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[1]Université du Québec en Abitibi-Témiscamingue, 445, boulevard de l'université, Rouyn-Noranda, Québec, Canada J9X 5E4
* Correspondence : Tel : (819) 843-3256; Email : martin.lavoie@uqat.ca; martin_skifond@hotmail.com
[2]Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Center
1055 rue du PEPS, P.O. Box 3800, Sainte-Foy, Québec, Canada G1V 4C7
[3]Northeast Science and Information, Ontario Ministry of Natural Resources
Ontario Government Complex, P.O. Bag 3020, South Porcupine, Ontario, Canada P0N 1H0
[4]Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Center
1219 Queen St. East, P.O. Box 490, Sault Ste. Marie, Ontario, Canada P6A 2E5

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Abstract

The Clay Belt region of Québec and Ontario supports a large forest resource and an important forest industry. In Quebec, the boreal forest is generally harvested with the "cut with protection of regeneration and soils" (CPRS) technique and in Ontario careful logging around advance growth (CLAAG) is utilized. There is currently a strong interest in forest management that emulates the natural disturbance regime in order to maintain forest composition and structure. The main objective of CPRS-CLAAG is the protection of soil and advance regeneration. In order to further protect soil and advance regeneration, forested peatlands are frequently harvested in winter. Despite general acceptance, the use of these methods is questioned in certain areas. Notably, in black spruce-feathermoss forests on the Clay Belt, growth problems have been observed due to paludification.

Paludification is the accumulation of organic matter (i.e.peat) over time that is generally believed to be caused by increasing soil moisture and *Sphagnum* colonisation. It is influenced by external and internal factors, and reduces 1) soil temperature, 2) decomposition rates, 3) microbial activity, and 4) nutrient availability. As a result, paludification may lead to lower site productivity with time since disturbance (wildfire or harvesting). Therefore, in harvested stands with a thick organic matter layer, low soil disturbance and water table rise (due to tree removal) may create favourable conditions for paludification that may ultimately be detrimental to timber production. Furthermore, this disturbance may be different from naturally regenerating sites following a wildfire. Consequently, evaluating the success of CPRS-CLAAG by only assessing regeneration density and stocking may be inadequate. We must also take into account the long-term effects of this treatment on site productivity and soil fertility.
In the literature, several solutions to prevent or control the negative effects of paludification are suggested. Drainage and fertilization are generally good techniques to control paludification and to improve tree productivity. On the other hand, site preparation (mechanical and prescribed burning) or drainage followed by burning may more efficiently control paludification at a lower monetary cost. These techniques may also have a greater potential to reverse paludification, specifically where peat accumulation was caused by natural succession or where lateral peat expansion has occurred.

This review was aimed at determining research needs for the Clay Belt. Several issues have been identified. First, the establishment of *Sphagnum* and the interaction *Sphagnum*-feathermoss is still not well understood. Second, even if the ecology of black spruce has been intensively studied, there are still large gaps in our knowledge, specifically for peatland black spruce. In the literature, almost all seedbeds have been reported as excellent for black spruce germination. Thus, the evaluation of seedbed quality and its interaction with environmental factors should be considered. Third, a lot of effort has been devoted to the study of black spruce germination, and we think that more efforts should be placed on substrate quality for tree growth in relation to the environmental factors particular to the Clay Belt. Finally, more fundamental research on peatland history with respect to topography, disturbance and climate using techniques such as paleoecological

reconstructions (peat stratigraphy) are necessary in order to understand and predict the effects of future management and climate change and to differentiate paludification caused by the chronosequence or toposequence. A better knowledge of topography and peat thickness will make it easier to locate small depressions, as well as primary peat growth and lateral expansion. Thus information will facilitate forest management. However, the Clay Belt will always remain an area susceptible to peat initiation, peat accumulation and lateral expansion, because the current climate, the topography and the mineral deposit are conducive to paludification

Résumé

La ceinture d'argile localisée au Québec et en Ontario, supporte une ressource et une industrie forestière importante. Au Québec comme en Ontario, de façon générale, la forêt boréale est récoltée avec la coupe avec protection de la régénération et des sols (CPRS) (CLAAG en Ontario). Actuellement, il y a un intérêt grandissant en aménagement forestier pour maintenir la composition et la structure forestière afin de simuler le régime naturel de perturbation. . L'objectif de la CPRS-CLAAG est de protéger les sols et la régénération adventive. Pour une protection additionnelle, la coupe est souvent exécutée au cours de la saison hivernale. Malgré une appréciation générale de cette technique, son utilisation dans la pessière noire à mousses sujette à la paludification dans la ceinture d'argile suscite des craintes quant au maintien de la productivité forestière.

La paludification est principalement influencée par des facteurs internes et externes et peut être définie par l'accumulation de matière organique (*i.e.* tourbe) causée par une augmentation de l'humidité du sol et de la colonisation par les sphaignes. La paludification a pour effet de réduire 1) la température du sol, 2) le taux de décomposition, 3) l'activité microbienne et 4) la disponibilité des éléments nutritifs. Ainsi, la paludification peut avoir pour effet de réduire la productivité des sites avec une augmentation du temps depuis la dernière perturbation (coupe ou feu). Par ailleurs, un horizon organique épais combiné avec une faible perturbation du sol et une élévation de la nappe phréatique, suite à l'enlèvement du couvert forestier, met en place des conditions différentes de celles qui suivent un feu et sont susceptibles d'être dommageables pour la production de bois. Conséquemment, utiliser la densité de régénération et la densité relative pour évaluer l'efficacité de la CPRS-CLAGG est inadéquat. Nous devons également prendre en considération l'effet à long terme de ces pratiques sur la productivité des sites et sur la fertilité des sols.

Dans la littérature scientifiques des solutions sont proposées pour contrer ou prévenir les effets négatifs causés par la paludification. Le drainage et la fertilisation sont généralement de bonnes techniques pour contrôler la paludification et pour améliorer la productivité des arbres. D'un autre côté, la préparation de terrain (mécanique et brûlage dirigé) et le drainage suivi d'un brûlage dirigé peuvent contrôler plus efficacement la paludification et ils ont surtout un potentiel plus élevé de renverser la paludification, surtout dans les endroits où l'accumulation de tourbe fait suite à la succession naturelle ou à une expansion de la sphaigne.

Cette revue de littérature nous a permis de définir les besoins futurs en recherche pour la ceinture d'argile. Tout d'abord, des ressources devraient être allouées pour étudier l'établissement des

sphaignes et l'interaction sphaignes-mousses puisque ces deux champs de recherche sont toujours mal compris. Deuxièmement, même si l'écologie de l'épinette noire est bien connue, il y existe toujours des besoins. Dans la littérature, il est pratiquement possible de conclure que l'ensemble des lits de germination sont excellents pour la germination de l'épinette noire. Ainsi, nous croyons que des besoins en recherche sont nécessaires pour déterminer quels sont les meilleurs lits de germination pour l'épinette noire en fonction des variables environnantes particulières à la ceinture d'argile. Troisièmement, beaucoup de temps et d'énergie ont été alloués à la recherche sur les lits de germination. Nous croyons également que des ressources devrait être investies dans la recherche sur les meilleurs substrats de croissance pour l'épinette noire en fonction des variables environnantes particulières à la ceinture d'argile. Et finalement, nous croyons que la priorité en recherche pour l'aménagement forestier dans la ceinture d'argile devrait être allouée à la reconstruction paléoécologique (stratigraphie) et aux études portant sur la topographie à différentes échelles. Il est essentiel de connaître l'histoire de ces tourbières boisées pour être mieux outillé pour prédire, avec la modélisation, les réponses suite au réchauffement climatique et aux activités humaines, mais également pour être capable de mieux distinguer les causes de la paludification par chronoséquence ou par toposéquence. Une meilleure connaissance de la topographie ainsi que de l'épaisseur de tourbe nous permettra également de bien localisé les dépressions ainsi que les endroits où il a eu paludification primaire et expansion de sphaigne. Ces informations vont faciliter l'aménagement forestier. Mais, il demeure que la ceinture d'argile sera toujours un milieu propice à l'accumulation de tourbe et à l'expansion de la sphaigne puisque le climat actuel, la topographie et le dépôt minéral sont très favorables à la paludification.

Mots clés: paludification, tourbière boisée, productivité, feu, coupe, perturbation du sol.

1.0. Introduction

1.1. Background

The Clay Belt region of Québec and Ontario supports a large forest resource and an important forest industry. Because of a strong demand for wood products, as well as increasing pressure to set land aside for conservation purposes, forestry operations are pushed towards the northern limit of the commercial forest. In the James Bay Lowlands physiographic region of Quebec and Ontario, the majority of the harvested volume allotted to forest companies is in forested peatlands stands, which are considered to have low productivity (Prévost et al., 2001). In Quebec, the boreal forest is generally harvested with the "cut with protection of regeneration and soils" (CPRS) system, and in Ontario careful logging around advance growth (CLAAG) is used. But, there is currently a strong interest in the development of forest management systems that maintain forest composition and structure in an attempt to emulate the natural disturbance regime (*e.g.* ecosystem management with multiple-cohorts) (Bergeron et al., 1999, 2001, 2002; Nguyen-Xuan, 2000; Harvey et al., 2003; Lieffers et al., 2003).

The aim of CPRS and CLAAG harvesting techniques is the protection of soil and of advance regeneration. In order to further protect soil and advance regeneration, forest harvesting in wooded peatlands is often carried out during winter (Haavisto, 1979; Groot, 1987, 1995). Currently, when the pre-harvest density of advance regeneration is high, CPRS and CLAAG are generally regarded as good harvesting methods, as they maintain regeneration density and stocking (Harvey and Brais, 2002). Despite general acceptance, the use of these methods is called into question in certain areas. Notably, in black spruce-feathermoss forests located on the Clay Belt, growth problems have been observed due to paludification.

Paludification is the accumulation of organic matter (*i.e.* peat) over time and is generally believed to be caused by increasing soil moisture and *Sphagnum* colonisation. It is influenced by external and internal factors and reduces 1) soil temperature, 2) decomposition rate, 3) microbial activity, and 4) nutrient availability (Payette, 2001; Taylor et al., 1987). It has also been suggested that some disturbances (*e.g.* wildfire) can favour paludification by decreasing interception and evapotranspiration (Wilde et al., 1954). As a result, paludification may lead to lower site productivity with time since disturbance (wildfire or harvesting) (Larsen, 1982; Payette, 2001). Therefore, in harvested stands with a thick organic matter layer, low soil disturbance and water table rise (due to tree removal) may create favourable conditions for paludification, which may ultimately be detrimental to timber production. Furthermore, these sites may be different from those typical of naturally regenerating sites following a wildfire. Consequently, relying only on the density and stocking of natural regeneration after cutting to evaluate the quality of a CPRS-CLAAG is insufficient. We must also take into account the long-term effects of this treatment on site productivity and soil fertility.

Climate, topography (flat plain broken by gentle undulations or ridges) associated with surficial deposit (*i.e.* clay) make the Clay Belt a perfect area for peat development and landscape paludification (Wilde et al., 1954; Vincent, 1962; Jeglum, 1991; Riley, 1994). Since the Clay Belt is subject to peat accumulation any silvicultural treatment that could favour paludification of upland soils will have a long-term impact on tree productivity and soil fertility.

1.2. Objective of this review

A review of the scientific literature related to paludification was undertaken with the initiative of Lake Abitibi Model Forest (LAMF), in collaboration with the Canadian Forest Service, the Ontario Ministry of Natural Resources, and the Université du Québec en Abitibi-Témiscamingue. The objective was to synthesize the literature on the impact of natural disturbances and harvesting on paludification. This review will focus primarily on paludification research completed in the North American boreal forest, but will assess the pertinence of this literature, based on the similarity of the climate and terrain to the Clay Belt. In the last part of this review, solutions to prevent, control and reverse paludification will be discussed.

2.0. Definitions and terminology

To understand the processes related to paludification in the boreal forest, a review of literature concerning peatland ecology is essential. In the literature, several terms related to peatlands may have different meanings for researches in different disciplines, which may lead to confusion and misunderstanding. In order to avoid confusion, some definitions will be introduced. Wetland, is the must common group and is defined as: an area that is saturated with water long enough to promote wetland or aquatic processes as indicated by poorly drained soils, hydrophytic vegetation and various kinds of biological activity that are adapted to a wet environment (NWWG, 1988). Wetlands can be subdivided into two broad categories: **minerotrophic** or **organic wetlands**. Minerotrophic wetlands are found in areas where an excess of water collects on the surface and for geomorphic, hydrologic, biotic, edaphic, or climatic reasons produce little or no organic matter or peat. Gleysolic soils or peaty phases of soils are characteristics of these wetlands (NWWG,

1997). Minerotrophic wetlands are also areas of shallow water, generally less than 2 m deep (NWWG, 1997). Any wetlands with a significant component of woody vegetation, regardless of the size of the plant is considered as a **forested wetland**. Organic wetlands are more simply referred to as **peatlands**. In Canada, peatlands contain more than 40 cm (moderately or highly decomposed) or 60 cm (poorly decomposed) of peat accumulation on which organic soils develop. This depth limit is consistent with soil classification standards established by the Canadian Soil Survey Committee (1978). However, in Finland and in Scandinavia, the depth limit is set at 30 cm (Pakarinen, 1995). Peatlands may also include some wetlands and organic soils where aquatic processes are not operating (e.g. drained or afforested peatland) (Charman, 2002). As for wetlands, any peatland with a significant component of woody vegetation is a **forested peatland.** In Europe, the term peatland is not widely used, and the more generic term **mire** is used. The term mire means all ecosystems described in English as swamp, bog, fen, moor, muskeg, and peatland (Gore, 1983). The term **muskeg**, which is an Algonquin term for peatland, is also present in the literature. It is usually applied to areas with *Sphagnum* mosses, tussocky sedges and an open growth of scrubby trees (Harris et al., 1996). **Forests prone to paludification** (future minerotrophic or organic peatland) are not currently defined in the literature. In this review these are stands characterized by 1) a climate and physical and chemical properties favouring peat accumulation, 2) the presence of mosses (mainly feathermoss with a increasing cover of *Sphagnum*), 3) an increasing organic matter layer (< 30 cm), and 4) have soil properties (*ex.* nutrient concentration) similar to those of mineral and organic peatlands. Upland sites surrounded by lowlands sites may also be prone to paludification via the lateral expansion of *Sphagnum*.

The Canadian Wetland Classification Systems contains three hierarchical levels: (1) class, (2) form, and (3) type. However, for the purpose of this review, only the class level is considered. In the Canadian Wetland Classification, 5 classes are recognised: bog, fen, swamp, marsh, and shallow water. A similar classification is found in Finland and Scandinavia (Pakarinen, 1995). These classes are strongly linked to the concepts of trophy and nutrient status of the site. Only, bog, fen, swamp and marsh will be described.

Bogs are characterized by a variety of shapes and sizes. The bog surface, which is raised or level with the surrounding terrain, is virtually unaffected by runoff waters or groundwaters from the surrounding mineral soils. Generally the water table is at or slightly below the bog surface. Precipitation, fog, snowmelt and nutrient deposition are the primary water sources and mineral element flux and thus, all bogs are ombrogenous (and ombrotrophic) and mostly oligrotrophic (*i.e.* nutrient poor). Given that precipitation does not contain dissolved minerals and is midly acidic, surface bog waters are consequently low in dissolved minerals and are acidic (NWWG, 1997). Bogs may be treed, semi-treed or treeless (open), and they are usually covered with *Sphagnum* spp. and ericaceous shrubs (Vitt and Belland, 1995; NWWG, 1997). Over time, bogs have develope through terrestrialization or paludification. Many forms and subforms exist, including basin, blanket, domed, flat, palsa, riparian, and intermediate bogs (NWWG, 1997). Riley (1998) has documented that bog cover about 50 % of the peatland area of northeastern Ontario.

Fens are peatlands with a fluctuating water table. The waters in fens are rich in dissolved minerals and are therefore minerotrophic. Ground and surface water movement is a common characteristic of fens. The dominant peat materials are moderately decomposed *Sphagnum* in poor fens and sedges and brown mosses of variable thickness in rich fens (Vitt and Belland, 1995; NWWG, 1997). In general, graminoid vegetation and some bryophytes dominate wetter fens where the water table is above the surface. Shrubs are prominent in drier fens where the water table is lower. Trees occur in the driest fen sites where microtopographic features such as moss hummocks provide habitats as much as 20 cm above the water table (NWWG, 1997). Fens also range from acidic to alkaline and nutrient poor to nutrient rich (*i.e.* mesotrophic to eutotrophic) (Sims and Baldwin, 1996). Fens have developed by terrestrialization or by paludification. Many forms and subforms exist, including basin, channel, feather, palsa and riparian fens (NWWG, 1997).

Swamp is a term that has been used in Canada and the United States in reference to forested or wooded wetlands and peatlands. However, it should be noted that in British (and much European) literature, it refers to habitats, mostly dominated by plants of graminoid life form, in which the water level is above the ground surface for all, or much of the year (Wheeler and Proctor, 2000). However, as only the North American definition will be used in this review, a swamp can be defined as a wetland dominated by trees or tall shrubs (also called *thicket*) that is influenced by minerotrophic groundwater on either mineral or organic soils. The essential features of swamps are the dominance (over 30 % cover) of tall woody vegetation,, and the wood-rich peat laid down by this vegetation (NWWG, 1997). Swamps are not as wet as marshes, fens or open bogs, but they are comparable to treed bogs. The driest treed swamps grade into upland forest on mineral soil, and the wettest treed swamps grade into treed fen,

which is wetter with less tree canopy cover (NWWG, 1997). Swamps have developed via terrestrialization or paludification. Many forms and subforms exist, including discharge, flat, inland, riparian and slope swamps (NWWG, 1997).

Marshes are a wetland that has shallow water, with levels that usually fluctuate daily, seasonally or annually due to tides, flooding, evapotranspiration, groundwater recharge, or seepage losses. A marsh is a minerotrophic, and usually eutrophic, wetland. Nutrients are derived from the substrate through periodic aeration. High nutrient levels give rise to the characteristically high productivity of vascular plants and high decomposition rates of plant material at the end of the growing season. Marsh vegetation comprises emergent aquatic macrophytes, mainly graminoids such as rushes, grasses and sedges, and shrubs and other herbaceous plants, and non-vascular plants such as brown mosses, liverworts, and macroscopic algae (NWWG, 1997). Many forms and subforms exist, including basin, estuarine, slope and spring marshes (NWWG, 1997).

Three terms have been frequently used in the literature to describe a bog, peatland or wetland with a significant component of woody vegetation: forested, wooded and treed. To our knowledge, there are no clear distinctions made in the literature among these terms. Two very general definitions are given in the dictionary: wooded refers to covered with growing trees and bushes, forested refers covered with forest and treed is not defined. However, in discussion with different peatland ecologists, these three terms may actually different meanings that may lead to uncertainty and misinterpretation for some readers. For some, forested contains dense mature trees, while treed is used to indicate a sparser density and generally smaller size trees (Tim

Moore, *personal communication*) For others, forested refers to a closed canopy while wooded or treed is limited to open canopy (Jeglum, 1991; Vitt et al., 2003b, *Personal communication*). Finally, wooded (or woodland in this case) is used for a mix of wood and grass land, mostly savanna (some scattered trees in grassland), while forested designates an area covered by trees. The minimum percentage covered by trees might in that case be as low as 25% (Altaf Arain, *personal communication*). Consequently, in future research or evaluations standard definitions for wooded, forested, and treed should be provided.

To comprehend the processes related to the paludification of boreal forest, this review of literature will look deeper at the processes related to bog, fen and swamp formations. Consequently, in the following text, peatland will be used to refer only to bogs, fens and swamps.

3.0. Peatland distribution

3.1. The Global picture
As we have seen in the previous section several terms are used in the literature to define peatland. Consequently, the distribution of the world's peatlands is not accurately known. Peatlands are estimated to occupy roughly 500 million ha, or 3.8 % of the global land surface (Paavilainen and Päivänen, 1995). Boreal and subarctic peatlands are located mostly in the former Soviet Union, Canada, USA, and the Fennoscandian countries, with a total area of 346 million ha (Gorham, 1991). In Canada, peatland cover is estimated to be between 105 (> 40cm) and 170 (>30 cm) million ha with about 18 million ha of forested wetland (Dahl and Zoltai, 1997). Peatlands occupy 43 million ha, 21 % of the total landbase of Alberta, Manitoba, and Saskatchewan (Dahl and Zoltai, 1997; Vitt et al., 2000). Of this 43 million ha, 6.3 million ha is estimated to

be forested. In Newfoundland-Labrador wetlands cover approximately 6.5 million ha with about 77 % forested (Dahl and Zoltai, 1997). It is in Ontario where wetland and forested wetland occupied the greatest surface area with a 42.8 and 8 million ha respectively (Ketcheson and Jeglum, 1972). Lastly, in the province of Québec, estimations of the surface area occupied by peatlands range from 8 to 12 million ha (Dahl and Zoltai, 1997; Rochefort, 2001) where approximately 2.2 million ha is located south of the 50th parallel (Bolghari, 1986). The surface area occupied by forested wetland is about 3.8 million ha.

The percentage of cover of forested peatland in Canada remains uncertain and clearly more studies are needed across the Canadian boreal forest. Consequently, studies on the percentage of forests that are prone to paludification are also very rare.

3.2. The Clay Belt

The Clay Belt covers a broad east-west band of land that spans the Ontario and Quebec border, and covers about 125 000 km^2 (Lefort et al., 2002). The southern portion is situated in the boreal mixedwood forest, whereas the black spruce boreal forest dominates the landscape north of the 49th parallel. The Clay Belt support research activities conducted by a number of groups and organisations: 1) by the Ontario Ministry of Natural Resources, the Lake Abitibi Model Forest and associated a universities, 2) the Lake Duparquet Research and Teaching Forest, the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management and by the Québec Ministry of Natural Resources and 3) the Canadian Forest Service. The forestry companies operating in this area (Tembec, Norbord and Abitibi Consolidated) have to deal with a significant proportion of minerotrophic and organic peatlands in their territories (James Bay Lowlands,

northwestern Abitibi and northeastern Ontario). The Clay Belt is characterized by important glacial lacustrine deposits left 10 000 years ago by the glacial lakes Barlow and Ojibway (Boissonneau, 1966; Hardy, 1977; Vincent and Hardy, 1977; Veillette, 1994) which form the basis of much of the surficial deposits on the Clay Belt. 8000 years ago, when the ice front was roughly at the northern boundary of the Precambrian with Mesozoic and Paleozoic sediments, it made a series of readvances over the lacustrine deposits of much of Lake Barlow-Ojibway, which resulted in redeposition of till, known also as "Cochrane Till", and compaction of the underlying clay (Vincent, 1962; Boissonneau, 1966; Hardy, 1977; Vincent and Hardy, 1977; Bergeron et al., 1998). Argillaceous depositis with an organic horizon are prevalent but till and glacial lacustrine deposits are also found. The territory is made up of plains and is characterized by low hydraulic conductivity and imperfect to very bad drainage classes. This area is characterized by extensive black spruce peatlands and an age structure that includes large areas of forest cover over 100 and even 200 years old. However, in Quebec, no extensive studies have been conducted on the surface occupied by forested peatlands (Prévost et al., 2001). However, Ketcheson and Jeglum (1972) estimated that in Ontario 43 % of the Clay Belt is covered by wooded peatlands. This may be a function of the flat topography and small depressions that leads to slow runoff, collection and stagnation of water. As a result, decomposition is decreased, and organic residue increases. This accumulation may range from a moorlike raw humus horizon of a few centimetres thickness to several feet of peat in peatlands (Stanek, 1961).

4.0. Peatland initiation

Most peatlands begin their existence as minerotrophic wetlands and turn into an organic peatland over time, either naturally through successional processes, external factors, or with the assistance of humans. Peatlands are formed by allogenic (*i.e.* external to the ecosystem) and autogenic (*i.e.* internal to the ecosystem) factors (Payette, 2001a; Charman, 2002). In essence, peat accumulation begins when production of organic matter exceeds decay (Paavilainen and Päivänen, 1995; Charman, 2002). However, this process is not that simple as there are several factors that influence *Sphagnum* establishment that increases peat accumulation There are five main factors essential for peat initiation: climate, geomorphology, geology and soils, biogeography, and human activities (Gorham, 1957; Heinselman, 1975; Liu, 1990; Kuhry et al., 1993; Kobak et al., 1998; Halsey et al., 1997, 1998; Charman, 2002; Crawford et al., 2003). Clearly, *climate* must be of central importance in determining whether there is likely to be a surplus of water available for peat initiation. The precipitation-evaporation balance is critical and a surplus can result from low precipitation-low temperature or high precipitation-high temperature regimes as well as high prepcipitation-low temperature conditions (Charman, 2002).
Geomorphology involves topography, which creates spatial diversity in the hydrological characteristics of the landscape. The magnitude of the effect of geomorphology is seen in the situation of the two major peatlands in the world (Gorham 1991). The largest lies on the vast and nearly level West Siberian Plain between the Ob and Yennisey rivers in the ex-USSR. Slopes may vary from 0.1-0.8 in 1000 in wet peatlands to as much as 4 in 1000 in less wet sites. The next largest peatland occupies the Hudson/James Bay Lowlands of Canada, another region of

flat topography where the slope is commonly less than 1 in 1000, and where rather impermeable marine silt/clays and other deposits favor waterlogging (Riley, 1982). *Geology and soils* (bedrock and texture) are also very important in peat initiation, (Halsey et al., 1997) as mineral soil composed of heavy clay act as an impermeable substrate that facilitates water accumulation. However bogs are reported to form on glacial till, sand, blue clay, gravelly outwash, soil formed *in situ*, and rock (Riggs, 1925; Gorham, 1957; Hulme, 1994). Particular areas of the world (*Biogeography*) may be more susceptible to peat development because of the presence of animals (*e.g.* Beaver, *Castor canadensis*), particular plants or group of plants. And lastly, *human interventions* by agricultural activities or by forest management may modify the hydrological balance of the peatland and it may also change peatland development. Consequently, when these five main factors create conditions promoting excess of water and establishment of *Sphagnu*m, it can result in two main pathways of peat formation, termed **paludification** and **terrestrialization** (Romell and Heilberg, 1931; Millar, 1940; Gorham, 1957; Payette, 2001a; Charman, 2002). Terrestrialization is a process by which a shallow water body is gradually infilled with accumulated debris from organic and inorganic sources. This continues to a point where the water table is at or below the surface for at least some of the year, and peat accumulates over the previously deposited limnic (lak) sediments (Payette, 2001a; Charman, 2002). However, a greater proportion of peatlands are created via paludification than terrestrialization, (Payette, 2001a; Charman, 2002), and peat accumulation by terrestrialization is not affected directly by forest management and can hardly be reversed by silvicultural treatments. Therefore, for the purpose on this paper only paludification will be reviewed.

5.0. Paludification

5.1. Definitions

Several different definitions of paludification are found in the literature : (i) the conversion of dry land to peatland (Anderson et al., 2003); (ii) wetland expansion caused by gradual rising of the water table as peat accumulation impedes drainage (NWWG, 1988); (iii) conversion of a mineral soil site to a mire due to a rise in the groundwater (Paavilainen and Päivänen, 1995); or (iv) process that describes peat formation directly over a mineral substrate with no fully aquatic phase and no limnic sediments laid down. (Charman, 2002). However, for the purpose if this review, paludification will be refered to as (v) a dynamic process involving a gradual rise in the water table as peat accumulation impedes drainage and *Sphagnum* spp. ground cover continues to grow and expand (Sims and Baldwin, 1996).

5.2. Processes leading to paludification

The development of a paludified soil requires a precipitation/evapotranspiration ratio above 1 during the growing season (Taylor et al., 1987; Payette, 2001a). For paludification of dry land to occur, a shift in local hydrological conditions to produce waterlogged conditions in the soil to reduce the decay rate significantly below the production rate is required. This shift may be due to an increase in water inputs (precipitation, surface runoff and inflow runoff) or a decrease in outputs (evapotranspiration, outflow from surface runoff, and outflow to groundwater through seepage) (Charman, 2002). Many processes may cause a change in inputs or outputs, among them, human activity, tree removal, presence of charcoal, increase in precipitation, and podsolisation (Charman, 2002). For example, Hu and Brubaker (1996) found that in northwestern Alaska, a

climatic shift 4000 yr ago towards wetter climate probably induced permafrost aggradation, which impeded drainage in lowland areas and lead to the development of waterlogged soils. Once present, waterlogged soils may contribute to (1) an invasion of *Sphagnum* spp., which can via its ability to bind cations, lower pH, reduce microbial activity, lower nitrification rates, and reduce nutrient cycling, which all; (2) a reduction of microfaunal and microbial activities; (3) a decrease of redox potential; (4) deterioration in aeration conditions; and (5) a reduction of nutrient availability (Charman, 2002). All of these processes may further facilitate peat initiation and development.

AUTOGENIC VS ALLOGENIC
Peat initiation (section 4.0) and peat accumulation are mainly influenced by external factors such as climate or topography but it is important to remember that external and autogenic factors are constantly interacting (Glaser and Janssens, 1986; Kuhry et al., 1993; Jeglum and He, 1995; Payette, 2001a, Charman, 2002, see also Hu and Brubaker, 1996). Changes due to autogenic processes always occur against a background of external conditions. Interractions between autogenic and allogenic factors occur in three ways (Charman, 2002): (i) stable external conditions as a background against which autogenic processes take place; (ii) changing external conditions accelerate an autogenic process, or (iii) changing external conditions inhibit an autogenic process.

Autogenic processes that contribute to paludification are biological, physical, and hydrological. The biotic aspect includes growth, decay, and accumulation of organic matter, plant morphology, and animal behaviour (*e.g.* beaver). Physical processes associated with the movement of sediments and soils, and the freeze-thaw cycle in cold

climates, and hydrological processes that cause an increase or reduction in surface water may influence the development of a paludified soil.

Allogenic processes also determine where and when peat growth can occur, and include climate (temperature and precipitation), hydrological changes, volcanic influences, human activities (Charman, 2002), and fire (Kubiw et al., 1989). A favorable climate for peat initiation is essential, and influences other processes, such as hydrology, physical processes (*e.g.* permafrost aggradation), peat accumulation (via soil temperature and moisture), and to a lesser extent on biotics changes (*e.g.* plant responses) and peatland morphology. Human activities (tree harvesting for the purpose of this review), and fire, will be discussed later in this review (section 7.0). Hydrological changes include tree removal by human activities, sea level variations, and changes in groundwater supply. Lastly, studies on the effects of fire, via ash, on peatlands are limted and it is suggested that it might have a role on the vegetation and on the climate.

PATHWAY OF PEAT GROWTH

There are three main pathways of peat growth: primary, secondary and tertiary (Moore and Bellamy, 1973). Primary peats are those formed in basins or depressions where water collection is at a maximum and they are often preceded by a limnic phase of development. Many peatlands, including bog systems, have elements that evolved from primary peat formation. Secondary peats form as a result of expansion of a primary peatland due to waterlogging of the soil. Again, most peatlands have elements that can be regarded as secondary. Tertiary peats are those that develop above the influence of groundwater and where conditions allow the peat to cover most areas of the landscape.

When terrestrialization is the cause of organic matter accumulation, it is generally quite easy to identify peat initiation in pollen analysis due to the change in the vegetation. Howerver, peat formation by paludification may not be as easy to recognize. The transition beween mineral soil and organic soil is more gradual and it is unclear when the soil, with an increasingly thick organic matter layer, becomes a true peatland. As a result it is difficult to determine precisely when peat initiation took place. Peat stratigraphy, pollen, charcoal and radiocarbon data, as well as plant macrofossils and geochemistry are used as evidence to identify peat initiation in soil profiles (Charman, 2002), however the attribution of cause and effect of these indicators remains difficult.

HUMID BASIN AND WELL-DRAINED SOIL

Paludifcation is most often seen in basins and depressions, where there is an appropriate climate to allow an excess of water (Payette, 2001a). After initiation, autogenic and allogenic processes control or modify the peat accumation rate in these systems. As the depth of the organic matter increases, peat will be isolated from the mineral soil and the transition from fen to bog will occur. As the peat grows, eventually the peat may expand beyond the deepest parts of the depression onto the surrounding landscape.

Paludification also occurs outside of basins on unlikely terrain. Paludification on sloping terrain (20%) has also been reported (Gorham, 1957; Payette, 2001a; Charman, 2002). In such situations, as the bog grows, it must either develop its own internal drainage system or it will eventually become so big that the accumulation of water during heavy rain may exceed the holding capacity of the peat, and lead to a flow of the whole mass downslope (Gorham, 1957). Acid peat may form on upland soils even when they

are relatively rich. Moreover, if the atmosphere is sufficiently humid, and precipitation exceeds evaporation at all seasons, some species of the bog moss *Sphagnum* may grow where the ground is not saturated. And if rainfall is high, even fairly rich soils may be leached of nutrients at the surface, as a result of creating favourable conditions for the establishment of the bog mosses, and unsuitable conditions for the rapid breakdown of their dead residues (Gorham, 1957).

It is often assumed that peat initiation requires an external factor such as climate, but it may also be just a result of natural succession (*i.e.* autogenic) (Riggs, 1925; Zack, 1950; Heilman, 1966, 1968; Viereck, 1970; Engstrom and Hansen, 1985; Davis, 1988; Smith and Taylor, 1989; Mäkilä et al., 2001). In the absence of fire, there is a build-up of organic matter and an increase in *Sphagnum* cover in a black spruce-feathermoss community. This may lead 1) to the reduction in soil temperature, soil aeration, nutrient availability, decomposition rates, 2) to the formation of permafrost in certain areas, 3) an increase of the water table level, and finally 4) a decrease in tree productivity. Thus, with time, a black spruce stand may turn into an organic peatland (see Appendix 1). And, once *Sphagnum* is established, it seems unlikely to disappear as long as climate and hydrological conditions remain stable (Charman, 2002). Ultimately, it remains very difficult to determine if paludification of these black spruce stands originated from a chronosequence or a toposequence. Thus, it is not always possible to distinguish paludification by natural succession from lateral expansion from surrounding bogs or depressions. Peat stratigraphy and an understanding of local and surrounding topography are essential to discriminate between these two causes. Because forest management strategies differ

between the two situations, understanding the origin of peat is important.

An alternate pathway, not actually caused by natural succession but rather by soil development, has been documented by Ugolini and Mann (1980) in conifer forests near the northern limit for tree growth. The release of organic acids as from *Sphagnum* as a result of growth and decay causes the complexing of iron deposits in spodosols under old conifer stands. The iron oxides then become a cementing agent and bind soil particles into a hardpan, which hinders drainage. The resulting waterlogging leads to the establishment of *Sphagnum*-dominated peatland that eventually replaces the conifer stand.

5.3. Peat accumulation

Carbon and peat accumulation in peatlands is the difference between production of living plants atop the acrotelm and decomposition in both the acrotelm and the catotelm. The acrotelm is described as the active layer and is characterized by variable water content, variable soil aeration, high microbial activity and high hydraulic conductivity. Between the acrotelm and the catotelm is a transition zone where the water level fluctuates and water moves laterally. Below this, is the catotelm that is permanently saturated with water, is anaerobic, has low hydraulic conductivity, and as a result, has little biological activity (Paavilainen and Päivänen 1995). Peat accumulation occurs through the combined processes of production, decomposition and compression of organic matter derived from mosses and vascular plants. Each year's cohort of litter undergoes aerobic decay and is buried under the weight of younger material, until eventually the main plant structure collapses. Carbon is sequestered over long periodes of time as organic matter is submerged into the catotelm where decomposition rates are very low (Clymo, 1984; Belyea and Clymo, 2001).

PRODUCTION

Production is the positive side of the mass balance equation that determines peat accumulation. One might expect that areas with high productivity would also have high rates of peat accumulation, but in reality, because decay rates are often also high in very productive systems, they frequently accumulate less matter. Tropical peatlands are a good example of this situation, as the accumulated peat layer is less thick than in northern peatlands.

Although production is difficulty to estimate precisely, there are numerous studies that measure the primary production of wetlands and peatlands (Charman, 2002). For marshes and swamps, aboveground productivity ranges from 125 - 2590 g $m^{-2}yr^{-1}$, while belowground productivity ranges from 150 – 1800 g $m^{-2}yr^{-1}$ (Bradbury and Grace, 1983; Mitsch and Gosselink, 2000; Charman, 2002). In peat bogs and wet tundra, aboveground productivity range from 40 - 1400 g $m^{-2}yr^{-1}$, while belowground productivity range from 70 – 1460 g $m^{-2}yr^{-1}$ (Reader and Stewart, 1972; Bradbury and Grace, 1983; Van Cleve et al., 1983; Thormann et al., 1999; Mitsch and Gosselink, 2000; Vitt et al., 2000; O'Connell et al., 2001; Charman, 2002). Bryophyte production may be a significant contributor (30-50%) to total primary production in many poor fens and bogs. Aboveground production for bryophytes ranges from 5- 1660 g m$^{-2}yr^{-1}$ (Bradbury and Grace, 1983). Production is affected by light and nutrient availability, as well as by soil temperature, soil moisture, and soil aeration.

Sphagnum

As mentioned above, bryophyte production can be an important component of total primary production in many peatlands. Among bryophytes, *Sphagnum* spp. have a key role in controlling peat accumulation (see section **5.4** and **9.0** for further details on *Sphagnum* properties). *Sphagnum* spp.

production and growth (in height and lateral) rates are highly variable across the northern hemisphere (Appendix 2). Height growth can vary from less than 1 to 60 mm yr^{-1}, while *Sphagnum* production ranges from 3 to 250 g C m^{-2} yr^{-1}. *Sphagnum* is known as a paludifier in cool humid areas because of the expansion of carpets from peatlands into the surrounding forest (Andrus, 1986). Noble et al. (1984) have shown the capacity of *Sphagnum girgensohnii* to expand, as they measured a 2% increase/year in patch area in 7 plots in Alaska. An experimental trial held by the Ministry of Natural Resources in British Columbia showed an increase of approximately 20 % in *Sphagnum girgensohnii* cover during a single year (Asada et al., 2003a). This variability in growth and productivity is explained in part by the different niches occupied by different *Sphagnum* spp. (Vitt and Slack, 1984). Consequently *Sphagnum* productivity and distribution are influenced by mean temperature, water table level (Noble et al., 1988; Moore, 1989; Gerdol, 1995; Grosvernier et al., 1997), light availability (Bisbee et al., 2001) and peat characteristics (Grosvernier et al., 1997). For example, under conditions of average rainfall, lawn *Sphagnum*, section Cuspidata, grow at a faster rate than *Sphagnum*, section Acutifolia, on hummocks. Under low rainfall conditions, with lowered water tables, lawn growth can be severely reduced, whereas *Sphagnum* growth on the hummocks can be maintained at normal levels (Moore, 1989). Hummock species (*ex. Sphagnum fuscum, capillifolium*) form dense mats of individuals capable of retaining water in the spaces between individuals, allowing the hummock to remain relatively moist during dry periods. In comparison, species in hollows (*e.g. Sphagnum fallax*) have lower water retention abilities than hummock species, and may become quite dessicated under water stress.

DECOMPOSITION

Soil humus is composed of the recalcitrant products of decomposition. Decomposition of humus occurs in 2 phases. During the early stages, there is a rapid loss of solubles and a fairly rapid loss of cellulose. During this early phase, carbon is relatively available and nutrients are limiting and there is an immobilization of the limiting nutrient (usually nitrogen). Once the litter reaches the second stage, it can be considered as humus. This later stage coincides with a net loss of lignin and net nitrogen mineralization (Bridgham et al., 1998; Prescott et al., 2000). Decomposition rate in peatlands is controlled by climate, soil temperature, soil moisture, soil aeration, soil pH, *Sphagnum* properties, chemical and physical characteristics of litter and peat, substrate quality and abundance and composition of soil microbial and faunal communities (Clymo, 1965; Heinselman, 1970; Van Cleve et al., 1983; Damman, 1988; Szumigalski and Bayley, 1996; Charman, 2002). Thus, as recently produced litter and new peat in the acrotelm are exposed to oxygen and varying water levels, they are subject to a higher decay rate. Once in the catotelm, the decay rate declines sharply and becomes independent of minor climatic fluctuations. Decomposition in the catotelm occurs primarily in anaerobic conditions, producing CH_4 and CO_2 (Clymo et al., 1998). The rate of peat transfer from the acrotelm to catotelm, or the acrotelm residence time, therefore largely determines net peat accumulation (Yu et al., 2001b). Several authors have suggested that peat accumulation is controlled by slow decomposition rates rather than rapid net primary production rates (Clymo, 1965, Damman, 1979, 1986; Malmer, 1986; Farrish and Grigal, 1988). However, this affirmation is not entirely true. High peat accumulation rates in bogs appear to be maintained by low rates of decomposition, but peat accumulation may occur in rich fens because of greater production. The equilibrium point is reached earlier in fens than in bogs (Thormann et al., 1999). This equilibrium is reached when addition from the acrotelm into the catotelm equals material lost from the catotelm due to decomposition (Clymo, 1984; Clymo et al., 1998; Thormann et al., 1999). In addition, Bridgham et al (1998) suggest that, over time, the decay rates of organic matter in different wetland communities converge towards a common rate.

ACCUMULATION DATA

Appendix 1 shows current (ARCA) and past (LORCA) carbon (C) and peat accumulation rates according to peatland type, age, topography, and geography. C accumulation rates range from less than 5 up to 260 g C m^{-2} yr^{-1} and peat accumulation from 0.06 to 3.8 mm yr^{-1}. These long-term estimates of peat accumulation may not take into account repeated peat fires, which could remove surface layers, thereby underestimating actual peat accumulation rates. Differences in long-term comparisons of peat accumulation may depend on whether mass or height increment is used and what dating technique is employed (^{210}Pb vs ^{14}C). A good example of the difference in the use of height versus mass as units is Reader and Stewart (1972) (Appendix 1) who found peat mass accumulation rates were higher in the lagg (depressed margin of a peatland, generally wetter and often contains open water) (26.7) than the nearby bog forest site (18.8) or muskeg (13.9). However, the bog forest had a greater height increment (0.41) than the lagg (0.28) or muskeg (0.26). The accumulation of C as well as peat is a function of production and decomposition influenced by allogenic and autogenic processes as well as compaction (Malmer and Holm, 1984) and subsidence. Peat thickness and long-term accumulation rates are however imperfect indices of the present capacity of a site to gain carbon, as they do

not take into account variations in bulk density, carbon content, the declining rate of net accumulation in mature bog or the remnant status of some peat deposits (Kobak et al., 1998; Vitt et al., 2000).

MODELLING

While long-term peat or C accumulation rates can be estimated using peat cores, developing models of peat accumulation can help to understand processes and to predict peatland response to forest management or global warming. There are many models, in the literature that can be roughly grouped into two basic categories: conceptual models and simulation models (Yu et al., 2001a). The first group describes the relationship of different processes and can be used to examine the consequences of various assumptions, while the second is built upon the conceptual model, and its purpose is to mimic and reproduce the behavior of real world systems, through changing a parameter or a set of parameters over time (Yu et al., 2001a).

In peatland ecology, a number of studies have used Clymo's model to investigate rates of peat accumulation in different deposits (Clymo, 1984; Charman, 2002). Clymo's (1984) approach applies an exponential decay constant (k value) to the entire acrotelm (0.04-0.004), and a separate decay constant to the entire catotelm (10^{-5}-10^{-7}). One notable conclusion of Clymo was that long-term peat accumulation depends primarily on 2 parameters: the rate of transfer of peat from the acrotelm to the catotelm and the decay rate (k value) within the catotelm. Later, Clymo et al. (1998) further developed and extended his model, testing different proportional decay rates: α (1) constant model (constant α); (2) linear model (α decrease linearly as a function of proportion of original dry mass remaining); and (3) quadratic model (α decrease quadratically with proportion remaining).

Gorham et al. (2003) and Yu et al. (2001b) concluded that there is evidence that the autogenic Clymo model of declining rates of peat accumulation over time (Clymo, 1984; Clymo et al., 1998) is less applicable in North America. One explanation for these results may be that some sites are more susceptible to allogenic influences such as fire and drought, which could make production and decay rates more variable (Belyea and Warner, 1996). Thus, the implication of these results is that the steady state of production-decay for acrotelm peat assumed by Clymo's model is not realistic, as hummocks and hollows would develop unsustainable height differences. A more variable rate of decay in the acrotelm and the catotelm would be more probable. For example, Yu et al., (2001b) and Vitt et al. (2000) have reported acrotelm (0.017 yr^{-1}) and catotelm (0.43 and 2.6 x 10^{-4} yr^{-1}) decay rates for some sites in western Canada. Feedbacks between *Sphagnum* growth, decay, and moisture restrict peat accumulation overt time, and create a stable equilibrium with local climate within a decade. This feedback appears responsible for the long-term maintenance of bog hummocks and hollows and their adaptation to changing environmental conditions (Nungesser, 2003)

Recently, new models have been developed but none of them are complete. Some 1) do not have an interaction between the acrotelm and the catotelm (Hilbert, 2000), 2) are proposed only for regions with an oceanic climate (Clymo, 1984; Hilbert, 2000), 3) are only built to evaluate C balance during the last 100-200 yr (Wieder, 2001), 4) assume constant vegetation production and decomposition (static) (Frolking et al., 2001), or 5) are limited to reconstruction of a bog (Korhola, 1996). In Canada, Yu et al (2001a) have proposed a new model, still in development, which is dynamic and that will

consider peatland initiation from mineral soil, to lateral expansion and vertical growth.

As modelization is not the objective of this review, this section is not exhaustive; however, we consider modelization as a very useful tool for forested peatland mangement. In spite of this, research still needs to be done. An ideal model would be applicable to all peatland types and all regions should also be dynamic instead of being static and finally this model should also include autogenic as well as allogenic factors. This model should also be applicable to short-term as well as long-term predictions. Estimation of aboveground and belowground productivity for vascular and non-vascular plants also need to be improved. In the short-term, we suggest that resources should be allocated to develop a model specifically for the characteristics and history of the forested peatland located on the Clay Belt.

5.4. Paludification and tree productivity

Paludification has been associated with forest disappearance (Crawford et al., 2003) and reduced tree productivity in black spruce forest (Rigg, 1917; Vincent, 1965b; Heilman, 1966; Larsen, 1982; Reiners et al., 1970; Van Cleve et al., 1983; Munson and Timmer, 1989a; Paré and Bergeron, 1995; Payette, 2001; Boudreault et al., 2002; Harper et al., 2002, 2003). However, there is some disagreement concerning the definition of site productivity. In its simplest form **site productivity** is the ability of a given site to accumulate biomass during a period of time, commonly expressed in kg ha^{-1}yr^{-1}. This is essentially NPP (net primary productivity), and represents the base on which all other trophic levels obtain energy (Morris, 1997). On the other hand, **forest productivity,** refers to the growth and maintenance of all or any part of the assemblage of plants and animals (all trophic levels) that exist in a forested ecosystem (Morris, 1997). Finally,

our concern with paludification regards **timber production.** Timber production or tree productivity represents that portion of net primary productivity that is partitioned into commercially useable biomass (Morris, 1997). These different types of site productivity will be addressed in this review.

In the extreme, paludification is believed to sometimes cause forest retreat, as in many areas the treeline is now at latitudes where thermal conditions are adequate for tree growth but regeneration is prevented by peat growth (Crawford et al., 2003). But in a short-term perspective, black spruce growth is affected by paludification in three ways: 1) accumulation of organic matter, 2) increase of the water table level and 3) colonisation of mosses and *Sphagnum* spp. (see also **section 9.0. Promotion of paludification** for further details). However, these factors can be explained in terms of soil aeration and nutrient availability. Deep peats do not limit growth *per se*, but are related to poor growth because peat accumulation is favoured under conditions of low nutrient availability and low organic matter decomposition (Heinselman, 1963; Gorham, 1957; Tilton, 1978). The existence of occasional good stands on deep peat illustrates that a thick peat layer is not necessarily limiting (Heinselman, 1957a; 1963). Similarly, edaphic factors such as site wetness, depth of water table, water table fluctuations and microtopography (Hörnberg et al., 1997; Roy et al., 1999), do not in themselves control growth or nutrient availability in peatland ecosystems. These factors, however, do influence soil aeration, which in turn affects the processes controlling nutrient cycling and primary production.

ORGANIC MATTER

Heilman (1968) reports that total quantities of P, K and Mg in available and exchangeable forms are consistently lower in *Sphagnum* soils. Moreover, peat accumulation results in a distribution of nitrogen in the soil that is unfavorable for its mineralization. Instead of being concentrated in the surface horizons of the soil, the bulk of the nitrogen becomes located in deeper and colder layers (Heilman, 1966). Accumulation of organic matter through slowed decomposition would be associated with increased soil acidity through incomplete oxidation of organic matter, and with accumulation of acidic end-products of microbial metabolism. Under these conditions, nitrification would be inhibited and ammonium would be the principal form of inorganic nitrogen available for plant use (Van Cleve and Alexander, 1981). It should be noted that even if the depth of peat is not always related to low tree growth, Heinselman (1963) reported a common characteristic in poor sites in Alaska: a thick accumulation of poorly decomposed *Sphagnum* in the uppermost layer. We observed the same phenomenon on the Clay Belt. Damman, (1988) reports those periods of fast *Sphagnum* growth produces poorly decomposed peat with a low N content whereas periods of slow growth increase decay and raise the N concentration of the peat. It would be appropriate to investigate in the field the importance of the ratio fibric/humic on black spruce growth and also try to relate this ratio to the topography. We might expect more fibric peat in basins whereas humic peat would be found in secondary peat (natural succession or where lateral expansion occurred).

Watt and Heinselman (1965) suggested that higher levels of nitrogen on good sites may be attributed to nitrogen fixation by speckled alder, more rapid decomposition of litter, (indicated by less peat accumulation),

movement of enriched water, and proxiomity of mineral subsoil. Data from the Clay Belt have shown that total volume production in mixed stands was, as a rule, slightly greater than in pure black spruce stands. This suggests that managing black spruce on some sites would likely result in smaller loss in total volume, but would definitely result in an increase in commercial volume (Whynot and Penner, 2000). In addition, Paré et al (1993) reports with the exception of N, that the availability of all nutrients declined with time-since-fire in the southern boreal forest in Abitibi. They suggest that the maintenance of hign N-mineralization rates could be explained by the persistence of *Betula papyrifera* in late successional stages. They also proposed that the presence of deciduous trees may limit the development of moss cover. Moreover, in the same area, Légaré et al. (2004) have shown that the presence of aspen (between 0-41% basal area) also had a positive effect on black spruce growth (dbh and height). They suggested that presence of aspen enhanced soil fertility by its influence on nutrient availability.

WATER TABLE

Black spruce foliar N and S concentration, needle length, and periodic annual increament in basal area are positively correlated with depth to water table showing the importance of aeration for roots and microbial activity (Lieffers and Rothwell, 1987b). In Ontario, across different peatland types, Jeglum (1974) reports that moisture-aeration balance and nutriment regime explain a large proportion of the variation in vegetation and tree growth on black spruce peatlands. Root growth, elongation and biomass are controlled by soil temperature (Tryon and Chapin, 1983) and correlated with depth of the water table level (Lieffers and Rothwell, 1986). Low oxygen concentration in the rooting medium due to waterlogging reduce root and shoot growth

of trees by affecting many plant physiological processes, including net assimilation, transpiration, stomatal conductance, carbohydrate metabolism and respiratory activity (Islam and Macdonald, 2004).

SPHAGNUM
Grigal et al (1985) have shown that total productivity of all strata of six ombrotrophic sites approached that of upland sites in the same region. Although bog types have lower total woody productivity than the upland sites, the ground layer composed of mosses, partly compensated for this loss and substantially increased the NPP of these ecosystems. By promoting cold soil temperatures and in some areas permafrost, mosses and specially *Sphagnum* spp. reduce decomposition rates, microbial activity, and nutrient availability (Payette, 2001a; Taylor et al., 1987; Bonan and Shugart, 1989). The reduction in mineralization may be due to immobilization but also to the chemical composition of *Sphagnum* litter that contains refractory cell-wall material, or toxins produced by living *Sphagnum* plants (Weber and Van Cleve, 1983; Verhoeven et al., 1990).

Thus, forest management that will try to control or reverse paludification in forested peatland will need not only to eliminate *Sphagnum* but also need silvicultural treatments that will arrest the declining nutrient availability founded under the natural succession in forest.

5.5. Paludification and forest management in the literature
Few studies were found in the literature concerning paludification and forest management. The only one, to our knowledge, is an experiment held in British Columbia by the Ministry of Natural Resources (Banner and Shaw, 2001; Banner and Smithers, 2001; Banner et al., 2002;

Asada et al., 2003a; Asada et al., 2004). This work on paludification is part of a multidisciplinary study called HyP[3] project (Pattern, Process, and Productivity in hypermaritime forests). The effect of forest management on paludification is a particularly concern for the hypermaritime north coast of British Columbia. But currently, forestry researches in peatland ecology are not concerned by paludification and its effect on site productivity.

5.6. Paludification and the Clay Belt
Generally, it is quite difficult to distinguish the original cause of peatland formation in a specific area. It is also hard to tell apart what proportion of peat formation is caused by chronosequence vs toposequence. Peatland stratigraphy is considered as an essential tool in understanding processes and patterns responsible for peatland formation. But, very few tools exist to predict where peat formation will occur. And as we have seen above, there are important factors, both allogenic and autogenic, which iniate and regulate the formation of peat: climate, topography and surficial deposits.

With respect to the Clay Belt, during the last 2350 years, the climate has cooled down and become more humid, which has likely contributed to the establishment of peatlands (Potzger and Courtemanche, 1954). The current climate is also very favorable for peat accumulation (Jeglum, 1985; Sundström, 1992). In the northeastern part of the Clay Belt, the mean annual temperature recorded is 0.1°C (-19°C in January and 16°C in July) (Environment Canada, website) with mean annual precipitation of about 892 mm of which 30 % falls as snow. The average number of degree-days (> 5°C) is 1249 and the period without frost-free days is 64 days although freezing can occur occasionally throughout the growing season. In the southern part of the Clay Belt (close to Iroquois Falls) the mean annual temperature

recorded is 0.9 °C and mean annual precipitations approximately 776 mm. The potential evapotranspiration in this area ranges from 400 to 450 mm per year.

The topography of the Clay Belt, which gives the impression of flatness, is in reality broken by gentle undulations or ridges (Vincent, 1962), which probably facilitate peat accumulation (Figure 1). In small depressions, water stays within the basins creating waterloggedconditions. Consequently, when these small depessions are filled by peat, lateral expasion occurs on flat topography or onto upland sites, and thereby increasing the surface area occupied by peatland. On the Clay belt, the main mineral deposit is clay, which prevents water percolation and therefore facilitates peat initiation. In western Canada, peat stratigraphy is a well know tool to study peatland (Appendix 1), but in eastern
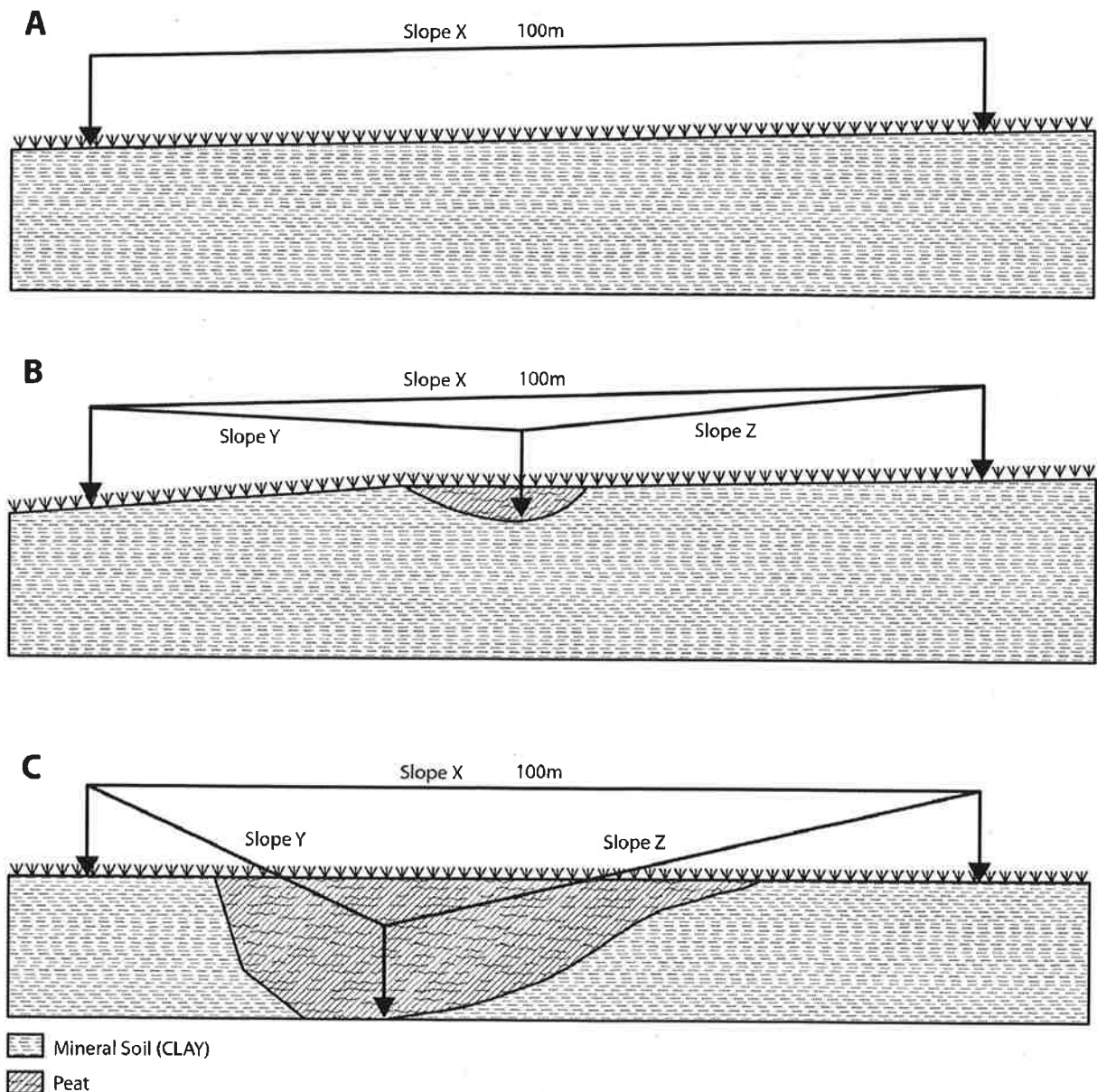

Figure 1

Canada and on the Clay Belt, there has been very few peat profiles sampled. Obviously, there is a need for more peat stratigraphy to learn more 1) on cause of peat initiation and 2) about the factors (allogenic and autogenic) that have been important in regulating peat accumulation. This knowledge will be valuable for forest management and in the prediction peat and C accumulation in a global warming perspective.

Major paludification and development of *Sphagnum*-dominated peatlands throughout the continental and temperate interior Canada occurred between 4000 and 6000 yr BP (Halsey et al., 2000). The oldest basal peat dates (6800 yr BP) at an elevation above sea level of 240 m and the youngest date (3800 yr BP) at 60 m above sea level have been reported for the Clay Belt (Dionne, 1979). Dionne (1979) also documented a delay of about 400 to 900 yr between forest occupation and the establishment of peat accumulation. Although it is very difficult to predict future areas that will be affected by paludification, it is clear that upland sites are vulnerable to lateral peat expansion in the context of forest management and future climate change (see section 11.0). On the Clay Belt, control, reduction or reversal of paludification by natural processes seems to be unlikely in a short-term perspective, while human interventions may have an impact (see section 10.0). Control of paludification and tree improvement are the only possibilities in limiting the effect of paludification of tree productivity in this humid basin.

5.7. Knowledge gaps regards to paludification

Particularly in the Clay Belt, very few experiments have measured the production of peatlands and more specifically *Sphagnum*. More studies should also evaluate the rate of peat accumulation for each peatland class of the Clay Belt in order to permit modelling, as it would be assist in the development of predictions concerning peat accumulation rates following natural and human disturbances (and climatic change). Fundamental research on peatland history with respect to topography, disturbance and climate using approaches such as paleoecological reconstructions, which have seldom been used in the Clay Belt, should also be encouraged. Paleoecological reconstructions are necessary in order to understand and predict the effects of natural and human disturbances on peat accumulation and to differentiate paludification caused by chronosequence vs toposequence. Furthermore, a better knowledge of the topography, the thickness and degree of decomposition of the peat layer will facilitate the location of small depressions, as well as primary peat growth and lateral expansion. This information is essential to facilitate forest management.

6.0. Black spruce requirements

Black spruce is presently considered the main tree species growing on mineral and organic peatlands. Black spruce is also the most important tree species present in forest stands prone to paludification. The main topic of this review is clearly paludification. However, concerns on paludification are quite related to possible reduction in black spruce growth. For this reason, a short section on black spruce requirements follows.

SEEDBEDS AND MICRO-SITES
It is well known in the literature that *Sphagnum* moss and *Sphagnum* peat provide better substrates for black spruce seed germination and seedling survival than do feathermosses, mainly because of better moisture and water supply (Roe, 1946, 1949; Heinselman, 1957a, b; Jarvis and Cayford,

1961; Vincent, 1966; Johnston, 1975, 1980; Jeglum, 1979; Ohlson and Zackrisson, 1992; Groot, 1994). *Sphagnum* moss is an excellent rooting medium due to its extreme porosity, large water-holding capacity, and good aeration. Living *Sphagnum*, *Sphagnum* peat, mineral plus organic mixed, mineral B and C horizons, pioneer moss, compacted *Sphagnum*, thin F, thin H, shallow mineral soil, displaced *Sphagnum*, poorly decomposed *Sphagnum* and sheared *Sphagnum* have also been reported as good receptive seedbeds for black spruce (Jarvis and Cayford, 1961; Jeglum,1984; Fleming and Mossa, 1994; Groot and Adams, 1994). It should be noted, however, that following soil disturbance black spruce seedlings colonized more frequently *Polytrichum sp.*than minerals soils (Linteau, 1957). We can observe frequently the same phenomenon after wildfire on the Clay Belt (*Personal observations*). However, with the number of good seedbeds listed, there is confusion and contradiction in the literature. For examples, *Polytrichum* has been qualified as both good and bad seedbeds. Thus, we think that this issue sould be clarified.

Although, *Sphagnum* moss is a good germination seedbed, once the root systems of seedlings become established, nutrient supply becomes more important than water supply to seedling growth. Furthermore, black spruce seedling growth is reduced because of smothering by the faster growing *Sphagnum* moss (Roe, 1949, McEwen, 1966; Arnott, 1968; Johnson, 1977; Jeglum, 1981; Wallén et al., 1988; Van Breemen, 1995). The literature suggests that growth of black spruce is better on feathermoss than on *Sphagnum* (Wilde et al., 1954). Few studies have been conducted on the growth of black spruce on various substrates. Arnott (1968) grew black spruce on *Pleurozium schreberi* and on *Sphagnum capillifolium (synonymous : S. nemoreum)*. His results, although not

significant, showed higher shoot weights and higher foliar level of P and lower level of K on *Pleurozium schreberi*, than on *Sphagnum capillifolium*. Jeglum (1981) also grew black spruce on *Pleurozium schreberi* and also *Sphagnum fuscum, S. angustifolium, and S. magellanicum*. Seedling grew significantly better on *Pleurozium schreberi* than on *S. angustifolium and S. fuscum*. While *S. magellanicum* produced seedling crown length closer to those of *Pleurozium*. In general, the better growth of black spruce seedling on *Pleurozium* was related to a better nutrient supply (Wilde et al., 1954, Jeglum, 1981; Klenk, 2001). However, Jeglum (1979) showed that black spruce growth was better on *Pleurozium* than on *Sphagnum* only when there was a daily watering. Consequently, *Pleurozium* is a better growth substrate but it also forms a rather dry seedbed in the field which can be a disadvantage for germination (Arnott, 1968; Wood and Jeglum, 1984). Deluca et al. (2002b) recently reported that *Pleurozium schreberi* was a host for an associative or symbiotic *Nostoc sp.* that has a N fixation potential of 1.5-2.0 N ha^{-1}yr^{-1} which could significantly contributed to the total N balance of boreal ecosystems. In addition, Klenk (2001) also report that organic matter under feathermoss have greater rates of decomposition and nitrogen mineralization than organic matter under *Sphagnum* mosses and thus their presence results in faster nutrient cycling in forested peatland. O'Connell et al. (2003), suggest also that soil organic matter decomposition is slower in black spruce-*Sphagnum* community than in black spruce-feathermoss community.

Linteau (1957) observed a tendency for spruce to have a more rapid height growth on moss-covered soil than on bare mineral soil. Differences were small but it was noted that the stocking was much lower on bare mineral soil. In opposition, Vincent (1965a) reports better growth on mineral soil than

moss duff. Nevertheless, investigations in the field are necessary to evaluate the quality of different substrates for black spruce growth following natural (mainly wildfire) and mechanical disturbances (harvesting and mechanical site preparation). Finally, seedbed quality is not synonymous of good growth and these properties should be evaluated separately. For example, after a wildfire in a peatland, the organic layer becomes very warm and dry and forms a crust. These conditions prevent germination thus black spruce growth is unknown on this substrate.

NUTRIENT REQUIREMENTS AND HYDROLOGY
Although, black spruce is well adapted to grow on wet and low nutrient sites (Van Cleve et al., 1983; Viereck et al., 1983), experimental studies have shown positive effects of fertilization on black spruce growth (see section peatland fertilization). Lowry, (1975) reports that N and P limit mostly tree growth over a broad range of site conditions. Deficiency and optimal levels for black spruce are for N, P and K are 1.20 % and 1.50 %, 0.14 % and 0.18 % and 0.30% and 0.40 %, while for Mg and Ca deficiency and optimal levels are 0.10 % and 0.15 %, and 0.09 % and 0.12 % (Swan, 1970). Studies show that black spruce growth is related to drainage (Stanek, 1961; Lowry, 1975; Lieffers and Macdonald, 1990) and bulk density (Prévost and Bolghari, 1990) showing the importance of aeration for roots (Lieffers and Rothwell, 1987b). The root systems of black spruce is dominated by a horizontally spreading lateral roots and occurred mostly within 3-20 cm of the surface (Strong and La Roi, 1983; Personal observation, 2003). To prolonged soil flooding black spruce seedling black spruce have developed adventious roots (LeBarron, 1945). Lastly, black spruce is known as a shade tolerant species, but it develops better in full light than in reduced light (Vincent, 1965a; Wang and Macdonald, 1993).

KNOWLEDGE GAPS FOR BLACK SPRUCE
The evaluation of seedbed quality and its interaction with environmental factors should be considered for black spruce. Moreover, a lot of effort has been devoted to the study of black spruce germination, and we think that more efforts should be placed on substrate quality for tree growth in relation to the environmental factors particular to the Clay Belt.

7.0. Wildfire-Logging

Disturbance events on the ClayBelt are not limited to fire, and windfall, insect outbreaks and other disturbances do occur in the boreal forest on the Clay Belt; however the discussion in the following section will be limited to wildfire because fires have been the dominant natural disturbance affecting the structure and composition of the Clay Belt landscape. Fire reconstruction studies on the Clay Belt have indicated that the average age of the forest (average number of years without fire) decreases from the LAMF region (172 yr), to the Abitibi west (139 yr), and Abitibi east (111 yr) regions, with a slight increase in central Quebec (127 yr) (Bergeron et al., 2001). On the Clay Belt, studies have shown that the length of the fire cycle has been increasing over time. Before 1850, the length of the fire cycle was 103 and 132 years for Québec and the LAMF respectively. This increased in length between 1851 and 1920 to 133 and 234 years, and since 1920 the fire cycle has increased dramatically to 398 and 521 years (Gauthier et al., 2000; Bergeron et al., 2001). This trend is explained in part by climate change and fire suppresion (Lefort et al., 2003), although the exact causes are still a matter of discussion (Miyanishi and Johnson, 2001; Ward et al., 2001).

EFFECTS OF FIRE AND LOGGING
While, wildfires have played a major role in the boreal forest dynamic since the last

glaciation, logging has become one of the main disturbances in the boreal forest in the last century. Consequently, in the past five decades, wildfires and logging have affected equivalent areas (Schroeder and Perera, 2002). Foresters have historically believed that from a stand perspective, clearcuts have similar effects as severe wildfires, as both initiate stands and modify the soil microclimate (temperature and moisture) (McRae et al., 2001; Simard et al., 2001). Currently, it is accepted that, while similarities exist, fires and clearcuts have distinct suites of effects on the boreal forest.

These different suites of effects can be seen in many aspects of the forest landscape and stand, including geographic scale, rotation period, structure and composition of post-disturbance stands, and effects on soils. Wildfire has several regulating factors such as weather, abundance and nature of fuels, wind, and topography. As a result, wildfire and forest harvest currently operate on different scales. Through interaction of regulatory factors, wildfires can vary in size from less than 0.1 ha to a conflagration covering thousands or hundreds of thousands of hectares. In contrast, the regulated size of clearcuts in Canada has varied through time, but has generally remained under or close to 100 ha, with 90 % under 260 ha in size (McRae et al., 2001). These differences in disturbance scale have consequences on landscape pattern. In a large-scale spatial vegetation analysis, Schroeder and Perera (2002) found that patch size was larger, and patch number was lower in a post-fire landscape compared to a post-clearcut landscape. This may relate to the greater severity of large fires compared to large clearcuts.

The rotation period of fires and harvestes also differ, which has consequences for the abundance of different forest structures on the landscape (McRae et al., 2001; Bergeron

et al., 2001, 2002). For example, the fire-return interval on the Clay Belt ranges from 139-172 yr, while harvesting frequencies, dictated primarily by the rotational age at merchantable size, typically ranges from 40 to 100 yr (Bergeron et al., 2001; McRae et al., 2001). On the Clay Belt, the current age structure has more than 50 % of the area older than 100 yr. Therefore, because the age structure of the natural black spruce stands varies from even-aged in young stands (< 160 years) to uneven-aged in older stands, with a harvesting age of 100 yr, this means that 50 % of the stand age structure (*i.e.* structures associated with stands >100 years) would disappear from the landscape (Bergeron et al., 2001; Haeussler and Kneeshaw, 2003). In contrast, stands derived from CPRS-CLAAG, an uneven-age structure from a young age (Horton and Groot, 1988; Groot and Horton, 1994; Lussier et al., 2002).

The level of soil disturbance also differs between fires and clearcuts. While soil disturbance is relatively even across the stand in clearcuts, after a fire soil disturbance severity is heterogeneous. CPRS-CLAAG may also increase soil compaction and rutting (Brais and Camiré, 1998; Harvey and Brais, 2002), and as a consequence reduce soil hydraulic conductivity. Depending on intensity and frequency, fire can partially or entirely remove the soil organic layer, the feathermoss and the *Sphagnum* layers (Lutz, 1960; Carleton and Maclellan, 1994). Moderate and severe fires have a variety of impacts on forest soils. These include an increase in soil fertility via an increase in soil temperature and decomposition rates (Lutz, 1960), an increase in soil pH and exchangeable cation availability (Lutz, 1960; Dyrness and Norum, 1983; Van Cleve and Dyrness, 1983; McRae et al., 2001; Simard et al., 2001), mineralization of immobilized nutrients (turning organic matter into ash) and reduction of the organic carbon and the

microbial biomass (Dyrness and Norum, 1983; Fritze et al., 1993; Pietikainen et al., 1993, 1995; Simard et al., 2001). Harvesting also has a great influence on nutrient cycling, but unlike wildfire logging also removes large amounts of P, K, Ca, and Mg contained in the tree biomass. These materials are mostly conserved *in situ* during a wildfire (McRae et al., 2001).

In addition, several studies suggest that the deposition of charcoal after a fire may also be favourable. Charcoal has the ability to absorb phenolic compounds and Zackrisson et al. (1996) and Wardle et al. (1998) concluded that charcoal might catalyse important ecological soil processes in early-successional boreal forests. This effect diminishes as succession proceeds, and ultimately may have important long-term consequences for stand productivity and ecosystem function, especially in forests dominated by ericaceous shrubs that are under strict fire control (Zackrisson et al., 1996; Wardle et al., 1998; DeLuca et al., 2002a).

Fires also affect the composition and diversity of the herbaceous and shrub layers (Dyrness and Norum, 1983; Aksamit and Irving, 1984; Foster, 1985; Carleton and Maclellan, 1994; Rees and Juday, 2002; Haeussler and Kneeshaw, 2003). Tree species composition and structure are also altered (Foster, 1985; Nguyen-Xuan, 1999; Nguyen-Xuan et al., 2000; Haeussler and Kneeshaw, 2003); and sexual reproduction by seedling is facilitated (Lussier, 1992). In contrast, following a CPRS-CLAAG, the understory may be affected, but with different results from fire (Zackrisson, 1977; McRae et al., 2001). Furthermore, protection of the feathermoss and *Sphagnum* layers facilitates vegetative reproduction by layering (Stanek, 1968a; Arnup, 1996). Forest health may also be degraded by forest harvest and planting via the use of inbred

seedlots in planting and the promotion of forest pests and pathogens by clearcutting compared to fire (McRae et al., 2001). However, Reich et al (2001) contest these differences between harvested and burned stands. The authors found no evidence of differing species diversity (tree, shrubs, herbaceous and bryophytes) and composition in forested stands of comparable age and forest types (Aspen; Jack pine; Black spruce) that originated after logging compared to after wildfire.

In light of these differences between fire and forest harvest, using CPRS–CLAAG and clearcutting as a harvesting methods, which result in a longer time since the last fire (for the next rotation), may reduce site productivity and promote site deterioration because of 1) enhancement of paludification (Hills and Boissoneau, 1960; Weetman, 1962b; Larsen, 1982; Brumelis and Carleton, 1988; Keenan and Kimmins, 1993), 2) stand opening (Reiners et al., 1970; Halvorsen, 2000; Dussart and Payette, 2002), and 3) the maintenance of ericaceous shrubs, plants that are well-known to inhibit black spruce growth and which have harmful effects on soil fertility (Yamasaki, et al., 2002). Second, partial harvesting is considered as a better alternative than clearcutting with respect to conservation of 1) vascular plants and bryophytes (Hannerz and Hånell, 1997) and 2) wildlife. Finally, forest roads are an element of managed forests with major environmental impacts across a full range of spatial scales aspect (Haeussler and Kneeshaw, 2003). Roads disturbance are well outside the scope of natural variability at all ecological scales.

LAYERS VERSUS SEEDLINGS
Recently, layers have been accepted as adequate type of reproduction and regeneration. Some studies (Doucet and Boily, 1986; Lussier et al., 1992) showed that the wood volume (*i.e.* production) from

layers could be comparable or even larger with one coming from seedlings when the advance regeneration density before a CPRS-CLAAG is adequate (Stanek, 1968a; Morin and Gagnon, 1991, 1992; Paquin and Doucet, 1992; Ruel, 1992; Doucet, 2000). The annual growth (*i.e.* productivity) in seedlings is higher than in layers, but the initial height of the latter compensates for their lower growth (Lussier et al, 1992). Moreover, black spruce advance regeneration often responds to overstory removal with an increase in growth (Boily and Doucet, 1991; Paquin and Doucet, 1992; Pothier et al., 1995; Groot and Hökkä, 2000). Pothier et al. (1995) showed that stands with the tallest regeneration at time of release produced the largest yields for a given site quality and number of years since harvesting. Therefore, the preservation of advance growth, which is most abundant on the wettest, most nutritionally and floristically poor sites, will reduce the delay period associated with planting or seeding and will also reduced the cost associated with planting. This results in shortened rotations and increases in long-term growing stock and harvest volume (Archibald and Arnup, 1993; Arnup, 1996; Groot, 1996a). In contrast, some researchers believe that growth of black spruce regeneration is influenced by the site quality rather than by the type of reproduction (Boily and Doucet, 1993; Paquin, et al., 1998). Therefore, even though the production of the layer and seedling can be equivalent, CPRS-CLAAG may have a negative impact if it facilitates stand paludification (Larsen, 1982).

FIRE SEVERITY

The position of the water table in forested peatlands relative to the surface is of great importance when assessing the susceptibility of peatland (and to a lesser extent paludified forest) to fire, and ultimately the severity of fire (Zoltai et al., 1998). Seasonality of water table position is also important because of a direct change in fuel moisture that affects flammability (Ryan, 2002). **Surface peat fires** consume most of the aboveground biomass. The susceptibility to fire is higher in permafrost peatlands, followed by swamps, bogs and fens. The estimated biomass burned annually for surface peat fires is 6400 10^3t (Zoltai et al., 1998). Zoltai et al. (1998) estimated that the long-term average annual burn area was approximately 6420 km^2 and that the fire return period for surface fires of North American boreal peatland is between 75 and 1000 years, depending on the region and the kind of peatlands. **Shallow peat fire** burns part of the underlying peat as well as the aboveground biomass (10- 15cm). The moisture content of the surface peat and mosses determines whether the peat can ignite and sustain combustion. Zoltai et al. (1998) summarize observations of moisture content of surface peat. Their data indicate that under normal conditions, a small proportion of bogs have moisture levels at or below ignition levels ($< 25\%$ m.c.). However, the proportion of bogs with surface peat layers that can sustain combustion ($< 235\%$ m.c.) is much higher than those that are ignitable. Shallow peat fires occur more frequently in bogs and conifer swamps. Zoltai et al. (1998) indicated that in North America, based on average moisture content, about 0.5% or 6420 km^2 of the peatlands can be expected to burn annually. But, only a small 20% (1160 km^2) of this area is expected to be shallow peat fires, with the majority burned by surface peat fire. Based on the frequency of charcoal layers in peat deposits, it has been estimated that the fire return period for shallow peat fires is between 250 and 1000 years and the estimated biomass burned was 14 500 10^3t (Zoltai et al., 1998). In very droughty years or after drainage, fires can burn deep into the peat (Zoltai et al., 1998). Thus, **deep peat fire** is very rare, but peat

may burn to a considerable depth, sometimes down to the underlying clay.

Peat surface fires do not influence the long-term vegetation development of *Sphagnum*-dominated boreal peatlands, as the *Sphagnum* resprouts from the remains (Kuhry, 1994; Charman 2002). In an organic peatland, fire may only slow down the paludification process. However, in mineral wetland, paludified forest or in permafrost peatland, the effect of 1) shallow and deep fires or 2) a very high frequency of fire on the reduction of peat accumulation may become significant (Miyanishi and Johnson, 2002).

FIRE CONSUMPTION
Generally, a high rate of fire spread is reported for conifer forests (Fuel type: C-2 (Boreal spruce)). Conifers produce a greater abundance of fine fuels in the form of needles, small twigs, resinous products and small bark flakes than do most deciduous trees. Also lichens and mosses are common on the forest floor (Johnson, 1992). These live fuels dry as rapidly as dead fuels. Conifers retain more dead branches of all sizes than do deciduous trees. The crown shape of conifers also allows easy access of flame from the ground into the crown. Leaf moisture content is also higher in deciduous trees than conifers (Johnson, 1992; Johnson et al., 2003). However, forested peatlands differ from some boreal forest stands in their large surface area of *Sphagnum* and a thick layer of moist peat (duff), which reduces fire consumption.

Smoldering combustion has been recognized as the major process by which duff is consumed. Duff consumption is determined by **bulk density**, **moisture content** and duff **depth** (Dyrness and Norum, 1983; McRae, 1985; Miyanishi and Johnson, 2002). Smoldering combustion differs from flaming combustion in being a much slower,

nonflamming oxidation of a porous charforming solid. Smoldering is generally modeled as a two-step process: an endothermic process of pyrolis (thermal degradation) of the solid fuel, releasing volatiles, and forming char and an exothermic process of char oxidation. Thus, factors that explain extinction of smoldering are those that influence either the rate of heat generation by oxidation or the rate of heat transfer from the oxidation zone to the virgin fuel. The rate-limiting factor for smoldering of dry fuels is oxygen availability, which determines the rate of oxidation and hence the rate of heat generation (Miyanishi and Johnson, 2002; Johnson et al., 2003). To better predict pattern of duff comsumption both within stands and across the landscape, we need to have better hydrologic models that predict patterns of duff moisture at varying scales.

Thus, peat (as duff) combustion in peat fires is highly variable. This variability is explained in part by differences in moisture content on peatland sites. First, canopies of all trees intercept precipitation with differing efficiencies, resulting in differences in moisture inputs to duff at the scale of a meter or less (Johnson et al., 2003). Second, the interception of solar radiation decreases surface evaporation, while the interception of terrestrial radiation decreases surface cooling at night, and inhibits dew formation (Johnson et al., 2003). Third, microtopography also explains part of this variability. Benscoter and Wieder (2003) reported that organic matter lost by combustion was higher in hollows than in hummocks. They explained this observation by the fact that in dry periods, hummock species (*e.g. Sphagnum fuscum*) form a dense mat of individual capable of retaining water in the spaces between individuals, therefore allowing the hummock to remain relatively moist. In contrast, species in hollows (*e.g. Sphagnum fallax*) have lower

water retention abilities than hummock species, and may become quite desiccated under water stress.

ON THE CLAY BELT
Johnson (1992) mentioned that the mineral soil exposed by fire results in greater recruitment for most boreal trees than does a duff-covered surface. In the context of the Clay Belt, it may not be very realistic to aim for a thin organic layer. Although, mineral soil has been considered as a good seedbed for black spruce (Jeglum, 1984; Simard et al., 2001), mineral soil is a borad concept including clay, sand and silt proportions. On the Clay Belt, the mineral soil has a very high clay proportion. Consequently, during dry periods, the mineral layer becomes very hard, and prevents germination. During wet periods, depending on local topography, this low porosity substrate restricts the penetration of water, even on sloping terrain, which results in the accumulation of water in small depressions (*Personal observation*). These conditions may lead to high black spruce seedlings mortality. On the other hand, we also observed that after fire, charred (scorched or lightly burned) humus is a highly unfavourable micro-site, as a consequence of the low albedo and low density the black surface organic layers undergo rapid and extreme fluctuations in moisture content (Foster, 1985). These harsh conditions may prevent black spruce germination (Zasada et al., 1983; Engstrom and Hansen, 1985; McRae, 1985; Personal observations).

KNOWLEDGE GAPS
Estimates of the long-term frequency and average annual burn for surface, shallow and deep peat fire should be evaluated for the Clay Belt. Moreover, the issue of fire severity is very important and should try to address the question: what should be the frequency of surface, shallow or deep peat fire in order to stop paludification? We think that an experiment examining seed germination and tree growth in relation to environmental variables, should be tested on burned sites in order to investigate the low tree density following fire.

9.0. Promotion of paludification

Some harvesting systems have recently been proposed to reduce soil disturbance (rutting and soil compaction) and advance regeneration mortality. Over the last decade, CLAAG in Ontario and CPRS in Quebec, have become the most common harvesting methods on the Clay Belt. CPRS-CLAAG confines the movements of machinery to regularly spaced corridors, thus reducing overall site disturbance, favouring advance regeneration and reducing regeneration costs (Archibald and Arnup, 1993). Other harvesting systems, known as HARP (harvesting with regeneration protection) in Ontario and CPPTM (cutting with protection of small merchantable trees) in Quebec, are also used to protect small merchantable trees (diameter up to 15 cm) in multi-storeyed, uneven-aged stands (Lefort et al., 2001). These techniques 1) reduce time between harvests, 2) improve visual aspect, 3) allow habitat conservation through improved protection of residual trees, 4) allow maintenance of uneven-aged structure characteristics of older stands, and 5) reduce invasion of stands by deciduous trees (Lefort et al., 2002). While, CPRS-CLAAG currently account for over 80 % of logged areas on the Clay Belt (Lefort et al., 2002), the suitability of generalizing this type of harvesting across all ecosites has been questioned (Bergeron et al., 1999, 2002). Consequently, CPPTM-HARP has been proposed as an appropriate harvesting method in uneven-aged stands because it maintains or creates the irregular and more open structure of old-growth black spruce forests (MacDonell and Groot, 1996; Lefort et al., 2002; Deans et al., 2003). Recently,

Bergeron et al. (1999) have introduced the cohort model, which emphasizes in maintaining a forest age structure and composition (which are important to maintain biodiversity) similar to those generated by the regional disturbance regime driven by fire. This three cohort model includes three broad successional stages: even-aged-pioneer; uneven-aged and overmature; and uneven-aged, irregular or open old growth (Bergeron et al., 1999; 2001). Currently, two trial experiments are in progress on the Clay Belt. Both projects involve the utilization 1) of partial cutting treatments, including successional cutting, to create residual stand structures and compositions that resemble those of older stages; 2) of diverse harvesting treatments to maintain or generate the structural and compositional attributes of a regional forest mosaic similar to what the natural disturbance regime would produce (Lefort et al., 2002).

On the other hand, increasing concerns indicate that CPRS-CLAAG, HARP-CPPTM, and partial harvesting may led to an increase in paludification and reduction of tree growth in some boreal stands. In opposition to CPRS-CLAAG and clear-cutting, paludification should be less problematic following partial harvesting and shelterwood harvesting since the intensity of soil disturbance, the percentage of tree removed, and the amount of light available to *Sphagnum* should be lower, while the amount of rainfall interception should be higher. Therefore the combined effects of these processes and the site type considered will determine if these forest harvesting techniques enhance paludification or not. It can be suggested that the amount of canopy removed and the amount of disturbance to the soil, which are opposite to one another, are key processes in the limitation of paludification. Here will follow a short description of post-logging consequences that may facilitate paludification.

In the literature, the main post-logging effects that may lead to paludification are: 1) accumulation of organic matter; 2) watering-up; 3) increase in *Sphagnum* cover versus feathermoss; 4) increase in cover of ericaceous shrubs; 5) soil disturbance.

ORGANIC MATTER THICKNESS
As previously noted, harvesting methods that keep the soil organic matter almost intact leads to the preservation of a thick organic matter layer that has accumulated with time since the last fire. The progressive accumulation of a deep organic horizon and the preservation of the moss layer produces a cold, water-saturated environment of low pH, decreased microbial activity, and diminished availability of N and P (Heilman, 1966, 1968). Low soil temperature is particularly critical to the physiological activity of the root system. Reduced soil temperatures result in restricted decomposition and are conductive to low nutrient content because trees growing on organic substrates typically show reduced foliar level of P. N, and K and slower growth rates than comparable stands on mineral soils (Heilman, 1966, 1968)

WATERING-UP
One of the major changes following clear-cutting is the rise of the water table in the surface layer, referred to as watering-up. Watering-up has been documented worldwide (see review in Dubé et al., 1995) and recently in Canada (Berry and Jeglum, 1988, 1991a; Haavisto et al., 1988; Dubé et al., 1995; Roy et al., 1997; Jutras et al., 2002; Asada et al., 2003a; Pothier et al., 2003). The rise of the water table ranges from 4 to 22 cm (Berry and Jeglum, 1991a; Dubé et al., 1995; Roy et al., 1997, 2000a; Verry, 1997). However, Groot (1998) in an organic peatland located on the Clay Belt,

did not find evidence of disruption of surface drainage immediately after site disturbance. The magnitude of the rise of the water table is generally related to the period during which water is present near the soil surface (Verry, 1980), the depth of the original water table (Heikurainen, 1967, Päivänen, 1980) and the percentage of basal area removed (Heikurainen and Päivänen, 1970; Päivänen, 1980; Roy et al., 2000). In some cases but not always, a small proportion of tree removal creates a greater water table rise. Watering-up is also correlated to the soil porosity, as soils with higher porosity will have more space to absorb the excess water. Therefore the average water table rise after clear-cutting is greater on sites covered with a thin organic layer than on sites covered by a thick organic layer (Dubé et al., 1995).

The general conclusion is that watering-up is caused by a reduction in interception and evapotranspiration rates (Heikurainen, 1967). Silvicultural treatments that will maintain interception and transpiration by leaving logging debris, small trees and advance regeneration should limit water table rise. CPRS-CLAAG, HARP-CPPTM, sherlterwood methods and thinning have been considered efficient in 1) reducing water table rise after the first cut and 2) in promoting vigorous regeneration stratum that should also mitigate water table rise following the final cut (Heikurainen, 1967; Heikurainen and Päivänen, 1980; Roy et al., 1997; Pothier et al., 2003). Watering-up can also be limited by leaving debris and vegetation after logging (see review in Dubé et al, 1995).

Logging generally contributes to rutting and compaction as well as watering-up. But it is also important to note that wildfire may also 1) cause water table rise (Wilde et al., 1954; Kubiw et al., 1989; Crawford et al., 2003) favoured by lower evapotranspiration (Walter, 1977, Gorham, 1991), deposed

particles of ash and carbon into the soil profile (Crawford et al., 2003) and 3) allows establishment of *Sphagnum* spp. on the newly burned surfaces. Thus, fire may also be a factor leading to paludification.

SPHAGNUM AND FEATHEARMOSS COVERS
In the boreal forest, ericaceous shrubs and mosses are the dominating constituents of the forest floor vegetation. Moss growth and productivity are promoted by low soil temperature and high moisture content – conditions that, in turn are promoted by moss growth (Oechel and Van Cleve, 1986). Feathermosses grow best in heavy shade, and often die out and dry up after exposure by clear cutting (Groot, 1996b). In contrast, *Sphagnum* which prefers open areas, tends to thrive after clearcutting (Wilde et al., 1954; Heinselman, 1959; Groot, 1996b; Nguyen al., 2000). While feathermoss and *Sphagnum* both act as black spruce seedbeds, they also compete for nutrients with the growing seedling (Van Cleve and Alexander, 1981; Van Breemen, 1995; Zackrisson et al., 1997). Mosses are quite efficient for interception of nutrients from precipitation, throughfall, and litter decomposing on the moss surface (Oechel and Van Cleve, 1986; Laine et al., 1995). Once established *Sphagnum*, as opposed to feathermosses, make the local environment more acidic by the release of 1) polyronique acid which decreases the CEC, 2) organic acids, and 3) humic and fulvics acids during decomposition (Clymo, 1963; van Breemen, 1995). *Sphagnum* may also be able to draw up water from the water table (Bisbee et al., 2001). In addition, some *Sphagnum* species grow faster than the tiny spruce seedlings and can engulf them (LeBarron, 1948, Roe, 1949; Hörnberg et al., 1997).

Competition among bryophytes occurs in similar ways as in vascular plants. Studies of bryophyte competition suggest that competition is primarily for space, nutrients

and light (Mulligan and Gignac, 2001). The processes that allow *Sphagnum* establishment and expansion over feathermoss are still not well understood. In a short-term experiment, Mulligan and Gignac (2001) after a reciprocal transplant experiment showed that the depth to water was the most important factor for determining the distribution of *S. magellanicum, S. angustifolium* and *Pleurozium schreberi* except *S. fuscum*. *Pleurozium schreberi* exhibited the narrowest potential distribution. In addition, Mulligan and Gignac (2002) have measured after 2 yr, the competitive ability of 5 mosses species. They reported that the stronger competitor was *S. magellanicum* followed by *S. angustifolium, S. fuscum, Pleurozium schreberi* and *Ptilium crista-castrensis*. It is likely that the limited distribution of *Pleurozium schreberi* and *Ptilium crista-castrensis* are the result of both competitive exclusion by *Sphagnum* mosses and habitat limitation (Mulligan and Gignac, 2001; 2002). Although, feathermoss and *Sphagnum* are both controlled by light and water availability, temperature, and their interaction, they have different physiological and structural features that determine their physiological niche (Heinselman, 1963; Bisbee et al., 2001).

COVER OF ERICACEOUS SHRUBS
Ericaceous shrubs have been reported to increase in cover following harvesting (Groot, 1996b; Norberg et al., 1997; Dussart and Payette, 2002), although a temporary decrease might occur immediately after logging (Harvey and Brais, 2002). Higher soil moisture, and watering-up after logging may combine with an increase in light availability, and favour ericaceous growth. Ericaceous shrubs compete for light, soil water and nutrient availability with black spruce. Shrub cover also affects soil temperature and consequently soil decomposition and soil nutrient availability.

On the Clay Belt, competition with ericaceous species occurs mainly with *Kalmia angustifolia* (Inderjit and Mallik, 1996a; Inderjit and Mallik, 2002; Yamasaki et al., 2002; Wallstedt et al., 2002), and *Ledum groenlandicum* (Inderjit and Mallik, 1996b, 1997; Zackrisson et al., 1997; Prégent and Végiard, 2002). Most of the studies have examined *Kalmia* rather than *Ledum*. Based on various field and greenhouse trials, it has been suggested that *Kalmia* may impede black spruce growth by a number of mechanisms (Inderjit and Mallik, 1996a, 2002; Yamasaki et al., 1998, 2002), including (i) diminution of N mineralization, (ii) decrease in soil nutrient availability, (iii) production of allelochemicals, and (iv) interference with mycorrhizal colonization of spruce roots. At present, there is no compelling direct evidence that supports allelopathy as a mechanism by which *Kalmia* interferes with black spruce. However, secondary metabolites released into the environment may influence soil mineralization, mycorrhizae, nutrient dynamics, and soil microbial ecology (Inderjit and Mallik, 2002; Yamasaki et al., 2002).

As early as in 1948, LeBarron reported the inhibitory effects of *Ledum groenlandicum* (Labrador tea) on early growth of black spruce. *Ledum* is common in *Sphagnum* bogs and in moderately wet soil with thick humus layers. Although the interactions between *Ledum* and black spruce need to be further studied, it has been suggested that *L. groenlandicum* may interfere with black spruce growth by (i) allelopathic compound, or phenolics that could stimulate microbial activity which reduces soil nitrogen, (ii) competition for nutrient, (iii) alteration of soil chemistry, (iv) allelopathic compounds that affect spruce-mycorrhizal symbiosis, and (v) phenolics that may have directs effects on plant growth (Inderjit and Mallik, 1996b, 1997).

Obviously, there is competition between black spruce and *Kalmia angustifolia* and *Ledum groenlandicum* and further investigations are needed to determine the mechanisms by which they interfere with black spruce growth. Lastly, ericaceous shrubs may also contribute to paludification through interference with organic matter decomposition.

SITE DAMAGES

Careful logging was initiated to protect advance regeneration and to reduce soil disturbance, but this has not been completely eliminated (Groot and Haig, 1991; Groot, 1996b). It has been demonstrated in British Columbia that rutting was promoting paludification because *Sphagnum* was able to establish in the ruts (Asada et al., 2003a; Asada et al., 2004). Site disturbances may also vary according to peatland classes. For example, compaction, rutting and erosion may be more frequent in mineral wetlands, while in peatlands, rutting is the dominant disturbance. However, these site disturbances could be further reduced. An experimental trial in the UK showed that using slash roads provided an effective mean of limiting soil disturbance on sensitive deep peat and peaty gley soils, despite high trafficking intensities (Wood et al., 2003).

10.0. Control of paludification

On the Clay Belt, current harvestings techniques, combined with fire suppression and the expected reduction in fire frequency (due to climate changes), creates conditions favorable to paludification. It should be noted that the options available to forest managers is the amount and type of harvesting and not whether to burn or harvest a stand Thus, silvicultural treatments are necessary to control, reduce or reverse paludification. In the following section, drainage, fertilization and site preparation will be discussed as options to reduce paludification and increase site productivity.

10.1. Peatland drainage

The use of drainage in peatlands has been reported for quite a long time in former Soviet Union (17th century), Sweden (middle of the 19th century), Estonia (began in the 1840s), Norway (1952), Finland (1860) (Laine et al., 1995; Paavilainen and Päivänen 1995), and in USA (1920) (Averell and McGrew, 1929; Zon and Averell, 1929; LeBarron and Neetzel, 1942; LeBarron, 1948). However, drainage with the purpose of increasing tree productivity on peatland has started to be extensively used as a silvicultural technique in Russia and in Finland in the early part of the 20th century (Heikurainen, 1964). Because of this long history, drainage is well documented. Following positive results in Finland, this forest technology was imported into Canada and was experimentally used in Newfoundland (Päiväinen and Wells, 1977), Québec (Trottier, 1984), northeastern Ontario (Stanek, 1968; Payendeh, 1973a; Haavisto, 1984, Rosen, 1989), and in northern Alberta (Hillman, 1987; Hillman et al., 1990). Prior, to these trials, North American references to forest peatland drainage were occasional. Thus, most of the drainage experiments in Canada are very recent (Päivänen, 1997), even thought Canada possess large areas of peatland. Currently, about 14 to 15 millions ha of wetlands globally have been drained for forestry in the boreal and temperate zones (Päivänen, 1997; Prévost et al., 2001). The total forest drainage area is about 6 million ha in Finland, 5.5. million ha in Former Soviet Union, 1.5 million ha in Sweden, 420 000 ha in Norway, and only 25 000 ha in Canada (Päivänen, 1997). In Quebec, by the end of 1988, a total of 13 500 ha had been drained (Päivänen, 1997), but presently, 5000 ha yr^{-1} is drained (Prévost et al., 2001). On the Clay Belt, few drainage experiments

have been set up. To our knowledge, the Wally Creek area remains the main long-term drainage study (Belleau and Jeglum, 1991a, b; Roy et al., 1997).

EFFECTS OF DRAINAGE

Water table variations in forested peatlands are often small and are dependent on precipitation and evapotranspiration (Dai et al., 1974). Drainage allows the reduction of the water table level in undisturbed peatlands and of water table rise after clear-cutting. Tree productivity in natural peatlands is generally low because high water tables, cold substrate, poor aeration, excess moisture and inadequate available nutrient (Payandeh, 1973a; Lieffers and Rothwell, 1986, 1987a; Payandeh et al., 1997). Thus, the main objective of drainage is to adjust the water content of the surface soil to a level that ensures sufficient aeration for tree roots, and higher soil decomposition.

In the literature, tree growth improvement following drainage for pre- and mature stands (LeBarron and Neetzel, 1942; Stanek, 1977; Payandeh, 1973a; Hånell, 1988; Dang and Lieffers, 1989; Hillman, 1991; Sundström, 1992; Sundström and Jeglum, 1992; Macdonald and Yin, 1999; Prévost et al., 2004) as well as for seedlings (Roy et al., 1999; Jutras et al., 2002) are reported. In reducing the water table level (Belleau et al., 1992, Hillman, 1992), drainage improves soil aeration (Lieffers and Rothwell, 1986; Silins and Rothwell, 1999; Roy et al., 2000b), increases soil temperature and soil decomposition (Lieffers and Rohwell, 1987a; Lieffers, 1988; Rothwell et al., 1993; Prévost et al., 1997). It should be noted, however, that in the cold and humid climatic conditions found in Finland, Hökka et al. (1997) observed considerable cooling of peat due to intensive drainage. In Alberta, Lieffers and Rothwell (1987a, b) reported that drainage increased fine root biomass and the maximum rooting depth of black spruce

and tamarack. The improved aeration is related to the holding capacity and capillarity connection to the surface, which may change considerably after drainage due to peat subsidence (Rothwell et al., 1996). Near-surface soil temperature increases and accelerated organic matter decomposition leads to enhanced nutrient uptake and water absorption (Lieffers and Rothwell, 1987a; Lieffers, 1988; Lieffers and Macdonald, 1990; Mugasha et al., 1993, 1999; Laiho and Laine, 1994; Wells and Williams, 1996; McLaren and Jeglum, 1998). Macdonald and Lieffers (1990) have shown that trees in drained plots were characterized by higher rates of net nutrient assimilation, higher water-use efficiency, higher mesophyll conductance to CO_2, a lower ratio of intracellular to ambient partial pressure of CO_2, and higher foliar nitrogen content. The net assimilation and foliar nitrogen content were correlated with the leader growth.

Drainage also initiates subsidence on the peatland surface. At first the removal of water causes a physical collapse and compression in peat, and later, decomposition of the organic matter matrix further contributes to subsidence (Laiho and Laine, 1994). Subsidence brings a part of the nutrient stores immobilized in the deeper layers during peat accumulation back to nutrient cycling in the drained peatland forest ecosystem. In Finland, Laiho and Laine (1994) reported that N and P stores in a 0-50 cm peat layer increased with drainage age in oligo-ombrotrophic sites and remained unchanged in meso-ombrotrophic sites, even if large quantities were bound up in the increasing tree stand biomass. It suggests that these losses have been largely compensated by subsidence of the peatland surface (Laiho and Laine, 1994) and by the increased compaction and bulk densties (Minkkinen and Laine, 1998a) of peat after drainage.

Briefly, following drainage, Minkkinen et al. (1999) measured a drastic change in the species composition of the sites, especially at the minerotrophic sites, where almost all *Sphagnum* had been replaced by forest mosses. In future studies, it would be interesting to measure the germination rate of conifer trees knowing that *Sphagnum* is a good seedbed. On the other hand, *Sphagnum* is not considered to be a good growth substrate. Drainage may also influence ground frost. Ground frost can penetrate deeper in peat aerated by dewatering than in water-saturated peat of high specific heat. However, a low thermal conductivity of unsaturated peat delays thawing in spring. In these cases the beneficial effects of peat drainage might be reduced in cold climates by a significant reduction in the length of tree growth time, which is due to a drainage-induced increase in the period of ground frost (Swanson and Rothwell, 1986; Lieffers and Rothwell, 1987; Toth and Gillard, 1988). Finally, in reducing the water table level, specifically during severe drought, drainage may increase fire index and possibly fire severity. In this case, the combination of both treatments may be a very efficient way to reverse paludification particularly in mineral wetland or in organic peatland where the thickness of the organic layer is moderate.

FACTORS AFFECTING DRAINAGE EFFICIENCY
Results following drainage are highly variable. Drainage frequently gives positive tree growth results and a decrease in water table level. But drainage does not always limit water table rise after cutting on mineral (Dubé et al., 1995) and organic soils (Berry and Jeglum, 1988, 1991a). Drainage affects several processes and the effect of drainage can strongly vary according to several factors, of which here are some examples.

1) *Nutrient status*: Numerous studies, principally conducted in Fennoscandia, but also in Canada, have demonstrated that tree growth can be improved by forest drainage without fertilization, and the results are generally better on more fertile sites (Paavilainen and Päivänen, 1995). However, more generally, peatland drainage is experimented on pre-mature and mature stands and growth improvement following drainage seems to be relatively low without fertilization in these stands (Sundström, 1992; Sundström and Jeglum, 1992; McLaren and Jeglum, 1998).
Availability of nitrogen (N), phosphorus (P), and potassium (K) are major factors limiting growth of trees in natural and drained peatlands (Wells, 1991; Rothwell et al., 1993). Drainage improves soil conditions (*i.e.* aeration), but may not be sufficient to increase nutrient content or nutrient uptake. Thus, the alternative is to supplement drainage with fertilization.

2) *Peatland types*: Drainage response may also be related to peatland type (treed swamp, treed bog or treed fen) (Stanek, 1977; Hånell, 1988; Hillman, 1991; Paavilainen and Päivänen 1995; Nykänen, et al., 1997), mainly for two reasons. First, following drainage, nutrient content may decrease or increase according to wetland types (Laiho et al., 1999; Westman and Laiho, 2003). Second, as we mentioned in the definitions, bog and fen are differentiated among others by nutrient status. On the productive site (moderate to rich fen), decomposition may exceed organic matter input to the soil. However, on poorer sites (bog or poor fen), net organic matter accumulation in the soil will continue after drainage. Consequently, on poor sites, the sufficiency of nutrients for forest growth may become an issue over time, unless the influence of ground water flow through the peat deposit, about which we know very little, is significant enough to import nutrients to the rooting zone (Westman and Laiho, 2003). Thus, drainage in poor bogs

may not be sufficient to increase nutrient level signifcantly to improve tree growth.

3) *Stand and tree ages*: Growth improvement following drainage is greater in young and small compared to larger, older trees (Stanek, 1968b; Payandeh, 1973a; Hillman, 1991; Wang et al., 1985; Laine et al., 1995; Macdonald and Yin, 1999; Jutras et al., 2002; Sarkkola et al., 2003).

4) *Time since drainage and length of postdrainage measurement*: Generally, growth increase following drainage is not immediate because the limited resources are initially allocated to the development of the root system and leaf area. For black spruce, growth response following peatland drainage may take between 3 and 7 years before significant results are achieved (Dang and Lieffers, 1989; Sundström, 1992; Sundström and Jeglum, 1992; McLaren and Jeglum, 1998). In Québec, Dumais et al. (1998) report that it may take more than 10 years before positive results are observed.

5) *Site characteristics*: Characteristics such as peat depth, peat hydraulic conductivity, quality of micro-sites, microtopography and water stress may influence drainage responses (Lieffers and Rothwell, 1987a; Rothwell et al., 1993; Macdonald and Yin, 1999; Roy et al., 1999).

6) *Ditch spacing*: Soil bulk density and soil nutrient content, soil water content, soil decomposition as well as soil temperature can all vary according to ditch spacing (Wells and Williams, 1996; Prévost et al., 1997). Numerous studies show that drainage response is related to the ditch spacing (Berry, 1988; Berry and Jeglum, 1991a; Prévost et al., 1997; Roy et al., 1999, 2000b; Jutras et al., 2002) and the reduction in the water table may be inversely proportional to ditch spacing (Braekke, 1983; Belleau et al., 1992). However, in a treed fen in Alberta,

Hillman (1992) showed that drainage had made the site more hydrologically uniform and the drops in water levels were, respectively, 79, 66, 56, and 73 cm for the 30, 40, 50 and 60 m ditch spacing.

7) *Subsidence*: Changes to soil water properties resulting from non uniform peatland subsidence appear to be important in modifying the spatial distribution of soil water in the unsaturated zone. Compaction is due to several factors including physical collapse of the pore structure after the water table draw-down, enhanced oxidation processes, loss of substrate through organic decompostion, gradually increasing weight of the tree stand and accelerated input of tree roots (Hillman, 1997; Westman and Laiho, 2003). Thereby, the positive drainage effect on soil conditions may be mitigated by subsidence (Rothwell et al., 1996). However, Silins and Rothwell (1998), illustrate that postdrainage subsidence increased both the amount of plant-available soil water and the ease with which the water could be transported to tree roots. This should be beneficial to trees growing within the drained area for the reason that trees could maintain soil water uptake for longer periods during the day with less rapid decreases in soil water potential and resulting water stress limitations to photosynthesis.

FOREST DRAINAGE TECHNIQUES
To get a complete overview of drainage techniques, readers are invited to consult the following documents: Päivänen and Wells, 1978; Braekke, 1983; Berry and Jeglum, 1991a; Belleau et al., 1992; Hillman, 1992; Paavilainen and Päivänen, 1995; and Vompersky and Sirin, 1997. Briefly, to get the maximum potential from drainage, appropriate techniques are essential. These documents provide specific information on 1) water table depth targets and 2) ditches information (type, form, depth, spacing, and size).

Drainage ditches need to be maintained and cleared of vegetation (Ahti and Päivänen, 1997). Ditch deterioration may be caused by: subsidence of the peat layer, collapse of ditch walls, blocking through vegetation, slash and other obstacles and erosion (Paavilainen and Päivänen, 1995). Maintenance is essential as, when the drainage network starts to become ineffective, the trees near the ditch, which initially showed greatest growth response, will be most severely retarded in growth, and some will even die (Vompersky and Sirin, 1997).

ENVIRONMENTAL IMPACTS OF FOREST DRAINAGE

Besides improving tree growth and changes in vegetation, drainage may also have an environmental impact. The main negative effects are: loss of biodiversity, increase in runoff, increase in flooding risk, increase in suspended sediments transport in aquatic ecosystem and decrease in the quality of surface water which influences stream beds and aquatic ecosystem (mainly temperature and oxygen concentration) (Laine et al., 1995; Klove and Bengtsson, 1999; Prévost et al., 2001). Forest drainage usually results in increased in suspended sediments, mainly during ditching and high flows in the following weeks or months (Ahtiainen, 1992; Joensuu, 1997; Aström et al., 2001; Prévost et al., 2001). Changes in pH are also reported (Belleau and Jeglum, 1991b; Laine et al., 1995). In the literature, nutrient (NO_3^-, NH_4^+, Ca^{2+}, Mg^{2+}, Na^+, and S) (Prévost et al., 1999; Prévost et al., 2001), (Ca^{2+}, Mg^{2+}, Na^+, K^+, Cl^-, SO_4^-, SiO_2, NH_4^+, P, Al, Fe, Cu and Mn) (Belleau and Jeglum, 1991b), (N, Ca^{2+}, Mg^{2+}, DOC) (Laine et al., 1995), (N, P) (Klove, 2001), (N, Ca^{2+}, Mg^{2+}) (Aström, et al., 2001), (K^+, Ca^{2+}, Mg^{2+}) (Laiho et al., 1999), and (N, P, K^+, Hg, Fe and Al) (Paavilainen and Päivänen, 1995) losses by leaching have been reported frequently. Nutrient losses are caused by two

mechanisms. Drainage increases soil decomposition, and thereby soil nutrient content. In addition natural peatlands affect water quality by intercepting and partially accumulating inorganic elements, and in this manner reduces their leaching potential (Oechel and Van Cleve, 1986; Laine et al., 1995; Inisheva and Inishev, 2001). However, since ditches prevent catchment nutrient inputs from reaching the surface layer of the peatland, therefore the potential for the peatland to act as a trap for elements carried by water is lost. Instead of being filtered through peat, the water sidesteps the peatland through the ditch network (Laine et al., 1995). When drainage is combined with fertilization, nutrient losses by leaching may be amplified (Paavilainen and Päivänen, 1995). Environmental changes caused by peatland drainage also include changes in water pathways, lake eutrophication and loss or change in biodiversity (Laine et al., 1995; Vasander et al., 1997; Klove, 2001). The effect of drainage on peatland hydrology may decrease with time since drainage or remain high (Päivänen, 1997).

In Québec and on the Clay Belt, few studies have examined the environmental impacts of drainage. In the Wally Creek area, Berry and Jeglum (1991b) report following drainage in ES 11, 12 and 14, an increase in concentrations of all major ions (see above), some heavy metals, ammonium, total phosphorus, and in pH, alkalinity, conductivity, suspended solids and temperature. However, for most measures, guidelines for freshwater aquatic life were seldom or never exceed. Only for ES 11, higher values could be explained by increased decomposition of peat resulting from increased aeration (Belleau and Jeglum, 1991b). Overall, they concluded that drainage has not significantly degraded downstream or on-site water quality. Indeed, pH and alkalinity conditions were improved for aquatic life. In southeastern Québec,

Prévost et al. (1999) report that drainage increased base flow, and suspended sediments only increased during rainfall events in the weeks following ditching. They also reported significant increases in nutrient losses (see above) by leaching but specify that nutrient levels remained within acceptable limits for aquatic ecosystems.

In a global warming perspective, peatland drainage has important effects on carbon sequestration (CO_2 and CH_4). Natural northern peatlands can act as either important sources or sinks for atmospheric carbon (Gorham, 1991). Water table level controls carbon dioxide and methane emissions from peatland soils (Moore and Knowles, 1989). Generally, drainage increases CO_2 emissions as a by product of decomposition of a larger pool of decaying biomass (Moore and Dalva, 1993). Drainage may increase CO_2 sequestration in biomass via improved tree growth. In addition, recent findings in Finland have indicated that the carbon density and store in peat soil may increase after drainage for forestry, even if soil respiration has clearly increased (Minkkinen and Laine, 1996, 1998a, b; Domisch et al., 1998). This is caused by the increased organic C flow from tree stands into soil and consequent retention in the peat matrix (Domisch et al., 1998).
Studies report that drainage usually reduces CH_4 emission (Martikainen et al., 1995; Nykänen et al., 1998). To reduce or eliminate CH_4 emissions, only a small persistent decrease in the water table may be necessary (Roulet et al., 1993). In the Wally Creek experimental forest drainage site, Roulet and Moore (1995) report lower CH_4 emission following drainage. But, this decrease was partially compensated by the quite high emissions measured from drainage ditches. CH_4 emissions by ditches are correlated to density of ditches. Thus, to prevent CH_4 emissions, Roulet and Moore (1995) suggest measurements of the predrained peatland CH_4 flux, an estimate of the expected ditch CH_4 flux and the density of ditches required to effectively drain the peatland. It must be noted that Minkkinen et al. (1997) reported from a Finnish study, that CH_4 fluxes from the ditches would be a small contribution to global warming since the proportion of ditches of the total peatland area is rather small.

RECOMMENDATIONS
Currently, it seems that drainage in the eastern Canadian boreal forest should be limited to the first cohort stand following logging, since the improvement in tree growth following drainage may be relatively low in pre- and mature stands without additional fertilization. Results from Jutras et al. (2002) show more encouraging results with small and young trees. But nevertheless, it remains that there have been few experimental peatland drainage studies on the Clay Belt. Clearly, more research into the short and long term response of black spruce to drainage according to stand age, ecological types (Québec), ecosites and wetland classification (Ontario) and vegetation types. Moreover, peatlands are known to be very sensitive to disturbance and the environmental impacts of management practices on peatlands must be considered before forest drainage is employed more extensively. Besides the evaluation made by Berry and Jeglum (1991b), few works have been completed on the Clay Belt and clearly the short and long-term environmental impacts need to be assessed. Third, an economic estimation of the balance between investment cost and return is essential. In 1973, Payandeh (1973b) completed this exercise, but the current situation is different and logging in remote areas is more frequent. Costs will also vary if drainage occurs in undisturbed versus a harvested peatland. Additional costs should be added if fertilizer is necessary and for proper ditch maintenance. Fourth,

drainage increases peatland nutrient content, suggesting that the nutrient pool will suffice for the production of one post-drainage tree crop according to peatland type. But, as we mentioned previously, fertilization is sometime needed in conjunction with drainage. Thus, regularly foliar analysis might be an indicator of future nutrient soil depletion. Finally, research is also needed on the effect of drainage on tree seedbed distribution, on black spruce germination, and on advance regeneration stocking to evaluate future black spruce density and stocking.

10.2. Peatland fertilization

Low nutrient status in forested peatlands suggests that nutrient elements supplied by fertilization should be an essential tool for improving tree productivity in peatland conifers. Early fertilization experiments are illustrated by Weetman (1962 a, b; 1968) in Ontario. According to Armson's (1967) compilation, there were only two trials established before 1964 in pre-mature natural black spruce forest in eastern Canada. Thus, the literature on fertilization in forested peatland in eastern Canada is quite recent. The aim of fertilization is to improve soil nutrient status and humus quality and, thereby tree growth and site productivity.

EFFECTS OF FERTILIZATION

First, as we mentioned previously, there is a clear correlation between peatland type and the concentration and amount of certain nutrients. For example, it is expected that bogs have lower nutrient contents than rich fens. The growth of tamarack and black spruce in natural peatlands in Canada is more often limited by nitrogen and phosphorus than by any other nutrient element (Macdonald and Lieffers, 1990; Mugasha et al., 1991, 1993). Consequently, before any fertilization, it is highly recommended to proceed with a soil and foliar analysis in order to have a nutritional diagnosis and to be able to indicate which nutrients and amounts are needed on different site types to increase tree growth.

In the literature, tree growth improves following fertilization (Weetman 1962a, b; 1968, 1971, 1975; Morrison and Foster, 1979; Morrison et al., 1976; van Nostran, 1979; Alban and Watt, 1981; Foster et al., 1986; Paavilainen and Päivänen, 1995; Wells and Warren, 1997; Gale et al., 1998; McLaren and Jeglum, 1998; Turkinton et al., 1998). In northern Ontario, Weetman (1962a, b) after fertilization (max. of 450 kg ha^{-1} of N) measured an increase in the average leader growth over the control of up to 40 % (from 25.2 to 36.6 cm) two years after treatment. In two poor site peatlands in Minnesota, Alban and Watt (1981) found an important increase in height and diameter growth following fertilization by hand (672:294 Kg ha^{-1} NP). Maximum height growth response occurred in the first or second year following treatment at which time the height growth for the maximum treatment in trial 1 was three times (from 6 to 20 cm yr^{-1}) the control and in the trial 2 was 2.5 times (from 10 to 24 cm yr^{-1}) the control. In their NP treatment, the increase in diameter growth was three times that of the controls during the first five years following fertilization. Grossnickle (2000) mentioned also for northern spruce species, the importance of early fertilization on recently planted seedling to reduce the nutrient stress and to improve early root development.

On the Clay Belt, Sundström (1992) and McLaren and Jeglum (1998), have fertilized (manual application of 150:100:100 kg ha^{-1} NPK) in ES 11 and ES 12 in the Wally Creek area. Their results show significant growth and yield responses (DBH increment) following the fertilization treatment. In both ES 11 and ES 12, the largest foliar macronutrient increase was by

P, suggesting that this element may be generally largely limiting in boreal peatland systems (Morrison et al., 1976; Alban and Watt, 1981; Munson and Timmer, 1989b; Mugasha et al., 1991, 1993), or that improvement due to fertilization were more prolonged for this element than for N or K (Weetman, 1971, 1975; Foster et al., 1986; Wells and Warren, 1997).

Tree growth improvement is induced by different changes in tree physiology and soil nutrient content. First, Mugasha et al. (1999) show in a short-term experiment that fertilization changed the phenology of needles, the seasonal foliar nutrient patterns and status, and fluxes.

Paquin et al. (2000) also report that fertilization significantly improves the water and nutrient status of slow-growing layers and enhanced their photosynthetic capacity. Two growing seasons after fertilization, fertilized trees (layers and seedlings) had higher net photosynthesis and maximum capacity of Rubisco for CO_2 fixation, as well as higher stomatal conductance, and higher water use efficiency. Additionally, fertilized trees had higher predawn and midday shoot water potential. They concluded that physiological changes of the leaf in combination with increased leaf area and root biomass explained the large growth response of the layers reported by Paquin et al (1998). Second, increases in i) nutrient foliar concentration and content, ii) nutients return through litterfall, iii) unit needle mass, iv) change in nutrient retranslocation (Weetman 1962a, b; Munson and Timmer, 1990, 1991; Mugasha et al., 1991; 1993; 1996) and v) needle length and weight (Alban and Watt, 1981) were also reported following addition of fertilizers. It should be noted, that even with tree improvement following fertilization, trees may be still under deficient levels (van Nostran, 1979; McLaren and Jeglum, 1998). Third, higher soil nutrient content can be attributed by direct addition of nutrient but also because

of higher soil decomposition and microbial activity (Wells and Williams, 1996). Fourth, fertilization may increase biological drainage by increasing tree stand growth and thereby interception loss (Päivänen, 1972; Paavilainen and Päivänen, 1995). This leads to a lowering of the groundwater level. Transpiration by tree stand and ground vegetation is probably also intensified. Fifth, besides field fertilization, in forestry nutrient loading in nursery fertilization is also suggested to build up plant nutrient reserves (Timmer and Munson, 1991; Grossnickle, 2000).

Few studies on the effect of fertilization on the understory exist. In northwertern Canada, Turkinton et al., (1998) report rapid changes in species composition in reaction to fertilizer. Graminoids and some dicots increased in cover, while other dicots, some species of dwarf shrubs, and some bryophytes and lichens declined. Also, in poor bogs in Minnesota, Alban and Watt (1981) measured a reduction in *Sphagnum* cover one year after fertilization. However, within 10 years after the treatment, the *Sphagnum* cover was back to pretreatment levels. Shrub biomass was increased by fertilization and *Ledum* increased markedly at the expense of *Chamaedaphne* (Alban and Watt,1981). Heinselman (1963) suggest that *Chamaedaphne* is an indictor of poor black spruce stands. Even if *Chamaedaphne* is adapted to low levels of nutrient supply, Bartsch (1994) reports subsequent to fertilization an increase in the production of vegetative and reproductive tissue, and an increase in content of P in shoots. Bartsch (1994) also reports an increase in *Sphagnum* productivity in response to addition of N, P, and K. Growth of above and belowground component of *Kalmia angustifolia* and increase in nutrient content of leaves was also measured (Mallik, 1996). Enhanced growth of *Kalmia* contributes to its competitive ability and allopathic

interference, which play a significant role in its spread and interference to conifer regeneration (Mallik, 1996). *Kalmia* have also a role in reducing the mineralization of N from humus which it have important implication for long-term site productivity (Yamasaki et al., 2002). In a 4-year fertilization experiment, Aerts et al (2001) studies the effects of increased N or P supply on productivity and potential decay in the acrotelm of *Sphagnum*-dominated Swedish peatlands at northern (low-N site) and southern (high-N site) sites. They found no significant effects of the nutrient treatments on cumulative length growth and productivity at either site. There were, however, significant effects of site and nutrient treatment on nutritional variables of *Sphagnum*. They also suggest that higher N concentrations in litter may lead to higher potential decay rate of the litter and this may seriously affect the carbon balance in the acrotelm of these systems. In the end, fertilization may increase *Sphagnum* growth but if the supply is in excess, it can have detrimental effects on *Sphagnum* mosses (Gunnarsson and Rydin, 2000; Malmer et al., 2003). Thus, Vitt et al. (2003a) have also measured *Sphagnum* growth after N fertilization., but in a review of N-deposition, they reveals a critical N-deposition value of between 14.8 and 15.7 kg ha^{-1} yr^{-1} for NPP of *Sphagnum* species.

Nevertheless, more studies on the effect of fertilization on 1) *Kalmia, Ledum* and *Chamaedaphne,* the three most important ericaceous shrubs in terms of competition, 2) mosses (feathermoss and *Sphagnum*), and 3) the interaction of vascular and non-vascular plants, on black spruce regeneration (germination and growth) are definitely needed.

FACTORS AFFECTING FERTILIZATION EFFICIENCY

1) *Peatland types*: As previously indicate, nutrient and foliar status differ between peatland types. Thus response to fertilization may vary according to peatland types (Tilton, 1978; Munson and Timmer, 1991; Sundström, 1992).

2) *Drainage*: Drainage combined with fertilization improves the effect of the fertilizers (Sundström, 1992; McLaren and Jeglum, 1998).

3) *Climate*: Finnish studies report differences in tree growth due to treatment because of the lower temperature in the northern part of Finland (Paavilainen and Päivänen, 1995). Thus, Starr and Westman (1978) found that the amount of available nutrients, especially N and P, in northern Finland was smaller than corresponding peatland site type in southern Finland.

4) *Tree stand*: First, the growth responses of different tree species to fertilizer are primarily dependent on their nutrient requirements, and the effectiveness of nutrient cycling. Second, the response to fertilizer is affected by the age and size of the trees and by the age of the stand (Weetman, 1962a, b; van Nostran, 1979; Paavilainen and Päivänen, 1995; McLaren and Jeglum, 1998). And third, the growth response to fertilization is usually correlated with the initial stand volume at the time of the fertilization (Paavilainen and Päivänen, 1995).

5) *Time since fertilization*: A lag between tree response and fertilization is likely, and future decrease in tree growth following fertilization is also probable (Paquin et al., 1998; Grossnickle, 2000).

6) *Fertilization techniques*: Possible reasons to explain low response after fertilization

include application rate (Morrison et al., 1976) and application date, winter being not recommended because of greater risk for leaching of nutrients (Paavilainen and Päivänen, 1995). Besides application rate and date, type of fertilizers and spreading methods (by air or by hand) are other choices to be made. Many type of fertilizer exist: N, P, K, separately or in combination; micronutrients; urea; lime; and wood ash (Paavilainen and Päivänen, 1995; Demeyer et al., 2001; Moilanen et al., 2002).

ENVIRONMENTAL IMPACTS OF FERTILIZATION

The most serious problem associated with fertilization is nutrient leaching. Weetman (1962) report nutrient losses of 10 to 17 % of nitrogen following fertilization, while nutrient losses from the root zones was measured by Morrison et al. (1976) and an increase of leaching of N, P, and K was reported in Paavilainen and Päivänen (1995). All the problems related to nutrient leaching we discussed in the section drainage and environment can also applied in this section. But, obviously, more research on the effect of fertilization on water quality or biodiversity is needed, especially if we are tempted to use it more extensively.

RECOMMENDATIONS

Fertilization is effective in increasing tree productivity and soil decomposition. However, more long-term experiments are needed to study fertilization responses according to ecosites, ecological types and vegetation types on the Clay Belt. Environmental impacts (water quality and biodiversity) of this management practice on peatlands should be considered before forested peatland fertilization is utilized more extensively. Further works on the effects of fertilization on micro-sites and seedbeds are required as well as long-term studies on mosses and ericaceous shrubs according to tree germination and growth.

Lastly, economic models should also be developed for future investment decisions.

10.3. Site preparation

In the silvicultural guide, **site preparation** is defined as disturbance of the forest floor and upper soil horizons (and/or vegetation) to create suitable conditions for artificial regeneration by mechanical or chemical means, or by prescribed burning (OMNR, 1997). The OMNR (1997) distinguishes between site preparation and **scarification**, the latter referring specifically to the mechanical preparation of a site for natural regeneration. The well-known objectives of site preparation are to: i) create enough suitable, well-spaced sites for seedlings or seeds established via artificial planting; ii) provide easier access for artificial regeneration; iii) limit competing vegetation and insect hazard; iv) reduce fire hazard and slash on the site; v) manipulate wildlife habitat; vi) increase soil temperature, soil oxygen and availability of soil nutrients; vii) decrease frost risk; viii) establish seedlings quickly; and ix) maximize seedling growth and survival rates (Sutherland and Foreman, 1995, 2000; OMNR, 1997; Frey et al., 2003; Lieffers et al., 2003; Prévost and Dumais, 2003).

On the Clay Belt, the application of site preparation is recent and remains, to our knowledge, a method that is rarely used in forested peatlands. In the Québec portion of the Clay Belt, during the 1999-2000 season, 39 000 ha of cutover were treated by scarification and 6 000 ha by shearblading. Although prescribed burning fulfills terms for the payment of royalties, almost nobody in the forest industry use this kind of site preparation. In Ontario, shearblading and prescribed burning have been applied since the beginning of the eighties. Currently in Ontario 90 000 ha (including 45 000 ha in northeastern Ontario) of cutover have been treated with different site preparation

techniques. In the black spruce forest, the most often used type of site preparation is winter shearblading, which is carried out when the soil is frozen with the help of a tractor provided with a sharp blade to eliminate most of the vegetation and to partly remove the thick organic matter. Shearblading is mostly used on the richest sites ("uplands"), where the organic horizon is relatively shallow (< 25 cm) and where black spruce is growing intermixed with jackpine and balsam fir. However, some forest companies (*ex.* Abitibi-Consolidated) have occasionally used shearbladding in lowland sites (R. Gemmell, *Personal communication*), where black spruce is the dominant tree species, and where the organic matter is thicker. No study to our knowledge examines the effects of site preparation on long-term soil fertility and on long-term black spruce productivity in lowlands.

Site preparation in lowlands is likely to have a major impact on soil fertility and on forest growth. This impact can be positive or negative depending on the treatment severity. Several studies suggest that soil disturbance is essential for the maintenance of soil fertility by direct effects (*ex.* soil temperature increase) but also by indirect effects on the composition and the dynamic of the plants colonizing the site (Nguyen-Xuan, 1999; Nguyen-Xuan et al., 2000; Yamasaki et al., 1998). Like a wildfire, site preparation can reduce the cover of feathermoss and *Sphagnum* and reduce the thickness of the organic layer. Consequently it can affect soil moisture and soil temperature, decomposition rate, nutrient availability, and the cover of competiting vegetation (Johansson, 1994; Sutherland and Foreman, 1995, 2000; Prévost, 1992; Trettin et al., 1996; Lundmark-Thelin and Johansson, 1997; Prévost et al., 1997; McLaughlin et al., 2000; Alcàzar et al., 2002; Prévost and Dumais, 2003). Moreover, site preparation involves significant changes in the composition of the flora. Nguyen-Xuan et al. (2000) showed that the exposure of the mineral soil in black spruce forests promoted the presence of plants that stimulate soil fertility, in particular deciduous trees and herbaceous species with broad leaves. Following logging (CPRS-CLAAG), the water table level increases in black spruce stands (Dubé et al., 1995; Prévost et al., 2001) and site preparation, in removing the competitive vegetation, may also contribute to a reduction of evapotranspiration. However, compared to logging, site preparation allows the creation of elevated micro-sites, and improves local drainage and aeration, while controlling the competing vegetation (Prévost, 1992).

The creation of micro-sites favourable to the plantation (Sutherland and Foreman, 1995) and germination of black spruce via site preparation is well understood. However, the long-term effects on soil fertility are not particularly well studied and the impact on forest growth for periods of more than two years is almost unknown (Burgess et al., 1995; Prévost and Dumais, 2003). Several authors have speculated that these practices could affect forest growth at mid-rotation, while the nutritive needs for black spruce stands are to their maxima, (Burgess et al., 1995; Piatek et Allen, 1999). In the literature, some authors report, nutrient losses and a reduction in site productivity at 7 and 27 years after scarification (Burgess et al., 1995; Wurtz and Zasada, 2001). In soils with a shallow organic horizon, this nutrient loss could become problematic. On the other hand, in the cold boreal climate, it is possible that the nutritional losses caused by the removal of the organic matter are more than compensated by beneficial effects due to stimulation of nutrient cycling. In short, for an optimal site preparation, a compromise must be made between adequate production of micro-sites for planted and seeded seedlings and reduction of competing

vegetation and the maintenance of soil fertility.

Site preparation can involve chemical applications, mechanical activities, prescribed burning or a combination of these techniques. In the following section, we will briefly define each technique, but readers are invited to consult more specific documents for more detailed information and technical procedures (Sutherland and Foreman, 1995; OMNR, 1997).

CHEMICAL SITE PREPARATION
Herbicides have been used for more than 50 years (Vincent, 1962), and are currently used in Ontario, but it is not permitted in Quebec. **Chemical site preparation** is the application of herbicide to a site prior to artificial regeneration or after logging to reduce competitive vegetation, mainly ericaceous shrubs, alder or aspen. On the Clay Belt, chemical spraying is applied in Ontario, however before undertaking a chemical spraying program, a wide range of technical, social, political and legal issues must be addressed.

Chemical application is the most effective site preparation technique in reducing competing vegetation (OMNR, 1997). This technique improves height growth, ground-level stem diameter, and health of the planted seedlings, because it removes the competitive vegetation and thereby increase soil temperature (Wood and von Althen, 1993; Sutherland and Foreman, 2000). Chemical site preparation may be broadcast, band or spot spraying (OMNR, 1997) and the timing of spraying should be considered (Wood and von Althen, 1993). This method is cost effective; however there are concerns about the environment side effects, including impacts on biodiversity and human and animal health (Lieffers et al., 2003). An alternative to chemical spraying presented by Norberg et al. (1997) is steam treatment.

They measured a significant effect of steam on the competitive ground vegetation. After four years, pine seedlings had greater height, needle dry weight, and nitrogen content compared with seedlings in the control.

It is important to note, that chemical spraying is not a technique to prevent paludification but is only a tool against competitive vegetation from ericaceous shrubs, herbaceous plants, alder or aspen that are found frequently abundant after logging in forested peatlands and in forest stands susceptible to paludification.

MECHANICAL SITE PREPARATION
Mechanical site preparation involves the direct use of machinery to modify a site to provide favourable conditions for artificial regeneration and/or to improve access (OMNR, 1997). There are five broad categories of mechanical site preparation, and they vary in the amount of disturbance of the forest floor, in the degree of mixing of the organic matter with the underlying mineral soil and in the persistence of treatment. The five categories are screefing, mounding, inverting, trenching, and mixing (Sutherland and Foreman, 1995; OMNR, 1997). These techniques were originally defined for upland black spruce and boreal mixedwood forests. On shallow soils of marginal fertility and on fine textured soils, mechanical site preparation for spruce regeneration should ensure that the organic layer is retained. The preferred method for mechanical site preparation on peatland areas for black spruce regeneration is winter shearblading (Haavisto, 1979; OMNR, 1997). This practice clears slash and shears and compacts *Sphagnum* moss but also minimizes the potential for erosion. Shearblading is not recommended when the water table level is close to the surface or when the existing advanced conifer regeneration is adequate. Optimum results from shearblading are obtained when the

ground is frozen. Few mechanical site preparations on lowland have been experimentd. Moreover, some have already suggested that scarification should not be used in wet sites since *Sphagnum* is an excellent receptive seedbed (Frisque and Vésina, 1977; Jeglum, 1987). Sutherland and Foreman (1995) have experimented with trenching and screefing/trenching on peat soils (V33 – Black spruce / feathermoss and V34 – Black spruce / Labrador tea / Feathermoss (*Sphagnum*)). These experiments gave close to or more than 2000 planting spots/ha, which is considered good. Gale et al. (1998), working in a mineral wetland, showed that site preparation by mounding increased jack pine seedling growth. On the same site, Trettin et al. (1996) showed that mounding and trenching increase soil temperature and soil decomposition. These increases were positively related to soil disturbance: greatest decomposition occurred on mounding treatment, followed by trenched and controls. N mineralization was also higher in the mounding treatment than the trenched and controls (McLaughlin et al., 2000). Prévost et al. (1997) in a mineral wetland in Québec, found that after scarification (trenching) ericaceous shrub cover significantly decreased (but paper birch establishment was promoted), stocking of black spruce seedlings slightly increased and part of the layering advance growth was removed. As noted earlier, layering can have similar growth potential than seedlings, but layers are one of the consequences of paludification. Finally, in a pre-mature black spruce-feathermoss stand showed an increase in the initial growth of black spruce regeneration (planted and natural seedling, and layer), and nutrient status (Prévost et al., 1996; Prévost and Dumais, 2003)

Exposing the mineral soil as found on the Clay Belt is not always positive, as mounds cannot be created without also creating wet depressions. Thus, in hollows, exposed mineral soil is highly susceptible to frost heaving, dessication, flooding and poor root penetration (Sutherland and Foreman, 1995; Arnup, 1998). In addition, seedling mortality will be higher in bottom positions, because of flooding (Hall, 1972). Moreover, small depressions may also revegetate with *Sphagnum* and other mosses (Banner and Smithers, 2002; Asada et al., 2003a; Asada et al., 2004). Mechanical site preparation of severely compacted areas, such as landing and skid trails, facilitates re-vegetation and may reduce erosion potential. Finally, proper selection of the appropriate equipment and technique for a given site condition (moisture, nutrient, soil texture, and topography) and type of competition should be tied to ecological classification rather than by cost of operation and access (Lieffers et al., 2003).

In summer 2003, in the northeastern part of the Clay Belt, an experimental trial was initiated in a black spruce stand prone to paludification. Three intensities of mechanical site preparation and prescribed burning were tested. The site preparation treatments were crushing with simultaneous scarification (scarifier-crusher), mounding (excavator mounding) and scalping using the dip and dive technique (scarifying rake mounted on a bulldozer). Black spruce seedlings will be planted during the summer of 2004. The initial results from these tests should be available in 3 years.

PRESCRIBED BURNING

Prescribed burning is the knowledgeable application of fire to a specific land area in order to accomplish predetermined forest or land management objectives. It is the site preparation technique that most closely emulates natural processes, especially in fire-evolved ecosystems such as jack pine and black spruce forests (OMNR, 1997). Prescribed burning has not been widely

applied in Canada, and its use is decreasing. There are several reasons for this: smoke from fires pose a health risk and a traffic hazard on highways; fear of loss of control of fires that may result in loss of forest, plantations, property or life (Lieffers et al., 2003). Prescribed burning is also time consuming and expensive, and is ultimately dependant on the required fire index rating. There is also an interaction between the success of a burn in achieving management objectives, and the likelihood of fire escape (Robinson, 1970; Weber and Taylor, 1992; Lieffers et al., 2003).

Objectives and benefits of prescribed burning include : i) production and modification of seedbeds and micro-sites; ii) removal of slash to provide planter access; iii) increase in soil nutrient cycling by increased level of cations, accelerated mineralization rates, and higher soil temperature; iv) removal or reduction of the forest floor; v) longer growing season with the removal of the insulating organic layer; vi) reduction in moss and ericaceous shrub cover; vii) insect and disease control (Chrosciewicz, 1976; Weber and Taylor, 1992; OMNR, 1997; Berger and Gilmore, 2003). For further information on the effect of fire on soil properties and micro-sites, readers are invited to consult section 7.0 Wildfire-logging.

Experimental burns in organic peatlands (Johnston, 1971, 1977; Chrosciewicz, 1976, 1990; Aksamit and Irving, 1983) or on the Clay Belt (McRae, 1979, 1985) are rather rare. In most cases experimental burn studies looked at short-term results, i.e. the effect on germination rate, slash removal, or reduction of competitive competition, etc. But we believe that more research should focus on the long-term effects of prescribed burning. For example, the amount of organic matter removed by prescribed fire as opposed to logging (with no further site preparation) or

mechanical site preparationshould be compared. As noted earlier, in forests prone to paludification, germination rate is not problematic; however organic matter build up may reduce nutrient availability.

Because prescribed burning remains the site preparation method that most closely emulates wildfire, and given the expertise in fire management available in Canada, this technique appears to be an option that should be favoured in the boreal forest. This is particularly true on the Clay Belt, where forested peatland is generally remote and and a fair distance from populationed areas.

SCARIFICATION
Scarification is the loosening of the top soil of open areas or the breaking up of the forest floor, to assist the germination of natural seed from either standing trees or slash, or to stimulate suckering and sprouting (OMNR, 1997). This method involves mechanical site preparation techniques, while relying on natural seed sources or root systems.

TENDING
Tending operations include cleaning (removal) of competing vegetation, via the use of herbicides, manual labour, or machines. It is usually applied during the first years after planting to assure increased tree growth rates in a competition free environment.

ENVIRONMENTAL IMPACTS OF SITE PREPARATION
Very few studies in the literature have looked at the environmental impacts of site preparation in forested peatland. Site preparation may have side effects similar to those of harvesting, among these the changes with the greates impact on long term site productivity are, reduction in soil organic matter, nutrient loss, soil erosion, soil compaction, rutting, and changes in biodiversity (Ahtiainen, 1992; Sutherland and Foreman, 1995; Alcàzar et al., 2002;

Haeussler et al., 2002). The severity of these negatives effects is related to the severity of the site preparation. Prescribed burning is also associated with side effects (*e.g.* nutrient losses by volatilization) but these imitate soil disturbance associated with natural fire. Lastly, chemical site preparation is certainly the treatment with the effects that differ the most from natural disturbace. For example, chemical spraying is a major concern for human health.

RECOMMENDATIONS

Long-term studies of the effects of mechanical site preparation (including scarification) and prescribed burning on site fertility and black spruce productivity in 1) boreal forested peatland and 2) black spruce stands prone to paludification are certainly needed. Experiments examining the effeciency and environmental impacts of mechanical site preparation following natural surface and shallow peat wildfire should be tested, since black spruce germination might be low following wildfire. It would be interesting to estimate if a certain amount of time (*e.g.* 2 to 4 yr) between a severe mechanical site preparation and plantation is desirable to allow the water accumulated in small depressions to dry out. Finally, in a trial experiment, a combination of drainage with prescribed burning should be investigated. This method could be the best solution (and with the most severe environmental impacts) to reverse paludification.

10.4 Knowledge gap

The effect of drainage and fertilization in forested peatlands are relatively well-known. On the other hand, very few experiments have measured the long-term effects of mechanical site preparation in forested peatlands. Thus, more experiments are needed. As for prescribed burning, quite a lot of work has been done on this topic, but it remains very unpopular because of major problems such as smoke from fires, traffic hazards on highways, fires spreading out of control, and risk to destroy intact forests or valuable plantations. However, prescribed burning is the site preparation method that most closely emulates wildfire and given the expertise in fire management available in Canada, this technique appears to be an option that should be encouraged in the boreal forest.

11.0. Global warming

As discussed previously, the climate has a great importance in the dynamics and formation of peatlands. Consequently, in a global warming perspective, we can expect a change in the peatland dynamics and in forest stands susceptibles to paludification. For the Clay Belt, an increase in the air temperature from 1 to 4°C is expected (Flannigan et al., 1998). However, the variation in precipitation will vary across the country. As opposed to western Canada, on the Clay Belt an increase in precipitations and reduction in fire frequency are expected (Weber and Flannigan, 1997) (Bergeron et al., 2001; Carcaillet et al., 2001a). Complex interactions of factors including CO_2 enhanced productivity and increased precipitation may favour forest paludification. In years to come, long-term experiments on the effect of global warming on forested peatland dynamics are truly needed.

12.0. Concluding remarks

In the present review, we have demonstrated that paludification is a very complex process and it is frequently observed in the Canadian boreal forest. The factors responsible for peat initiation, accumulation and lateral expansion are numerous. In the eastern boreal forest, which is highly susceptible to paludification, the harvesting techniques (CPRS-CLAAG) currently in use may

increase the risk of paludification. At the same time, partial harvesting has been proposed in uneven-aged stands to maintain or create the irregular and more open structure of old-growth black spruce forests. This technique might be effective for rain interception but it was also suggested that partial harvesting may facilitate paludification since it prevents soil disturbance and increases the amount of light available to *Sphagnum* and ericaceous shrubs. Future research in silvicultural techniques to control paludification should put an emphasis on two front methods 1) that will prevent or inhibit *Sphagnum* growth and expansion and 2) that will increase peat decay.

Black spruce is the main tree species on the Clay Belt. The ecology of black spruce is well known, however we think that further research should be completed on seedbed and growth substrates. Ironically, with so many studies done on this topic, almost all seedbeds have been contradictorally reported to be excellent seedbeds for black spruce. Thus, seedbed experiments related directly to ambient environmental factors should be considered. On the other hand, a lot of work has been done on seedbeds for black spruce. But very few studies have looked specifically at appropriate growth substrates for black spruce. Again, we think that works on growth substrates related to environmental factors particular to the Clay Belt should be considered.

Bryophytes are highly important in paludification. *Sphagnum* is a good seedbed but also inhibits black spruce growth. In contrast, feathermosses (mainly *Pleurozium schreberi*) are beneficial for tree growth. But, *Sphagnum* is very efficient in invading black spruce-feathermoss stands. Establishment of *Sphagnum* and the interaction between *Sphagnum* and feathermosses are still not well understood.

Thus, more research in this area is recommended.

However, priority for the Clay Belt in terms of advancing forest management, should be paleoecological reconstructions (peat stratigraphy) and studies examining topography at different scales (micro-, meso- and macro-). We think it is essential to know the history of these forested peatlands not only in order to be able to predict, with modelization, future responses to global warming and human activities, but also to be able to discriminate paludification caused by chronosequence versus toposequence. Also a more detailed knowledge of the regional topography will make it easier to identify small basins or depressions. As well, information on the thickness of the peat layer will be also appropriate, and primary peat growth and lateral expansion will be easier to locate. This information will facilitate forest management. As we already seen before, drainage and fertilization are generally good techniques to control paludification and to improve tree productivity. On the other hand, site preparation (mechanical and prescribed burning) and drainage followed by burning may not only control paludification but may also be able to reverse paludification, specifically where peat accumulation was caused by natural succession or lateral peat expansion has occurred. Obviously, important environmental and economical issues should be considered and investigated. In the end, the Clay Belt will always remains an area susceptible to peat initiation, peat accumulation and lateral expansion, because the current climate, the topography and the mineral deposit are very favourable to paludification.

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Appendex 1. Carbon accumulation and peat accumulation in peatland sites in northern hemisphere.

Site	Peatland type	C accumulation (g C m^{-2} yr^{-1})	Peat accumulation (mm yr^{-1})	Comment	References
Southern Sweden	Bog	20.7 to 25.9²			Mattson and Koulter-Anderson, 1954[5]
Washington, USA			0.52 to 0.62		Rigg and Gould, 1957
Alaska, USA			2.5-3.8	In less than 185 yr	Heilman, 1968
Alaska, USA			0.48		Heinselman, 1961[9]
Alaska, USA		1.4; 0.45		0-3160; 3160-10310 (yr BP)	Heinselman, 1970
Manitoba, Canada	Lagg – bog forest - muskeg	26.7; 18.8; 13.9²	0.28; 0.41; 0.26	LORCA[11]	Reader and Stewart, 1972
Peatland, unknown	Peatland		0.80 – 0.16	Present time at 6500 yr	Aaby and Tauber, 1975
England	Bog	24-36; 67-106²		2 sites	Jones and Gore, 1975[5]
Southern Finland		6 to 34²		LORCA	Tolonen, 1979[5], 1987[6]
Southern Finland	Bog	30.1 to 9.6²	1.13 to 0.18	200 – 7690 (yr BP)	
Finland	Bog		5.4 – 3.8	Over 50- and 100-yr period (mean of 2 cores)	El-Daoushy et al., 1982
Canada	Fen	19; 20; 22²	0.43; 0.52; 0.54	0-2350; 2350-3500; 3500-6600 (yr BP)	Zoltai and Johnson, 1985
	Edge	23; 23; 24²	0.60; 0.69; 0.54	0-2260; 2260-3500; 3500-6600 (yr BP)	
	Island	16; 19; 29.9²	0.49; 0.43; 0.58	0-2350; 2350-3500; 3500-6600 (yr BP)	
Alaska, USA		7 to 41		LORCA	Billings, 1987
Newfoundland	bog	11.6; 25.4; 18.3¹		0-2065; 2065-3375; 3375-5063	Damman, 1988
		18.5; 17.8¹		5063-7830; 0-7830	

Location	Type	Rate	Ratio	Period (LORCA / yr)	Age ranges (yr BP)	Reference
Yukon – Manitoba, Canada	Peatlands	11.0 – 35.0		LORCA		Tarnocai, 1988[6]
Canada	Subarctic	9.0 - 23.0		LORCA		
Alaska, USA		7.0. – 41.0		LORCA		Kubiv et al., 1989
Alberta, Canada, Muskiki lake	Fen	*48.6; 37.8; 32.4[1]*	0.68; 0.41; 0.34	2760-3670; 8084(yr BP)	3670-7080;7080-	
	Fen	*37.8; 48.6; 37.8[1]*	0.66; 0.67; 0.34	3300-4600;4600-6320;6320-7850 (yr BP)		
	Fen	*48.6; 27; 43.2; 81[1]*	0.57;0.37;0.51;0.79	2800-4910;4910-6260;6260-7530;7530-9000		
Alberta, Canada, Marguerite lake	Fen	*32.4[1]*	0.57	1810-2750 (yr BP)		
	Fen	*43.2[1]*	0.79	2670-3400 (yr BP)		
Scotland	Bog		3 – 2.0	Over 50- and 100-yr period		Clymo et al., 1990[8]
Central Sweden	Bog		0.09–1.1	On 1000 yr		Foster and Wright, 1990
Canada	Peatlands	10 to 35	0.1 to 1.0	LORCA		Ovenden, 1990
Monts du Forez, France		*5.7-7.8[2]*		LORCA		Francez, 1991
Boreal		23.0 to 29.0		LORCA		Gorham, 1991
Canada	Subarctic; Boreal; Canada		0.31-0.54-0.48	LORCA		
South Sweden and North Germany			0.70	LORCA		
South and Central Finland			0.75	LORCA		
Northern Europe			0.6	LORCA		
Boreal Former Soviet Union			0.6–0.8	LORCA		
Siberia palsa province			0.2–0.4	LORCA		
Eurasia			0.52	LORCA		
Western Canada	Boreal peatlands (n=93)	*292.6[2]*		<1500 yr		Zoltai, 1991

Western Canada	Subarctic peatlands (n=23)	171.2[2]		< 1500 yr	
Finland	Sedge – Sphagnum peat	4-13 to 6.7-21.2[2]	0.18-1.36	Long-term C accumulation potential	Tolonen et al., 1992
Maine, USA		10.3-13.4[2]			
Sweden	Bog (Hummock)	8.2 to 52.3[1]	0.15 to 1.0		Malmer and Wallén, 1993
Northwestern Ontario, Canada	Bog		9.2 – 2.9	Over 50-year period (Hummock-Hollow)	Belyea and Warner, 1994
Buffalo Narrows, Alberta Canada	Bog	14.1; 10.2; 11.8	0.35; 0.12; 0.16	0-2480; 2480-5230; 5230-7870 (yr BP)	Kuhry, 1994
Legend Lake, Alberta Canada	Bog	12.9; 6.1; 5.0	0.5; 0.1; 0.06	0-1180; 1180-4340; 4340-7950 (yr BP)	
Slave Lake, Alberta, Canada	Bog	18.1; 21.5; 37.1	0.44; 0.36; 0.5	0-2830; 2830-6430; 6430-8240 (yr BP)	
Zama, Saskatchewan, Canada	Bog	16.5; 18.5	0.45; 0.3	0-1990; 1990-6490 (yr BP)	
Wathaman, Saskatchewan, Canada	Bog	25.6; 19.95	0.98; 0.47	0-1390; 1390-4380 (yr BP)	
La Ronge, Saskatchewan, Canada	Bog	17.48	0.42	0-3710 (yr BP)	
Beauval, Saskatchewan, Canada	Bog	24.12	0.59	0-2790 (yr BP)	
Gyupsumville, Manitoba, Canada	Bog	28.65	0.82	0-1790 (yr BP)	
USA	Temperate bog, swamp	13.6; 11; 8	4.5; 3.1; 2.2	5 sites, top 2 cm; past 50 yr, 100 yr	Weider et al., 1994
Former Soviet Union	Mire, bog, fen, marsh	12.0 to 80.0		LORCA	Botch et al., 1995
Finland, Estonia, Maine (USA)	Peatlands	4.6 to 85.8		LORCA	Korhola, et al., 1995

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Location	Type				Reference
Scotland	Bogs (3)		1.15 ; 0.8	Over 50- and 100-yr period	Oldfield et al., 1995
Western Canada	Bogs (9)	11.0 to 32.0		LORCA	Kuhry and Vitt, 1996
Northwestern Ontario, Canada	Bog	34.0^2		LORCA	Belyea and Warner, 1996
Finland	Fens (4)	9.6 to 24.9		LORCA	Tolonen and Turunen, 1996
		10.7 to 17.0		Actual rate of C accumulation	
	Bogs (10)	13.7 to 35.2		LORCA	
		8.1 to 23.0		Actual rate of C accumulation	
Finland		$18.6\text{-}14.0^2$		Oceanic to continental	Turunen and Tolonen, 1996[7]
Finland	Fen	32-35 to 73		Hummock-laws-flarks	Alm et al., 1997
Norway	Bog		6.6 to 1.8	From 0.5 to 34.5 cm	Jensen, 1997
Sweden	Bog		4.9 to 2.0	From 1.5 to 33.5 cm	
Sweden	Bog		12.0 to 2.2	From 0.5 to 34.5 cm	
Norway	Bog		7.7 to 1.1	From 0.5 to 34.5 cm	
Sweden	Bog		7.9 to 2.8	From 0.5 to 44.5 cm	
Norway	Bog		3.8 to 1.5	From 1.5 to 45.5 cm	
Northern Eurasia	Peatlands (21)		0.07 to 1.1	0-2600 (yr BP)	Klimanov and Sirin, 1997
Saskatchewan, Canada	Treed dry bog	18.68	0.56	0-1870 (yr BP)	Kuhry, 1997
	Treed moist bog	35.18	0.66	1870-2790 (yr BP)	
	Total bog	24.12	0.59	0-2790 (yr BP)	
	Treed fen	45.04	1.15	2790-3260 (yr BP)	
	Total peatland	27.14	0.67	0-3260 (yr BP)	
	Pond with fen	49.58	0.85	3260-4330 (yr BP)	
	Pond with marsh	80.27	1.8	4330-4890 (yr BP)	
	Total pond	60.12	1.18	3260-4890 (yr BP)	

Finland	Total wetland	38.13	0.84	0-4890 (yr BP)	Mäkilä, 1997
Southern Sweden	Bog	16.7-22.3		Marginal - central part	Malmer et al., 1997
Finland	Bog	40		LORCA during 5000yr BP	Clymo et al., 1998
		12.4 – 37.2[2]		LORCA modelled[3]	
		30.0[2]		Current rate of C accumulation modelled[3]	
Northwestern Russia	Mire, bog, swamps, fen	11.4 to 50-75	0.15 to 1.0	LORCA	Kobak et al., 1998
Northwestern Russia	Mire, bog, swamps, fen		0.13 to 1.10	Model estimates	
Northwestern Russia	Bogs (n=2)	9.0; 18.0		0-2500 (yr BP)	
Karalia		17.0; 43.0		2500-4900 (yr BP)	
		27.0; 45.0		4900-7800 (yr BP)	
		34.5; 45.0		7800-9000 (yr BP)	
Norway	Bog	25.0 to 450.0	3.0 to 28.0	0-50 years	Ohlson and Okland, 1998
		100.0	1.0	50-200 years	
Manitoba, Canada	Fen	28.8		Current yr	Raphalee et al., 1998
	Bog	46 to 17		Current yr; 13 to >90 yr	
	Bog	21.7 to –13.6		Current yr; 13 to >90 yr	
Manitoba, Canada	Boreal permafrost peatland	169 to 318		6 cores means, Decrease with depth,	Camill, 1999
		184		Average period on 100 yr	
Southern Sweden	Raised bog	82.2; 89.7; 55.3[2]		Hummocks; hummocks; lawns	Malmer and Wallén, 1999
Finland	Fen (2) and bog (2)	17 to 26		Long-term average rate	Minkkinen et al., 1999
Northwestern, Canada	Northern peatlands	13.2	0.28	Peat plateau	Robinson and Moore, 1999
Alberta, Canada	Fens – bogs – marshes	83; 67; 50		C accumulation potential	Thormann et al., 1999

Location	Type			Description	Reference
Canada	Northern peatlands	19.3; 23.0	0.57	Hummock; hollows	Robinson and Moore, 2000
		19; 24; 13	0.57; 0.68; 0.28	Bog; transition zone; peat plateau	
Northern Alberta, Canada	Permafrost bog	*75–61*[2]	1.9; 1.3	Over 50- and 100-yr period (mean of 2 cores)	Turetsky et al., 2000
	Bog	*79–58*[2]	4.0; 2.6	Over 50- and 100-yr period (mean of 2 cores)	
	Internal lawn	*119–95*[2]	3.8; 2.6	Over 50- and 100-yr period	
Central Alberta, Canada	Bog	*87–57*[2]	4.1	Over 50- and 100-yr period (mean of 2 cores)	
Western Canada	Peatlands	19.4		Past 1000 yr	Vitt et al., 2000
Sweden	Bog	2.0; -7.6		0-2 yr	Waddington and Roulet 2000
Manitoba, Canada	Boreal permafrost peatland	*26.0 – 144.2*[2]		Permafrost Plateaus (6 ages 81 to 124 yr)	Camill et al., 2001
		114.3 – 196.5[2]		Collapse scars (6 ages 173 to 200 yr)	
Canada	Bog ; fen	*18.6 ; 16.0*[2]		LORCA	Frolking et al., 2001
		11.4 ; 5.1[2]		Current rate of C accumulation modelled	
Western European Russia	Bog		1.3	1400 to 2000 (calendar yr)	Klimenko et al., 2001
Alberta, Canada	Bog	34-52		Current rate accumulation	Wieder, 2001
Western Canada	Boreal peatland	*14.3*[1]		Current rate of C accumulation modelled	Yu et al., 2001b
North-Central Finland	Aapa mire	8.0	0.2	LORCA	Mäkilä et al., 2001
Finland	Fen	-7.0		Current yr	Ayrela et al. 2002
Western Siberia	Bog		1.9 to 0.3	9500 to 1500 (yr BP)	Glebov et al., 2002
Eastern Finland	Bog		0.1 to 0.15	6300 to 10 000 (yr BP)	Pitkänen et al., 2002
Western Canada	Peatland complex		0.37 to 0.94	Woody, *Sphagnum*, herbaceous peat	Bauer et al., 2003
North Dakota, USA	Peatland	*37.5*[2]	0.58		Gorham et al., 2003

Location	Type	Organic matter production	C accumulation	Notes	Reference
Minnesota, USA		*21.0 to 38.4²*	0.41 to 0.79	5 cores	
Québec, Canada		*21.9; 28.2²*	0.59; 0.83	2 cores	
Maine, USA		*21.9; 30.0²*	0.47; 0.56	2 cores	
New Brunswick, Canada		*22.1; 32.5²*	0.49; 0.79	2 cores	
Nova Scotia, Canada		*17.0;19.4²*	0.40; 0.48	2 cores	
Newfoundland, Canada		*18.9 to 41.2v*	0.39 to 1.05	5 cores	
Alaska, USA		*8.1; 16.1²*	0.18; 0.38	2 cores	
Southern Québec, Canada	Hydrosere[10]	*21; 3 to 6.2; 45.5²*		Early; mid and late Holocene; last 200 yr	Mueller et al., 2003
Central Finland	Mire	2.0 to 14.0		Mineral subsoil (150 to 3000 yr BP)	Turunen and Moore, 2003
Western Can	Fen	*25²,¹²*		0-4000 yr	Yu et al., 2003a
Western Canada		*41.4 to 248.2²*	0.5	4000-8000 yr BP (3 peaks)	Yu et al., 2003a
Western Can	Fen	31.5		LORCA	Yu et al., 2003b
Western Canada	Fen	100;140;190;270		0-8000 yr BP (4 peaks)	Yu et al., 2003b

Italic= data transformed from the original (organic matter production in $g\ m^{2}\ yr^{-1}$ to $g\ C\ m^{2}\ yr^{-1}$)

[1]54.5 % C content of dry mass; [2]51.7 % C content of dry mass (Gorham, 1991); [3]Based on Figure 15; [4] Present height of peat surface above water-table; [5]Data reported in Bozkurt et al., 2001; [6] Data reported in Botch et al., 1995; [7] Data reported in Francez, 2000; [8]Data reported in Turetsky et al., 2000; [9] Data reported in Reader and Stewart, 1972; [10]From pond to bog; 7 profiles; [11]Long-term average rate of C accumulation; [12]Estimations;

Appendex 2. Growth and primary productivity of mosses species.

Species and location	Growth (mm yr^{-1})	Production (g C m^{-2} yr^{-1})	References
Sphagnum angustifolium			
Norway (south)	14.7	250	Pedersen, 1975
Québec, Canada	4-17	15-64[1]	Moore, 1989
Finland	20–60	80-200	Lindohlm and Vasander, 1990
Ontario, Canada	20-39	49-99	Rochefort et al., 1990
Sphagnum magellanicum			
England	1.4-1.49	35[1]	Forrest and Smith, 1975
Norway (south)	10	35	Pedersen, 1975
Minnesota, USA	36	155[1]	Grigal, 1985
Sweden	16-22	NA	Wallén et al., 1988
Finland	8-20	105-115	Lindohlm and Vasander, 1990
Ontario, Canada	11-34	26-120	Rochefort et al., 1990
France	42	126-174	Francez, 1992
Italy	34-41	74-86[1]	Gerdol, 1995
Minnesota, USA	NA[3]	2.7-3.8-6.5[1,2]	Weltzin et al. 2001
Sphagnum capillifolium			
Québec, Canada	9	38[1]	Moore, 1989
France	19-27	64-103	Francez, 1992
Italy (Alpes)	20-23	186-235[1]	Gerdol, 1995
Sphagnum fuscum			
Manitoba, Canada	NA	3.6[1]	Reader and Stewart, 1972
Québec, Canada	6.8	39-43[1]	Moore, 1989
Finland	6-18	135-160	Lindohlm and Vasander, 1990
Ontario, Canada	7-31	35-152	Rochefort et al., 1990

Central Alberta, Canada	NA	54-78[1]	Li and Vitt, 1997
Central Alberta, Canada	NA	74-86[1]	Szumigalski and Bayley, 1997
Central Alberta, Canada	NA	81-138[1]	Thormann and Bayley, 1997
British Columbia, Canada	21.3	214[1]	Asada et al., 2003a
British Columbia, Canada	16	169[1]	Asada et al., 2003b

Sphagnum rubellum

England	9-38	67[1]	Clymo and Reddaway, 1974
England	NA	3-7[1]	Forrest and Smith, 1975
British Columbia, Canada	19.4	145[1]	Asada et al., 2003a
British Columbia, Canada	15	119[1]	Asada et al., 2003b

Sphagnum sp.

Alaska, USA	0.6-1.7	NA	Heilman, 1968
England	38-43	55-220	Clymo, 1970
Sweden	7-23	NA	Wallén et al., 1988
Unknown	NA	78-256-414[1,2]	van Breemen, 1995
Saskatchevan, Canada	NA	77	Bisbee et al., 2001
Minnesota, USA	NA	85-124-162[1,2]	Weltzin et al. 2001
Québec, Canada	2-14	NA	Heijmans et al., 2002

Pleurozium schreberi

Manitoba, Canada	NA	56[1]	Reader and Stewart, 1972
British Columbia, Canada	20.4 –23	148-166[1]	Asada et al., 2003a

Polytricum strictum

Minnesota, USA	NA	14-19-26[1,2]	Weltzin et al. 2001

[1]Transformed (g m^2 yr^{-1} to g C m^2 yr^{-1})= 54.5 % C content of dry mass;
[2]Related to hummocks, lawn and hollows;
[3]Not available;