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CONTROLS ON NUTRIENT AVAILABILITY IN BLACK SPRUCE FORESTS OF NORTHWESTERN QUEBEC

By Nicole Klenk

Department of Natural Resource Sciences, McGill University, Macdonald Campus, Ste-Anne-de-Bellevue, Quebec, June, 2001

A thesis submitted to the Faculty of Graduate Studies and Research in the partial Fulfillment of the requirements for the degree of Master of Science

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NUTRIENT AVAILABILITY IN BLACK SPRUCE FORESTS

OF NORTHWESTERN QUEBEC

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ABSTRACT

The presence of mosses in black spruce forests is known to have an important impact on the availability and abundance of nutrients in this ecosystem. Mosses contribute to longterm accumulation of organic matter and storage of nutrients as well as to short-term nutrient release. In the boreal forest of northwestern Québec, the effect of mosses on nutrient cycling was examined within the framework of a chronosequence ranging from 25 to 300 years of age. Laboratory and buried bag incubations, total nutrient digests, respirometric and root abundance measurements as well as moisture and temperature measurements were done to characterize the nutritional status of the organic matter profiles. In general, no change in moss accumulation, or nutrient storage or availability across the chronosequence could be detected. There were, however, differences between feather mosses and Sphagnum mosses, the latter having significantly lower levels of nutrients than the former in terms of mineralizable nitrogen and total carbon, nitrogen, phosphorus, magnesium and potassium content. The nutritional profile of moss cores showed different horizons, reflecting differences in organic matter quality down the organic layer. More specifically, nitrogen availability on a concentration basis as well as root abundance decreased with depth. Forest floor temperature seemed to confine the most biologically active horizon, referred to as the active layer, to a shallow depth, however neither temperature nor moisture seemed to explain the nutritional differences between feather mosses and Sphagnum mosses. These results may lead to practical consequences in that they show a clear distinction between the effects of feather mosses and Sphagnum mosses in nutrient cycling, suggesting that moss cover might be useful as an indicator of site nutritional status. The results also show that accumulation of nutrients

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in organic surface horizons, as has been observed elsewhere, does not appear to occur in black spruce systems in northwestern Quebec.

RÉSUMÉ

Dans les pessières à mousses, les hypnacées et les sphaignes controllent en grande partie le cycle des éléments nutritifs et l'accessibilité des nutriments à court-terme et à longterme. L'effet des mousses sur l'abondance et le cycle des éléments nutritifs dans la pessière à mousses hypnacées au nord-west du Québec a été étudié dans le cadre d'une chronoséquence don't l'étendue en age était de 25 à 300 ans. Des incubations en laboratoire, et in situ, ainsi que des mesures de respiration microbienne, d'abondance de racines, de temperature et humidité du sol ont été prises afin de charactériser le profile de la matière organique. Aucune accumulation de matière organique et de nutriments a été détectée à travers la chronoséquence, parcontre, des différences nutritionnelles significatives entre les mousses hypnacées et les sphaignes ont été constatées. La matière organique sous les mousses hypnacées contient plus d'azote minéralizable et, en contenu total, plus de carbone, d'azote, de phosphore, de magnesium et de potasse que les sphaignes. En faisant abstraction aux deux types de mousses, le profile de la matière organique démontre aussi la présence de plusieurs couches nutritionelles distinctes. Plus précisemment, l'azote mineralizable ainsi que l'abondance des racines décroissent en profondeur. La température du sol semble restreindre l'activité microbienne à une couche active peu profonde, mais ni la température et ni l'humidité du sol ne semblent expliquer la différence nutritionelle entre les mousses hypnacées et les sphaignes. Ces résultats suggèrent la possibilité d'utiliser l'abondance et le type de mousses comme Les résultats indiquent aussi que indicateurs du status nutritionel des sites. l'accumulation d'éléments nutritifs dans la matière organique, comme elle à été constatée ailleurs, ne semble pas prendre place dans la pessière à mousses du nord-west du Québec.

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FOREWORD

This thesis comprises three chapters: an introduction and two papers describing research findings. The two papers will be submitted for publication with the candidate as the first author, research supervisor Dr. J. Fyles, Dr. D. Paré and Dr. Y. Bergeron as coauthors. The content of these papers represents the research of the candidate and the coauthorship recognizes the conceptual contributions of others.

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INTRODUCTION

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0.0 Introduction

In Canada, the boreal forest spans across the country, from Newfoundland to the Yukon. The vegetation boundaries often follow the pattern of air masses; where the boreal forest meets the tundra is generally where the cold arctic air masses meet the warm moist southern air masses (Bonan and Shugart 1989). Black spruce forests are a major subtype of the boreal forest and are especially important in our nation's economy as well as for recreational values and other ecosystem services. The sustainable management of these forests requires an understanding of forest nutrition and productivity and given that long-term productivity of these forests may be declining, more research in this field is imperative. A key factor regulating to a large extent both forest floor nutrient dynamics as well as boreal forest nutrition is organic matter (Prescott *et al.* 2000). In view of its importance, its role in nutrient cycling and forest productivity will be examined.

0.1 Black Spruce Forest Decline

When measuring stand productivity, one might focus on many indicators including biomass production, site fertility and nutrient limitations, however these will vary with succession (Chapin *et al.* 1986; Mahendrappa *et al.* 1986). In the boreal forest, with time, after an initial increase and peak, biomass production generally either stabilises at a reduced level or declines, as available nutrients seem to be diminishing (Brais *et al.* 1995). Decline in nutrient availability with time is thought to be a result of the successional trends in the boreal forest, which tend to generate "climax" coniferous forests (Brais *et al.* 1995). Studies comparing hardwood forests to coniferous stands in the boreal forest generally report higher organic matter accumulation, higher C:N ratio, lower pH, reduced nutrient availability, lower nitrogen and base saturation and a tendency for lower forest floor temperatures as organic matter accumulates in coniferous or more exactly black spruce forests (Van Cleve *et al.* 1983a; Van Cleve and Yarie 1986; Bormann and Sidle 1990; Sharratt 1997). Although a decline in nutrient availability is thought to lead to lower forest productivity, it seems not to be fully supported by all field observations (Paré and Bergeron 1995). Nevertheless, some researchers assume that reduced nutrient availability as a result of succession will explain the decline of productivity in black spruce forests over time (Van Cleve and Yarie1986).

0.2 Nutrient Cycling in Black Spruce Forests

One of the main controls on forest nutrition and productivity in the black spruce forest ecosystem is the large amount of accumulated organic matter on the forest floor (Larsen 1980). Many factors govern its rate of accumulation and its consequential role in nutrient cycling. Organic matter quality may govern the rate of decay of the forest floor more than any other factor such as pH, microclimate and nutrient availability in different microsites (Flanagan and Van Cleve 1983). As a result of low organic matter quality, slow nitrogen mineralization in organic matter is thought to cause slow black spruce growth, low productivity and poor litter quality (Larsen 1980). The quality of the litter is determined mostly by its C:N ratio, its lignin and phenolic content (Bonan and Shugart 1989; Bauhus *et al.* 1998; Chapin *et al.* 1986). Plant tissues are composed to a large extent of complex carbohydrates such as cellulose, lignin and tannins while microbial cells often have a higher ratio of nitrogenous compounds to carbohydrates in their cell walls. Therefore, in the process of decomposition, microbes are generally not limited by carbohydrates, but relative to their needs, nitrogen may be limiting (Perry 1994). That is why nutrients are often immobilized in microbial biomass in the first stages of decomposition before being mineralized (Ausmus 1977; Berg and Staaf 1981). It seems therefore, that litter quality is responsible for the slow decomposition rates of organic matter in the boreal forest but nitrogen availability may be the most important control factor (Krause *et al.* 1979; Bonan and Shugart 1989, Paré and Van Cleve 1993).

Nitrogen is thought to be the most limiting nutrient in the boreal forest (Larsen 1980) and given that carbon release from organic matter will depend on the availability of nitrogen (Currie et al. 1999), the accumulation of organic matter in the boreal forest might be the result of low nitrogen availability. The understanding of the factors controlling nitrogen availability is thus quite important in terms of organic matter build up, nutrient storage and forest productivity. In the boreal forest the major pool of nitrogen is the forest floor organic matter, which may represent 1.5 to 7.3 times the amount in the above ground tree biomass (Krause et al. 1979; Larsen 1980; Van Cleve and Alexander 1981; Huang and Schoenau 1996). Most of the nitrogen, however, is thought to be unavailable and thus limiting forest productivity. Ammonium is the prevalent form of nitrogen in the boreal forest although nitrate is also present but in low quantity (Larsen 1980). There are a number of theories that try to explain the absence or reduced amounts of nitrate (NO₃) in the boreal forest. Some suggest soil pH and nutrient limitations for nitrifiers as factors controlling oxidation of ammonia to nitrate (Larsen 1980; Fyles and McGill 1987). Some studies suggest that plant uptake of the limited amount of available ammonium in boreal forest soils limits nitrification, ammonium being a precursor to nitrate in the process of nitrification (Brais et al. 1995). Stark and Hart (1997) have challenged the assumption, however, that nitrification in undisturbed mature coniferous forests is very low, they suggest that nitrification rates have been underestimated because of the high nitrate uptake from soil microorganisms. Also, some authors suggest that studies that focus on nitrate and ammonia availability are underestimating the total nitrogen availability because they are not measuring dissolved organic nitrogen, which may be an important constituent of soil solution and plays an important role in the N cycle (Smith *et al.* 1998). In addition, trees may be able to bypass decomposition by their association with mycorrhizae, some of which are thought to be able to take up nutrients, such as nitrogen in organic forms (Bowen and Smith 1981;Carleton and Read 1991; Näsholm *et al.* 1998). Nitrogen availability therefore, might be a function of other mechanisms that are not normally associated to the nitrogen cycle; however, evidence suggests that nitrogen mineralization is an important limiting factor in forest productivity (Larsen 1980; Pastor *et al.* 1987).

0.3 The Importance of Mosses in Nutrient Cycling in Black Spruce Forests

Nutrient cycling in black spruce/ feather moss, *Sphagnum* moss forests shows that, in general, rates of nutrient mineralization are slow because of the low temperature that is due in part to the low radiation input and cold climate. As a result of this, as mentioned above, nutrients are stored in unavailable forms in undecomposed organic matter (Larsen 1980; Prescott *et al.* 2000). The origin of the organic matter is mostly due to the presence of mosses. Cool summers with frequent precipitation (Collins and Oechel 1974) and long winters with very cold temperature (Miyawaki *et al.* 1994) are characteristic of the boreal forest. Low soil temperature and high moisture (Viereck 1975) which are

conditions resulting from the presence of mosses also promote their growth and production. In general, moss mats tend to encourage heat loss and discourage heat gain thus lowering soil temperature (Oechel and Van Cleve 1986). When wet, mosses conduct heat into the atmosphere while when dry they insulate the soil. By reducing soil temperature, the nutrient flux through the forest floor to vascular plants is also reduced (Oechel and Van Cleve 1986).

The types of mosses that grow in these forests will generate different types of organic matter and consequently will have different impacts on nutrient cycling. Which type of moss will be present in these forests will depend greatly on the moisture regime. Black spruce forests on wet sites are usually dominated by Sphagnum species that contribute to slow mineralization rates. Sphagnum species have a tremendous water holding capacity because of their unique hyaline cells. In bogs they are known to acidify the surrounding soil water solution because they exchange hydrogen ions for other cations (Clymo 1963; Kilham 1982). In general, the wet, low pH and nutrient impoverished environmental conditions in which they prosper are thought to lead to poor litter quality in Sphagnum species that contributes to slow rates of decomposition (Larsen 1982; Foster 1984; Belyea 1996). Scanlon and Moore (2000) showed that the degree of decomposition is the substrate property in peatland soil profiles that is the most strongly correlated to CO₂ production. Nitrogen has also been shown to limit bog peat decay, which may be the case as well in upland black spruce forest (Aerts et al. 2001). Because of its low decay rate, Sphagnum organic matter will accumulate over time (Johnson and Damman 1991).

Typically, better-drained black spruce sites have a continuous carpet of feather mosses such as *Hyloconium*, *Pleurozium* and *Ptilium* species that may affect soil

moisture in similar ways to *Sphagnum*. Feather mosses require organic substrates to grow upon and depend on precipitation and throughfall for their nutrient source (Chapin *et al.* 1987; Vitt 1990). They are poikilohydric, meaning that they can withstand periods of severe drought; their ability to resume physiological activity after a dry spell allows them to survive in relatively dry environments. In black spruce forests they contribute little to total biomass but they represent a large proportion of total nutrient uptake and total productivity (Oechel and Van Cleve 1986).

Both types of mosses can be found in upland black spruce forests, however few studies have examined their respective roles in nutrient cycling. Most studies have concentrated on feather mosses in upland sites. A study on well-drained deep coarse till in northeastern Quebec showed feather mosses to be nutritionally independent of black spruce because they obtain their nutrients from precipitation and throughfall whereas spruce obtain nutrients from the soil solution (Weetman 1968). Feather mosses prevent nutrient leaching and since they enhance spruce litter decomposition (Bernier and Roberge 1962) they supply black spruce with otherwise inaccessible nutrients (Weetman 1968). Overall, Weetman's research (1968) suggests that the presence of feather mosses maintains forest productivity.

In contrast, in Alaska black spruce forests with underlying permafrost, feather mosses limit nutrient cycling, and their presence is thought to explain long-term decreases in productivity (Oechel and Van Cleve 1986). It has been shown that feather mosses compete for nutrients with black spruce because they absorb nutrients from precipitation and throughfall and they prevent nutrients from reaching spruce roots, which are concentrated at a shallow depth (Tryon and Chapin 1983). Given that feather

mosses have inherently slow decay rates (Flanagan and Van Cleve 1977), moss growth is faster than moss decomposition and as a result, similarly to *Sphagnum* moss, feather moss organic matter tends to accumulate over time. As previously mentioned, this accumulation insulates the forest floor, leading to shorter growing seasons. Colder forest floors and shorter growing seasons lead to slow nutrient mineralization, low and limited nutrient uptake and is thought to be the cause of low black spruce productivity in Alaska black spruce forests (Van Cleve *et al.* 1981; Chapin 1986). Considering the contradiction between the studies of Van Cleve *et al.* (1983a) and Weetman (1968), in regards to the effects of mosses in nutrient cycling as well as to long-term forest productivity, it seems that distinguishing the contribution of the different types of mosses and their dynamics in time is essential in the understanding of forest nutrition.

0.4 The Effect of Forest Dynamics on Nutrient Cycling and Forest Productivity

The coexistence of both types of mosses in black spruce forests cannot be fully explained. *Sphagnum* is mostly found on poorly drained sites such as bogs and fens or in wet depressions in well-drained sites whereas most feather mosses prefer better-drained sites. Their coexistence may be a result of sites being inherently slightly wetter than usual black spruce-feather moss forests or there is a successional trend where *Sphagnum* replaces feather moss as the site moisture condition becomes wetter. It has been stated that paludification is an ongoing process across the boreal forest (Larsen 1980; Foster 1984). In this process, moss organic material accumulates over time, the moisture regime changes to wetter conditions and nutrient supply changes from minerotrophic to ombotrophic, the vegetation becomes independent from the underlying mineral soil

favoring oligotrophic vascular species and peatland development gradually ensues. The accumulation of feather mosses may change the moisture regime over time and generate moist acidic mor humus in which *Sphagnum* species can thrive given that *Sphagnum* mosses generally invade wet depressions (Foster 1984). Whether all black spruce/ feather moss forests follow this trend is unknown because of the frequent disturbance cycle, which prevents peatland formation (Foster 1984).

In "climax" black spruce/ Sphagnum forests, if no major disturbances such as fire return the forests to earlier states, the site may degenerate and become a forested bog through the process of paludification mentioned above (Foster 1984). In the other scenario, where a fire occurs in black spruce-Sphagnum forests, the outcome will depend on the severity of the fire. In any event, fire will result in higher forest floor temperature leading to increased rates of mineralization and release of a nutrient pulse for the first couple of years, consequently having an overall rejuvenating effect (Dyrness and Norum 1983; Van Cleve *et al.* 1983b).

The amount of residual accumulated organic matter after a fire will affect the rate of stand regeneration, vegetation composition and by consequence nutrient cycling. If burnt to the mineral soil then the site generally returns to a black spruce forest, but hardwoods such as white birch or trembling aspen may also invade it if there are seed sources present (Viereck and Johnson 1990). If the fire simply scorches the organic matter then black spruce regeneration may be limited by the poor substrate quality and moisture stress caused by the crusted, sun-exposed accumulated organic matter (Viereck and Johnson 1990). Thus, it seems clear that moss organic matter is a key controlling factor in black spruce forest regeneration as well as future nutritional status.

0.5 Research Perspectives

Knowledge on the exact mechanisms controlling nutrient cycling and black spruce forest productivity is lacking. Studies done by Van Cleve *et al.* (1983a) in Alaska in the late seventies have described among other things the effect of mosses on nutrient cycling. However, the contradictory evidence provided by Weetman (1968) suggests that the results from Alaska cannot be applied to all black spruce forest types, perhaps because of the variety of environmental conditions in which black spruce forests are found.

Given the state of our current knowledge and the importance of the effect of mosses on nutrient cycling in black spruce forests, it is relevant to pursue research in this domain. Hence, we focused on small-scale controls such as moss type, forest floor moisture and temperature on nutrient cycling in black spruce forests. Throughout the study, the role of mosses in overall forest nutrition and productivity is emphasized especially if it has any bearing on present and long-term managerial considerations. The first objective is to test the hypothesis that nutrient availability declines with time and the second objective is to compare feather mosses and *Sphagnum* mosses to clarify the contradictory evidence of Van Cleve *et al.* (1983) and Weetman (1968). Hence the first chapter examines the contributions of organic matter under feather mosses and *Sphagnum* mosses to nutrient cycling in a chronosequence in the Québec boreal forest, while the second chapter examines the role of forest floor moisture and temperature on the differences in nutrient cycling in organic matter under feather mosses and *Sphagnum* mosses and *Sphagnum*.

CHAPTER 1

Nutrient Availability in a Black Spruce Forest Chronosequence

in Northwestern Quebec

1.1 Introduction

Boreal forest floors, especially under coniferous canopies, are characterized by a deep layer of organic matter that accumulates due, in part, to slow rates of decomposition (Larsen, 1982; Perry, 1994; Prescott *et al.* 2000). Because of the recalcitrant nature of the organic matter (Flanagan and Van Cleve 1977) as well as low soil temperature, decomposition rates are slowest in black spruce (*Picea mariana* (Mill.) B.S.P.) forest types (Van Cleve *et al.* 1983a). Over time the build up of organic matter in these forests forms a pool of largely unavailable nutrients and is thought to cause forest productivity decline (Larsen 1980; Oechel and Van Cleve 1986).

In these ecosystems, mosses are important contributors to organic matter accumulation. Both feather mosses, such as *Pleurozium schreberi* (BSG.) Mitt. and *Hyloconium splendens* (Wedw.) BSG., as well as *Sphagnum* sp. mosses are ubiquitous in the boreal forest. Feather mosses cover 80 % of the forest floor under mature upland black spruce in the boreal forest of central Canada (Frego and Carleton 1995) while *Sphagnum* mosses dominate poorly drained sites or occupy wet depressions in upland sites of the boreal forest of southeastern Labrador (Foster 1984) which is similar to northwestern Quebec. Research focusing specifically on the effect of either of these types of mosses on nutrient cycling in upland black spruce forests has been limited since they contribute little to total above ground biomass and therefore, historically, have been ignored as factors controlling forest nutrition (Binkley and Graham 1981).

Two studies are notable for examining the effects of feather mosses on nutrient cycling in boreal forests. Weetman's (1968) research in eastern Canada suggested that feather mosses contribute positively to nutrient cycling and forest productivity in black

spruce forests by preventing the loss of nutrients and generating a continual release of nutrients for tree growth. In contrast, Oechel and Van Cleve (1986), working in Alaska, have emphasized the negative effects of mosses such as competition, nutrient immobilization and increased forest floor insulation leading to forest productivity decline. The model generated by the Alaskan research identified a positive feedback loop whereby the presence of mosses decreased forest floor temperature, leading to reduced nutrient cycling and tree nutrient uptake, while moss growth and accumulation was maintained or enhanced by these conditions (Van Cleve *et al.* 1983a). Together, the studies of Weetman (1968) and Oechel and Van Cleve (1983) indicate the potentially contrasting roles of mosses in this ecosystem.

The effects of *Sphagnum* mosses on nutrient cycling have been extensively studied in peatland sites (Johnson and Damman 1991, Hogg 1993, Belyea 1996) but limited information is available for upland black spruce/*Sphagnum* forests. It is known that *Sphagnum* decomposes slowly because of its recalcitrant nature, generally due to high C/N ratio and high lignin content. In addition the unfavorable habitat, preferred by *Sphagnum*, is typically wet and acid. *Sphagnum* contributes to these conditions by way of its high moisture holding capacity, drawing and retaining water from its surroundings and acidifying the soil solution by releasing H⁻ in exchange for cations (Clymo 1963; Foster 1984; Larsen 1982). The accumulation of *Sphagnum* mosses is thought to lead to the process of paludification whereby the moisture regime changes to wetter conditions and nutrient supply changes from minerotrophic to ombotrophic, the vegetation becomes independent from the underlying mineral soil favoring oligotrophic vascular species and

peatland development generally ensues (Larsen 1980; Foster 1984). The process of paludification will lead, in the long-term, to forest productivity decline.

Given that organic matter build up is an important process in nutrient cycling and forest nutrition, and that feather mosses and *Sphagnum* mosses may be contributing to the process differently, we decided to study the long-term accumulation of mosses and their effects on nutrient cycling in black spruce forests. We used the chronosequence approach to reveal changes in nutrient cycling and storage over time (Powers and Van Cleve 1991). We studied a chronosequence of 20 upland black spruce sites, covering a span of 300 years in age, and determined the effects of feather mosses and *Sphagnum* mosses on nutrient dynamics. Our objectives were: i) to determine the extent of nutrient storage and nitrogen availability in organic matter and, ii) to characterize the specific effects of feather mosses and *Sphagnum* mosses on nutrient cycling and storage.

1.2 Materials and Methods

1.2.1 Study areas and sampling site selection

This study was conducted in the black spruce/feather moss boreal forest type of the northern clay belt of western Quebec, in the Abitibi region, latitude ranging from $49^{\circ}00'$ to $50^{\circ}00'$ N and longitude ranging from $78^{\circ}30'$ to $79^{\circ}30'$ W. Part of the Mistaouac Lake region, is characterized by fine textured glacio-lacustrine deposits and flat topography with a few dispersed hills (Robitaille and Saucier 1998). Other studies in this region have identified the soil type as predominately Dystric Brunisols (Simard *et al.* in press). This region has an average annual temperature of 0.0° C, 2000 to 2200 degree

days above 5.6°C and an annual average precipitation of 700 to 800 mm (Robitaille and Saucier 1998).

In the summer 1999, 20 black spruce plots of 10 m x 10 m were chosen on the basis of their being on level topography with moderate to good drainage. Sites had a maximum of 60 cm of accumulated organic matter and had both feather mosses and *Sphagnum* moss present. A maximal depth of 60 cm of organic matter was chosen to limit the study to upland black spruce sites and avoid peatlands. All sites had originated by natural regeneration following wildfire. These sites constituted the chronosequence ranging from 25 to 300 years of age. The age of the sites was determined by tree ring analysis on several harvested trees per plot. Due to logistical constraints as well as the requirements of conducting a retrospective study, the site selection criteria were used to limit the amount of variability among the sites' physical characteristics thereby increasing the likelihood that the sites followed similar successional trends.

1.2.2 Sampling

Six organic matter profiles, approximately 30 cm x 30 cm square pits, were dug per site, three for each type of moss, and described by horizons (L,F,H) on the basis of a forest floor humus classification scheme (Table 1.1). In each profile a sample of organic matter from each horizon was used to estimate *in situ* nitrogen mineralization by the buried bag technique (Binkley and Hart 1989). Samples were inserted undisturbed into the polyethylene bags and returned to the holes from which they came. Bags were retrieved after one year and subsequently frozen until laboratory analysis could be performed.

In each profile an additional three series of samples were collected to measure total nutrient content, moisture holding capacity and microbial respiration. All samples were kept frozen until they were used for laboratory analysis.

In each site two diagonal transects were used to estimate moss cover for both feather mosses and *Sphagnum* mosses. The line intercept method was used to obtain the percentage cover per moss type, calculated by dividing the total length of the line by the total decimal fraction of the line covered by each moss type (Barbour *et al.* 1998).

1.2.3 Preliminary measurements

Initial moisture content was measured gravimetrically for all samples across the chronosequence by oven drying samples at 65 °C for 24 hours. To determine the appropriate moisture content for the laboratory incubation, a subset of samples of approximately 5 g of organic matter representing typical feather moss and *Sphagnum* moss horizons, with three replicates of each horizon per moss type, were used to obtain basal respiration measurements at different water contents. Samples were thawed and stored in the dark at 4°C in sealed polyethylene bags for a period of one week. Pre-incubated samples were transferred to a funnel incubation system (Fyles and Bradley 1992) to determine basal respiration at water tensions of 1, 2, 5, 10 and 20 kPa. Samples were soaked in water and left to equilibrate with the water columns for 12 hours before respiratory measurements. After the equilibration period, the samples were flushed with ambient air for 2 minutes using an aquarium pump and sealed for an incubation of one hour. Thereafter 3 cc air samples were taken from the head-space of the sealed buchner funnels and injected into a Hewlett Packard 5890-II gas chromatograph to determine the

 CO_2 concentration of the head-space air. The procedure was repeated with the same samples for all water tensions.

1.2.4 Laboratory Incubations

Based on the basal respiration data, we adjusted the moisture content in the samples collected from the 20 sites of the chronosequence to within a range of 400 % to 800 % moisture content for the aerobic incubation. Samples were sealed in polyethylene bags, and incubated in the dark for a period of 86 days at 25 °C. The time interval was calculated using the average degree-day above 5.6°C for a period of one year typical of the geographical location of the sites so as to be as similar as possible to the field incubations. Available nitrogen was extracted from a subset of the initial non-incubated samples and from incubated samples with 2N KCL and the concentration of NH₄ was determined colorimetrically using a Lachat Quickchem automated chemical analysis Mineralized nitrogen was calculated by subtracting the concentration of system. extracted NH₄ in the non-incubated samples from the concentration in the incubated samples. Preliminary analyses indicated that nitrate was of negligible concentration in all samples and was thus ignored. Buried bag samples collected from the field were thawed in the dark at 4°C until available nitrogen extractions were done following the same methodology as for the laboratory incubation samples.

1.2.5 Total Nutrient Digestions

Samples from the 20 sites were digested for total nitrogen, phosphorus, potassium, magnesium and calcium (Parkinson and Allen 1975). Total potassium,

magnesium and calcium concentrations were measured using a Perkin-Elmer atomic absorption spectrometer. Total nitrogen and phosphorus were determined colorimetrically as for mineralizable nitrogen. Total carbon was measured with a NC 2500 Automatic Elemental Analyzer (CE Instrument).

1.2.6 Statistical Methods

All nutritional data obtained from the 20 sites of the chronosequence fit a doubly repeated measures analysis of variance with 5 age classes, which were [0,50[, [50,100[, [100,150[, [150,200[and >200 years. The first repeated measure was the moss type and the second, the horizon. Because only complete data vectors are analyzed in a MANOVA, and some horizons were not present in some organic matter profiles, 14 sites were used in the analysis. It was not possible to predict the missing values in the incomplete vectors because they represented non-existing horizons. In other words not all organic matter profiles had all three horizons present. The analysis was done on a concentration basis (g of nutrient per g of soil) and an area basis (g of nutrient per m² of soil) for the nutritional data.

Because 6 sites were missing from all analyses, regular ANOVAS were done with the total 20 sites. We assumed that the addition of six sites to the analysis would increase the overall precision of the test and thus compensate for the lack of independence within the data due to the repeated measures that were taking. Therefore ANOVAS were assumed to generate a more representative picture of the underlying trends across the 20 sites.

Total depths and moss percentage cover were analyzed by a repeated measures analysis with 5 age categories and 20 sites.

All main effects were considered significant at the alpha level 0.1. Means were compared with unadjusted T-tests at an alpha of 0.05 because few repeated tests were done, thus limiting potential inflation of the alpha level. All data were tested for normality prior to analysis.

1.3 Results

1.3.1 Microbial Basal Respiration

Basal respiration did not vary with water tension across the range of 1- 20 kPa representative of field moisture conditions (Figure 1.1). Average *Sphagnum* moss field water content was 582 % \pm 18 % and 373 % \pm 16 % for feather moss (Chapter 2). Basal respiration of organic matter beneath feather mosses ranged from 40 to 110 µg of CO₂/g of soil per hour, which was significantly different to respiration under *Sphagnum* mosses, which ranged from 15 to 40 µg of CO₂/g of soil per hour (*p*=0.0001). The differences in respiration between the feather moss organic matter horizons are significant (L>F, p=0.0236 and F>H, *p*=0.0001) whereas no difference was detected between the *Sphagnum* organic matter horizons (*p*=0.9979 and *p*=0.1553).

1.3.2 Age Effect

The age effect refers to the age sequence within the chronosequence and is meant to represent changes occurring over time. No significant age effect or trend was observed for ammonium mineralization in either the *in situ* incubation or the aerobic incubation (Figure 1.3). As well, no age effects were noted for the total nutrient content across the chronosequence for: carbon, nitrogen, phosphorus, magnesium, potassium and calcium with probabilities of significance ranging from 0.20 to 0.94. Depth of organic matter did not increase with age class and neither did the total percent moss cover (Figure 1.4) nor the feather moss or *Sphagnum* moss cover, indicated by the non-significant moss cover by age interaction (p=0.78).

1.3.3 Organic Horizon Effects

Nutrient data expressed on a concentration basis indicates clear distinctions among the organic matter horizons regardless of moss type. The buried bag incubation and the aerobic incubation showed that the concentration of mineralizable NH₄-N decreased with depth (Figure 1.5). There were significant differences between the moss horizons for total nutrient concentration with respect to nitrogen (p=0.0018), calcium (p=0.04), potassium (p=0.0001) and magnesium (p=0.0336), however, there were no consistent trends down the organic matter profile among the different nutrient concentrations observed.

In contrast, nitrogen availability on an area basis (g/m^2) , in both the buried bag incubation and the aerobic incubation, was not significantly different between moss horizons (p=0.17 and 0.20 respectively) and did not decrease with depth. The total nutrient content per horizon, however, for nitrogen, phosphorus, carbon and calcium, increased with depth (Table 1.2).

1.3.4 Moss Effects
Based on field experience and our interpretation of this ecosystem, organic matter is mostly derived from the type of moss under which it is situated. It follows therefore that a distinction should be made between different types of mosses and their contribution to nutrient cycling. Organic matter beneath feather mosses generated a significantly higher amount of available nitrogen in both the *in situ* incubation and aerobic incubation compared to organic matter beneath *Sphagnum* mosses (Figure 1.6). Both types of moss organic matter, however, had higher nitrogen mineralization in the aerobic incubation than in the *in situ* incubation (figure 1.3). Feather moss organic matter had a higher nutrient content than *Sphagnum* moss organic matter with respect to nitrogen, phosphorus, carbon, calcium and magnesium (Table 1.3). It is also notable that mean total organic matter depth across the chronosequence was greater under *Sphagnum* mosses, $(0.32 \text{ m} \pm 0.022 \text{ m})$ than under feather mosses $(0.23 \text{ m} \pm 0.015 \text{ m})$ but that moss percent cover was not significantly different between feather moss and *Sphagnum* moss (p=0.16).

1.4 Discussion

1.4.1 Chronosequence

A broadly held hypothesis for the black spruce boreal forests is that mosses generate organic matter that accumulates over time to the extent it limits forest floor nutrient cycling processes, leading to lower forest productivity (Larsen 1980; Oechel and Van Cleve 1986). Nitrogen is considered to be a limiting nutrient in the boreal forest (Larsen 1980) and may be a key factor in spruce productivity decline (Pastor *et al.* 1987). Nitrogen is thought to become increasingly unavailable due to reduced mineralization rates as a result of low forest floor temperature and sequestration in organic matter (Viereck 1973; Oechel and Van Cleve 1986; Weber and Van Cleve 1984). Results from our chronosequence study do not indicate organic matter accumulation over time nor do they show a reduction in ammonium availability in the organic matter. The results for ammonium availability are consistent with the study of Brais et al. (1995) showing no variation in nitrogen availability with stand age in forests of balsam fir, white birch and white spruce of the southern part of the boreal forest of northwestern Ouébec. In contrast to Brais et al. (1995), however, we observed no decrease in total nutrient content over time. The fact that we were unable to detect nutrient accumulation or a reduction in nitrogen mineralization in the forest floor may indicate that organic matter is not responsible for long-term nutrient limitations in these forests or that long-term nutrient limitations do not exist. Nutrient cycling processes within the forest floor observed at one point in time, even in the context of a chronosequence, may better reflect present forest nutritional status than long-term trends in nutrient cycling and immobilization as generally hypothesized. These results also lead us to suppose that the process of organic matter accumulation may not be ubiquitous in the boreal forest.

Boreal forest succession is thought to lead to an increase in moss abundance and in some cases to the dominance of Sphagnum mosses over feather mosses (Larsen 1980; Foster 1984). Our results do not support the conclusion that Sphagnum mosses replace feather mosses. In fact this study shows neither increase in total moss cover nor an increase in either moss type percent cover with time.

1.4.2 Type of Moss

Given that organic matter under mosses has an important effect on forest nutrition it is important to understand the specific contributions of the different types of moss organic matter to nutrient cycling. The observation that the organic matter under feather mosses had consistently greater amounts of available ammonium, total nitrogen, phosphorus, carbon, calcium and magnesium, as well as greater microbial respiration, than organic matter under Sphagnum mosses, suggests the potential to use of moss composition as an indicator of forest nutrition and productivity. Since it was shown that feather moss organic matter does not accumulate as much as Sphagnum moss organic matter, our results seem to indicate that organic matter under feather mosses have greater rates of decomposition and nitrogen mineralization than organic matter under Sphagnum mosses and thus their presence results in faster nutrient cycling in black spruce forests. In addition, the fact that Sphagnum mosses consistently have a deeper organic matter profile than feather mosses may lead to greater forest floor insulation and a reduction in nutrient cycling. Our results suggest that research focusing on the effects of different mosses on productivity may lead to changes in forest management practices. The ability to predict forest nutritional status by estimating the abundance of mosses and their dynamics through time may prove to be a scientifically and practically sound indicator of sustainable forest management.

1.4.3 Organic Matter Horizons

One of the challenges forest nutritionists and soil scientist have in studying these systems is the lack of clarity in organic matter classification and the confounding effects of substrate quality and environmental conditions on nutrient cycling. Green *et al.* (1993)

suggested a classification and methodology for field description of humus forms that provide a tool for consistent identification and interpretation. Fyles *et al.* (1991) observed significant differences among organic materials that were morphologically and ecologically distinct, thus demonstrating the importance of distinguishing organic matter horizons. Moreover, considering the importance of the forest floor in black spruce forest nutrition, a clear description of the organic matter profile is essential to a better understanding of nutritional processes occurring within it. We have adopted the L, F, H nomenclature for forest floors and we refer the reader to Table 1.1 for a description of the respective horizons.

Our results show that there are clear distinctions between the organic matter horizons in terms of nutrient concentration down the organic matter profile. Since both the *in situ* incubation and the aerobic incubation showed that there was a higher ammonium concentration in the upper horizons, these results seem to indicate inherent differences in the quality of the organic matter instead of an environmental control on nitrogen mineralization. The greater amount of nitrogen mineralization in the laboratory incubation in comparison with the *in situ* field incubation, however, may indicate the influence of other control factors such as forest floor temperature and moisture. Our results support the conclusion that organic matter quality has an important role in controlling nitrogen availability that may in fact supersede forest floor temperature and moisture in black spruce forests in importance, although there are undoubtedly interactions between the factors (Flanagan and Van Cleve 1983).

The observation that the total amount of available ammonium was uniform down the organic matter profile is a result of the different thickness and densities of the

horizons. Similarly, the increase in total nutrient content with depth also results from organic matter horizon thickness. This might be explained by the fact that the results on an area basis (g/m^2) take into consideration the bulk density and the total thickness of the horizon. For example, a horizon in which the concentration of mineralizable nitrogen is greater than in another might have a similar total amount of mineralizable nitrogen on an area basis (g/m^2) because bulk density and total thickness differ between them. Thus the importance of the distinctions in organic matter quality is concealed by the amount of organic matter per horizon and therefore it is important in describing these systems, to be cautious of our interpretations. For site nutritional purposes, it isn't clear whether nutrient on a concentration basis or on an area basis is most relevant to nutrient uptake and cycling. Our results could indicate that the removal of the upper horizons, for site preparation for instance, may not lead to lower amounts of available ammonium for seedlings and may in fact lead to potentially increased amount of nutrient mineralization since total nutrient content increases with depth. These conditions however would be subject to other factors controlling nutrient cycling within the horizons, such as moisture holding capacity, temperature conductivity, root colonization and indigenous microbial populations.

1.5 Conclusion

Results from this chronosequence study indicate that organic matter depth does not increase with site age nor does ammonium availability and total nutrient content decrease with site age in black spruce forests of the Abitibi region in Québec. In addition no change in moss cover was observed with site age. It would seem that the effect of

moss organic matter on nutrient cycling processes might be more indicative of present forest nutritional status than of long-term changes in nutrient cycling, immobilization and forest productivity.

Also notable was the significantly greater ammonium availability and total nutrient content for feather mosses in comparison to *Sphagnum* mosses. In addition, the smaller accumulation of organic matter and the higher microbial respiration for feather mosses suggest a higher rate of nutrient cycling under this type of moss, thus leading to the possible use of moss composition as an indicator of forest nutrition and productivity. More research, however, is needed to decipher the relationship between the effects of moss type on nutrient cycling and forest productivity.

Our results also demonstrate the importance of in depth description of nutrient cycling processes within the organic matter profiles given that there are significant differences in ammonium availability and total nutrient content among organic matter horizons. The conclusions vary, however, depending on the units of measure used, therefore we advocate cautious interpretations of nutritional profiles, which reflect the compound effects of bulk densities, organic matter horizon thickness and other edaphic factors.



Figure 1.1 Microbial basal respiration at different water tensions for Feather Moss (FM) and *Sphagnum* Moss (SPG) organic horizons (L,F,H)



Figure 1.2 Water content at different water tensions for Feather Moss (FM) and Sphagnum Moss (SPG) organic horizons (L,F,H)





Figure 1.3 Ammonium mineralization across age classes for the buried bag incubation and the laboratory incubation. Note: Incubation periods were 86 days and a year respectively. (Values = means \pm SE)





Figure 1.4 Mean total depth of organic matter and mean moss % cover per age class. (Values are means \pm SE)





Figure 1.5 Ammonium concentration across moss horizons in the buried bag incubation and the laboratory incubation.

(Value are means \pm SE; Different letters = significant difference, $\alpha = 0.05$)





Figure 1.6 Feather moss and Sphagnum moss ammonium mineralization in the buried bag incubation and the laboratory incubation. (Values are means \pm SE; Different letters = significant difference, $\alpha = 0.05$)

Characteristics	Horizons			
	L	F	H	
Color	light	medium	dark	
	brown	brown	brown	
Fibres	intact	fibrous/humus	humic	
Texture	loosely matted	moderately matted	densely matted	

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Table 1.1 Moss organic matter horizon descriptions.

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	Moss Horizon	L	F	Н
Nutrient				
	C	1,5 ± 0,09 a	1,9 ± 0,2 b	2.0 ± 0.2 b
	N	25,9 ± 1,8 a	37.6 ± 3.2 ab	39.7 ± 2.8 b
	Р	2.3 ± 0.2 a	2,8 ± 0,3 b	2.9 ± 0,2 b
	Ca	16,9 ± 1,6 a	15.8 ± 1.8 a	22.7 ± 3.5 b

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Table 1.	2 Total carbon (kg/m ²	[!]), nitrog en (g/m ²), phosphorus	(g/m ²) and	calcium (g/n	n ²) per moss	organic horizon.
(Values	= means ± SE)						

Note: Different letters indicate a significant difference between horizons ($\alpha = 0.05$).

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	Moss Type	Feather Moss	Sphagnum Moss
Nutrient			
C		1,9 ± 0,1 a	1.7 ± 0.1 b
N		41.0 ± 2.3 a	28,3 ± 2,0 b
Р		3,3 ± 0,2 a	$2.1 \pm 0.1 b$
Mg		5,6 ± 0,6 a	$4.0 \pm 0.4 \text{ b}$
К		7.1 ± 0.5 a	4.2 ± 0.4 b

Table 1.3 Total carbon (kg/m²), nitrogen (g/m²), phosphorus (g/m²), magnesium (g/m²) and potassium (g/m²) in feather moss and in *Sphagnum* moss dominated microsites. (Values = means \pm SE)

Note: Different letters indicate a significant difference between horizons ($\alpha = 0.05$).

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CONNECTING PARAGRAPH

The first chapter focused on the accumulation of organic matter and the role of mosses in nutrient cycling in a chronosequence in black spruce forests of northwestern Quebec. The second chapter will look at the role of forest floor temperature and moisture in controlling nutrient cycling, root growth and nutritional differences in organic matter originating from two types of mosses.

CHAPTER 2

The Effects of Moisture and Temperature on Nutrient Cycling In Organic Matter in Northwestern Quebec Black Spruce Forests

2.1 Introduction

Organic matter in black spruce forests represents a large pool of mostly unavailable nutrients and is thought to control nutrient cycling and plant nutrient uptake (Larsen 1980; Weber and Van Cleve 1981; Prescott *et al.* 2000). Large accumulations of organic matter, mostly originating from partly decomposed moss tissues as well as from woody and foliar litter, are typical of boreal black spruce forests. The organic matter is thought to insulate the forest floor and lead to slower decomposition and mineralization rates, thus enhancing, in a positive feedback loop, the process of organic matter accumulation (Van Cleve *et al.* 1983; Flanagan and Van Cleve 1983; Chapin 1986).

Given the importance of the organic matter in nutrient cycling and forest productivity, understanding the nutrient dynamics within the forest floor is essential. Based on our current understanding of the ecosystem, we would expect lower forest floor temperature and potentially higher moisture contents at lower depths because of the insulating and water holding properties that characterize the accumulated organic matter. This would lead to a shallow active layer, where most of the microbial activity, nutrient cycling and root concentration would occur. The accumulation of organic matter, through its control of forest floor temperature and moisture availability, would control the depth and thickness of the potential active layer. For example, where black spruce forests are underlain by permafrost, the accumulation of organic matter over time and the consequential reduction in forest floor temperature has lead to the development of thinner active layers (Heilman 1968; Viereck 1970).

It is difficult to distinguish between the effects of temperature and moisture on nutrient availability, however in upland black spruce forests, temperature control is

thought to be the most important factor followed by organic matter quality and moisture, whose importance lies somewhere in between the two other control factors (Van Cleve and Yarie 1986). Van Cleve *et al.* (1981) showed that higher forest floor temperature result in a greater amount of nutrient cycling and tree growth in Alaska black spruce forests. Forest floor temperature is also correlated to the seasonal pattern of root elongation (Tryon and Chapin 1983). As well, there is the possibility that moisture conditions vary with organic matter depth and the importance of moisture availability could then be reflected in nutrient availability and root distribution down the organic matter profile. The moisture conditions might also have an impact on the type of moss that grows in these forests and consequently on the accumulation of organic matter that results from their presence.

Whether the concept of an active layer can be applied to the forest floor of upland black spruce forests might depend on the type and amount of organic matter accumulated. Both feather mosses and *Sphagnum* mosses are present in this forest and they contribute differently to total organic matter accumulation and nutrient cycling. In northwestern Québec black spruce forests, the former generate more mineralizable ammonium, total nitrogen, phosphorus, carbon, calcium and magnesium while the latter will accumulate to a greater extent (Chapter 1). It might be useful, therefore, to distinguish between feather mosses and *Sphagnum* mosses in terms of their moisture availability and temperature profiles and their respective effect on the hypothesized active layer.

The relationship between forest floor factors that control nutrient cycling is complex and numerous factors must be examined to understand the system. In this study the objectives were: i) determine whether or not an active layer is present in the organic

matter profiles of feather mosses and Sphagnum mosses and where it is situated, *ii*) characterize the root distribution within the organic matter profiles and *iii*) determine the role of forest floor moisture and temperature in controlling the depth of the active layer if it is present.

2.2 Materials and Methods

2.2.1 Study areas and sampling site selection

This study was conducted in the black spruce/feather moss boreal forest type of the northern clay belt of western Quebec, in the Abitibi region, latitude ranging from $49^{\circ}00'$ to $50^{\circ}00'$ N and longitude ranging from $78^{\circ}30'$ to $79^{\circ}30'$ W. Part of the Mistaouac Lake region, it is characterized by fine textured glacio-lacustrine deposits and flat topography with a few dispersed hills (Robitaille and Saucier 1998). Other studies in this region have identified the soil type as predominately Dystric Brunisols (Simard *et al.* in press) This region has an average annual temperature of $0,0^{\circ}$ C, 2000 to 2200 degree days of growing season above 5,6°C and an annual average precipitation of 700 to 800 mm (Robitaille and Saucier 1998).

In the summer 1999, 20 black spruce sites were chosen based on the following criteria: level topography, moderate to good drainage, a maximum of 60 cm of accumulated organic matter and both feather mosses and *Sphagnum* moss present. These site criteria were chosen to satisfy the requirements of the retrospective study and as a result of logistical constraints (Chapter 1). All sites had regenerated naturally following wildfire. In the summer 2000, nine sites out of the 20 were used for weekly temperature and moisture measurements as well as a root in-growth bag experiment.

2.2.2 Sampling

In each of the 20 sites a $10 \text{ m} \times 10 \text{ m}$ plot was established, within which the total depth of organic matter was measured and the percentage cover of the two types of mosses was estimated using two diagonal transect lines in each plot.

In 9 sites, weekly measurements of temperature and moisture were taken at 5 cm intervals down the organic matter profile in three pits per moss type. Two sites were visited every weekday and subsequently visited at the same day and time each week through July and August in the summer 2000. New pits were dug weekly to assure uniformity among sampling dates. Temperatures were taken with a thermistor probe (Fisher Scientific) and samples were collected for gravimetric measurement of moisture content

Root in-growth bags were installed in the 9 sites used for moisture and temperature measurements. Bags were made of nylon mesh and approximately 5 cm by 20 cm and were filled with 50 g of commercial peat moss. Prior to installation bags were soaked overnight in a nutrient solution of 5 g per liter of water of the common plant fertilizer, 20-20-20, before being inserted in 3 organic matter profiles per moss type. Soaking in a nutrient solution was done to induce root colonization by providing a nutrient rich microsite. There were two sets of root in-growth bags that were inserted in the forest floor; one set was collected in late August after 2 months and the other in late September after 3 months. Root in-growth bags were inserted in each of the horizons present within the organic matter profiles under each type of moss. Because the volume of the bags was not uniform, root distribution was calculated semi-quantitatively by root abundance classes, which were: none present, less than 5 roots, between 5 and 10 roots and more than 10 roots. Each class was given an arbitrary value, 0, 1, 2 and 3 respectively and a mean of the root abundance was computed for each of the moss types and for each horizon to indicate overall root distribution.

2.2.3 Statistical Methods

All main effects were considered significant at the alpha level 0.1. One-way ANOVAS were used to detect treatment effects for the root abundance-depth and moss cover-depth relationships. Means were compared with adjusted T-tests at an alpha of 0.05. All data were tested for normality prior to analysis.

2.3 Results

2.3.1 Forest Floor Temperature and Moisture

Weekly temperature measurements down the organic matter profile of both feather mosses and *Sphagnum* showed that there is an approximately 8°C difference between the top horizon and the bottom horizon, the top horizon being the warmest (Figure 2.1 and 2.2). There was no significant difference between the mean temperature in the feather moss and *Sphagnum* moss temperature profiles (p=0.7369). Temperatures appeared to rise gradually in all horizons until early August with temperature differences between the horizons maintained through the summer (figure 2.1). Surface temperatures dropped with cooler weather after mid-August so that temperature was uniform down the profile by the end of August. The temperature trends suggest that surface temperatures may be lower than temperatures deeper in the profile for a period in the fall. In contrast, no trend down the organic matter profile is apparent in the moisture measurements. Moisture content of samples within the organic matter profile ranged roughly from 200 % to 1000 % (Figure 2.3) with *Sphagnum* having higher average water content, $582 \% \pm 18 \%$ than feather moss $373 \% \pm 16 \%$. Laboratory measurement of the tension-water content relationship (Chapter 1) indicated that the field moisture contents represented low water tensions, and that organic matter profiles in the field remained near field capacity (about 10 kPa) throughout the study period.

2.3.2 Root Distribution, Moss Cover and Depth

Root abundance decreased with depth of organic matter (Figure 2.4). There were significant differences between all horizons (Figure 2.4). In terms of moss cover and depth, no trend was detected for feather mosses whereas the data suggests that there is an increase in *Sphagnum* moss cover with increasing depth of organic matter (Figure 2.5). Also, average feather moss cover is greater than *Sphagnum* moss cover (Figure 2.5).

2.4 Discussion

2.4.1 Moisture

Although moisture availability in forest floor organic matter is generally thought to distinguish forest types, little is known of its direct effect on nutrient cycling in upland black spruce forests (Van Cleve and Yarie 1986). Based on the field moisture observed, there were no trends detected within the 2000 growing season, suggesting that within the organic matter profile, moisture availability might not be delimiting an active layer. The incubation data seems to confirm this deduction (Chapter 1). The moisture contents of the laboratory incubations and buried-bag incubations were within the range of field moisture contents and the microbial respiration data seems to show that microbial activity does not vary within this range of water contents (Chapter 1). This indicates that in field conditions, moisture content does not have an overwhelming impact on microbial activity. The fact, however, that *Sphagnum* mosses held more water than feather mosses in the field might help explain the difference in nitrogen mineralization between the moss types (Chapter 1). Moisture might also be involved in the vegetation dynamics that occur in these forests.

Feather mosses mostly dominate this type of upland forest but in stands such as these, where different types of mosses cohabit, it is difficult to know why *Sphagnum* is present. This is also an important consideration in understanding nutrient cycling in this ecosystem because these types of organic matter do not generate the same nutritional organic matter profiles (Chapter 1). Relating average organic matter depth to moss cover in each site might reveal underlying moisture conditions that might indicate the suitability of the environment for the colonization of *Sphagnum* mosses. *Sphagnum* moss grows in wet conditions and the organic matter beneath it has lower microbial activity rates than feather moss organic matter, thus it tends to accumulate in greater amounts. If the proportion of *Sphagnum* cover is greater than feather moss cover with increasing average depth of organic matter. The results, however, show that feather moss has a larger proportion of the total cover than *Sphagnum* even with increasing average organic matter depth. The data does not indicate a significant trend either, although *Sphagnum* does seem to increase in cover with increasing depth of organic matter.

seem to suggest, therefore, that in these sites moisture availability is likely to favor feather moss growth, while still providing some favorable microsites for Sphagnum.

2.4.2 Temperature

When looking at the temperature variation within the 2000 summer growing season, we can see that there are no differences between the feather moss organic matter profile and that of Sphagnum moss. One would expect that under wetter conditions, where Sphagnum grows, temperature would be colder, however, the average temperature is similar for both types of mosses. Therefore temperature does not seem to explain the greater microbial activity and nitrogen mineralization in organic matter beneath feather moss compared to organic matter beneath Sphagnum moss (Chapter 1). In fact neither moisture nor temperature seem to have a dominating effect on the different rates of nutrient cycling that distinguish these two types of mosses. Organic matter quality might be the most important factor generating the difference in microbial activity between the two types of mosses. This would be consistent with Flanagan and Van Cleve's (1983) results showing how organic matter quality can be more influential on nutrient cycling than other edaphic factors. Temperature will, however, help to explain the decreasing microbial activity and nitrogen mineralization down the organic matter profile (Chapter 1) given that there is an important difference in temperature between the top horizon and the bottom horizon.

The seasonal temperature variation down the organic matter profile might be more relevant to the nutritional profile as a number of studies show (Weber and Van Cleve 1981; Van Cleve *et al.* 1983; Weber and Van Cleve 1984; Van Cleve and Yarie

1986). For both types of mosses, there was a maximum of 8 °C difference between the top and the bottom of the profile indicating an important temperature gradient. Greater temperature fluctuations in top horizons have been shown to generate greater amounts of nitrogen mineralization and immobilization (Weber and Van Cleve 1984). Seasonal patterns of root elongation also have been shown to be controlled by soil temperature, where roots were mostly concentrated in top organic matter horizons in an Alaska black spruce boreal forest (Tryon and Chapin 1983). Although our results cannot separate the effects of organic matter quality, moisture and temperature on nutrient cycling, it would seem most probable that the difference in temperature would lead to a shallow active layer. Based on field observations, the L horizon is typically located in the first 10 cm of the organic matter profile. Thus, one would expect that the difference in temperature down the organic matter profile would result in greater microbial activity, nutrient availability and root concentration in the L horizon.

2.4.3 Active Layer

Nutritional characteristics of the moss organic matter profiles (Chapter 1) suggest that temperature might be a very important control factor on nutrient availability. For example, in terms of the nitrogen mineralization, the laboratory incubation shows that organic matter quality decreases with depth, with a greater amount of mineralizable nitrogen in the L horizon compared to the H horizon. The data suggests, however, that the bottom horizon, despite having lower organic matter quality, does, nevertheless, contribute to a large extent to nitrogen mineralization. The presence of an active layer might therefore be unsubstantiated, but the buried bag incubation seems to indicate otherwise. Based on the temperature data, with a difference down the temperature profile close to 8 °C, and a Q10 assumed to be equal to 2, one would expect the top horizon to generate approximately 1.7 times more mineralizable nitrogen than the bottom horizon. In addition, in terms of substrate quality, the laboratory incubation data shows that the L horizon generates 1.8 times more mineralizable nitrogen than the H horizon (Chapter 1). Both temperature and substrate quality will influence field nitrogen mineralization, thus one would expect that the amount of mineralizable nitrogen in the L horizon of the buried bag incubation to be 3.1 times more than in the H horizon, as a result of the multiplication of both factors. The buried bag incubation data shows that it is in fact 2.9 times more (Chapter 1). These results imply that an active layer is present and occupies the L horizon, which is at the shallowest depth. The root distribution data also supports the hypothesis of an active layer as well, given that most roots are found in the top horizon, where most of the microbial activity occurs.

2.5 Conclusion

The importance forest floor temperature on nutrient cycling and root distribution in organic matter beneath different types of mosses in northwestern Quebec black spruce boreal forest seems to be consistent with other studies demonstrating its importance. Whereas temperature seems to be controlling to a great extent the presence and depth of an active layer, neither moisture availability nor forest floor temperature seem to be responsible for the differences in microbial activity and nitrogen mineralization between feather mosses and *Sphagnum* mosses. Organic matter quality seems to be the factor distinguishing feather moss and *Sphagnum* moss organic matter nitrogen mineralization. More research would be needed, however, to more fully characterize the contribution of both feather mosses and *Sphagnum* mosses to nutrient cycling and their control on forest floor moisture availability and temperature. This information would be a critical component of the understanding of boreal black spruce forest nutrition.





Figure 2.1 Temperature variation in organic matter under feather moss and *Sphagnum* moss from the first week in July to the last week of August, in the summer 2000.



Figure 2.2 Average temperatures, from the first week in July to the last week of August in the summer 2000, in relation to depth of organic matter under both *Sphagnum* moss and feather moss.





Figure 2.3 Moisture variation in organic matter under feather moss and *Sphagnum* moss from the first week in July to the last week of August, in the summer 2000. Note: The mean standard errors for feather moss and *Sphagnum* moss are 20 and 22 respectively.



Figure 2.4 Root distribution among organic matter horizons.



Figure 2.5 Moss cover as a function of the depth of organic matter. Letters compare moss cover across depths for each moss type.



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The results of this study indicate that the generally assumed hypothesis that organic matter is accumulating in black spruce forests due to the slow decomposition of mosses may not happen in northwestern Quebec. There are, however, a number of assumptions associated to the use of retrospective studies, such as the similar origins and successional outcomes of the sites in which the study was done. We are nevertheless confident that no blanket statement about an increase in organic matter over time in these forests can be made on the basis that similar amounts of organic matter were found in all age classes. No decline in nitrogen availability and total nutrient content was detected in the chronosequence suggesting that if there is a decline in black spruce productivity over time it may not be caused by long-term reductions in nutrient availability.

Nutritional differences between feather mosses and *Sphagnum* mosses, where the former generates more mineralizable nitrogen as well as total nitrogen, phosphorus, carbon, magnesium and potassium than the latter, suggests that it is worthwhile distinguishing the role of mosses in nutrient cycling in black spruce forests. In addition, moss cover and abundance might be used as potential indicators of site nutritional status and productivity, however, further research focusing on the relationship between tree productivity and mosses would be needed.

More research would also be necessary to clarify the role of forest floor temperature and moisture availability on nutrient cycling. Our results indicate that temperature seems to be the most important factor controlling the presence and depth of the active layer, where most of the nitrogen mineralization and root growth occurs. Moisture does not seem to play an important role in this respect, however, more data ranging from early spring to late fall might, for both factors, might prove to be helpful in

understanding the nutrient dynamics in the forest floor. There is a possibility that the bottom horizon stays warm and moist for a longer period of time than the shallow horizons in the fall, which might lead to a change in depth of the active layer. Nevertheless, the implications for silvicultural practices, such as the removal of organic matter for site preparation, are that the presence of organic matter might be more beneficial if left intact due to the presence of a shallow active layer.



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