandicus (Oeder) Fern.	ccg	
Comandra livida Richards	ccl	
Carex spp.	ccx	H
Carex aenea Fern.	ccxa	H
Carex deflexa Hornem.	ccxd	H
Deschampsia flexuosa (L.) Trin.	cdf	H
Epilobium angustifolium L.	cea	H
Gaultheria hispidula (L.) Muhl.	cgh	
Linnaea borealis L.	clb	
Ledum groenlandicum Retzius	clg	
Lycopodium annotinum L.	clya	
Lycopodium obscurum L.	clyo	
Maianthemum canadense Desf.	cmc	
Melampyrum lineare desr.	cml	
Nemopanthus mucronatus (L.) Trel.	cnm	D
Pteridium aquilinum (L.) Kuhn.	cpa	H
Pinus banksiana Lamb.	cpb	
Prunus pensylvanica L.	cpp	D
Pyrola secunda L.	cps	
Populus tremuloides Michx.	cpt	D
Ribes glandulosum Grauer.	crg	H
Rubus idaeus L.	cri	H
Sorbus americana Marsh.	csa	D
Solidago macrophylla Pursh.	csm	H
Salix spp.	csx	D
Trientalis borealis Raf.	ctb	

Vascular Plants (1 – 3 m)

Abies balsamea (L.) Mill.	dab	
Amelanchier spp.	dam	D
Betula papyrifera Marsh.	dbp	D
Kalmia angustifolium L.	dka	
Nemopanthus mucronatus(L.) Trel.	dnm	D
Picea mariana (Mill.) BSP	dpm	
Pinus banksiana Lamb.	dpb	

Populus tremuloides Michx.	dpt	D
Prunus pensylvanica L.	dpp	D
Sorbus americana Marsh.	dsa	D
Salix spp.	dsx	D
Viburnum cassinoides L.	dvbc	D