UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

QUALITÉ DES SUBSTRATS POUR LA CROISSANCE ET LA NUTRITION DE L'ÉPINETTE NOIRE EN RÉGÉNÉRATION DANS LES PESSIÈRES NOIRES À MOUSSES SUJETTES À L'ENTOURBEMENT

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AVANT-PROPOS

Cette thèse a été rédigée sous la forme de 5 articles scientifiques en anglais, et comporte un résumé, une introduction et une conclusion générale rédigés en français. Pour satisfaire aux exigences du jury de cette thèse, permettez-moi d'éclaircir le rôle de chacun des auteurs à la réalisation des différents chapitres.

Chapitre 1 : Martin Lavoie, David Paré, Nicole Fenton, Art Groot, et Kim Taylor
L'initiative scientifique provient de la Forêt Modèle du Lac Abitibi. La rédaction de l'article a été effectuée par Martin Lavoie avec l'aide de David Paré, Nicole Fenton, Art Groot et Kim Taylor. Cet article est publié dans la revue scientifique Environmental Reviews.

Chapitre 2 : Martin Lavoie, Karen Harper, David Paré et Yves Bergeron
L'initiative scientifique et le design expérimental est le fruit de la réflexion de M. Lavoie. Les analyses statistiques et la rédaction de l'article ont été effectuées par M. Lavoie avec l'aide de Mme Harper, M. Paré et M. Bergeron. Cet article est accepté (avec revisions) dans la revue Journal of Vegetation Science.

Chapitre 3 : Martin Lavoie, David Paré et Yves Bergeron
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RÉSUMÉ DE LA THÈSE

Dans la forêt boréale de l'est du Canada, la baisse de la ressource en bois incite l'industrie forestière à récolter la forêt vers la limite nordique des forêts dites commerciales et dans des peuplements moins productifs. Dans la pessière noire à mousses de l'ouest du Québec, et plus particulièrement dans la région de la ceinture d'argile, une proportion importante des volumes de coupe qui sont attribués à certaines compagnies forestières se retrouvent dans des tourbières boisées (i.e., pessière noire sur sol organique) des peuplements moins productifs que ceux sur sol bien drainés. La ceinture d'argile est une vaste région située de chaque côté de la frontière du Québec et de l'Ontario. Cette région est caractérisée par des dépôts importants laissés par les lacs proglaciaires et possède un sol minéral riche en argile et en limon. En plus, le passage d'une deuxième réavancée glaciaire dans une portion du territoire a eu pour conséquence de compacter le sol minéral et de le rendre difficilement perméable. Ces caractéristiques font de cette région un endroit propice à l'entourbement (i.e., accumulation de matière organique) et à la formation de tourbières. L'entourbement est favorisé par le relief relativement plat, la présence de dépressions, les conditions climatiques de la forêt boréale, le faible potentiel d'évapotranspiration de l'épinette noire, et la litière récalcitrante de la plupart des espèces (arbres et arbustes) présentes. Enfin, le taux d'accumulation de matière organique est également affecté par la présence de perturbations naturelles (e.g., feu, chablis, insectes) ou humaines (e.g., coupe, drainage, préparation de terrain).

Dans cette région, le feu est l'agent perturbateur majeur. Des travaux récents ont mis en évidence que l'entourbement successionnel (i.e., temps depuis le dernier feu) est fréquent sur ce territoire et que l'absence d'une perturbation du sol sur ce type de peuplement pourrait réduire éventuellement la productivité de ces sites. Le passage d'un feu sévère perturbe la couche de bryophytes, réduit l'épaisseur de l'horizon organique et augmente généralement la productivité des conifères. D'un autre côté, au Québec, la méthode de coupe la plus utilisée en forêt boréale est la coupe avec protection de la régénération et des sols (CPRS). La CPRS est souvent effectuée au cours de l'hiver dans cette région. Ce traitement perturbe très peu le sol mais favorise la croissance des sphaignes au détriment des mousses hypnacées, ce qui a pour effet de favoriser la conversion d'un peuplement forestier en une tourbière boisée. Par conséquent, l'utilisation de cette méthode de coupe est remise en question dans la ceinture d'argile et plus particulièrement dans les sites susceptibles à l'entourbement.

Afin d'améliorer la productivité de ces sites, une approche qui s'inspire des effets d'un feu sévère a été proposée. Elle implique l'utilisation de la préparation de terrain mécanique et/ou le brûlage dirigé. Toutefois, avant d'utiliser ces techniques sylvicoles, il est essentiel de 1) déterminer l'origine de l'entourbement (topographique vs. successionnelle) puisque le choix du traitement sylvicole en dépendra; et 2) connaître l'impact à moyen terme de ce genre de perturbation sur le sol et la végétation. On doit pouvoir déterminer les types de substrats disponibles, le potentiel de croissance des substrats qui seront exposés, et le type de végétation compétitrice présent. L'évaluation à moyen terme est également importante puisque les conditions environnementales (e.g., drainage, type de mousse, etc.) peuvent évoluer avec le temps depuis la perturbation. Les principaux objectifs de ce projet de doctorat étaient : 1) déterminer à l'aide de géostatistiques l'origine de l'entourbement dans deux sites; 2) identifier les meilleurs micro-sites pour la croissance de l'épinette noire dans la ceinture d'argile sept ans après perturbation (feu et CPRS); et 3) mesurer l'effet du contrôle du

Rhododendron groenlandicum (ancien nom *Ledum groanlandicum*) sur la croissance de l'épinette noire.

Notre étude propose les géostatistiques comme des outils utiles pour déterminer l'origine de l'entourbement et pour planifier la préparation de terrain. Nos résultats suggèrent que dans le site 2 (coupé en 1997), l'entourbement est d'origine topographique, alors que dans le site 1 (brûlé en 1997), l'entourbement serait d'origine successionnelle (avant la récente perturbation). Donc, dans le site 2, la présence d'une couche épaisse de matière organique peu décomposée et de la nappe phréatique plus près de la surface limitent l'utilisation de la machinerie lourde pour la préparation de terrain et réduisent les chances de succès d'un brûlage dirigé. Inversement, dans le site 1, la matière organique accumulée est mieux décomposée et le milieu est plus sec. Ces conditions sont plus favorables à la croissance de l'épinette noire et augmentent le succès de la préparation de terrain.

Nos expériences sur les substrats de croissances montrent que la croissance de semis d'épinette noire est supérieure dans les matériaux fibriques formés de *Pleurozium schreberi* (frais ou décomposés) que dans les matériaux formées de sphaignes (frais ou décomposés). De plus, la croissance de l'épinette noire est très faible, voir nulle dans le sol minéral et dans la tourbe humique (i.e., matière organique bien décomposée). Nos résultats montrent également l'importance de l'azote et du phosphore pour la croissance. Bien que les peuplements d'épinettes noires semblent uniformes et homogènes à première vue, l'étude rétrospective sur le terrain nous a permis de découvrir qu'en réalité la pessière à mousses de l'ouest au Québec est très hétérogène, et que la croissance de l'épinette noire est très variable et difficilement explicable sur la base de variables environnementales. Enfin, les faibles différences observées dans les taux de croissance entre les substrats en surface sur le terrain suggèrent que les substrats en profondeur sont de meilleurs indicateurs pour déterminer le potentiel nutritif.

Dans la forêt boréale au Québec, le *Rhododendron groenlandicum* est considéré comme une espèce compétitrice et par conséquent comme une espèce ayant un impact négatif sur la croissance de l'épinette noire. Bien que ce constat soit fondé sur très peu d'études, le contrôle mécanique du *Rhododendron* se voulait un choix logique pour augmenter la croissance de l'épinette noire. Pourtant, nos résultats démontrent que le contrôle mécanique du *Rhododendron* a diminué la croissance (approx. 25%) de l'épinette noire. Par conséquent, nos résultats suggèrent que le contrôle mécanique du *Rhododendron* ayant pour but d'accroître la croissance de l'épinette noire peut s'avérer inutile pour certains sites. Puisque le *Rhododendron* croit sur différents types de sites, il est probable que la présence de cette espèce ne soit pas nécessairement un indicateur de problème avec la régénération (croissance et germination) de l'épinette noire.

Pour conclure, ce projet a mis d'abord en évidence le besoin d'effectuer des travaux supplémentaires pour mieux identifier sur le terrain les sites propices à une remise en production et les sites entourbés de façon permanentes. Nos résultats remettent également en question l'utilisation de la CPRS. Par conséquent, nous recommandons: 1) l'utilisation de la préparation de terrain (mécanique ou brûlage dirigé) pour favoriser la croissance du *Pleurozium schreberi* au détriment des mousses de sphaignes (frais et décomposée), et pour prévenir l'accumulation excessive de matière organique; 2) d'éviter l'exposition du sol minéral et de la tourbe humique sur de grande surface; 3) la sélection des micro-sites lors de la plantation; et 4) d'éviter le contrôle mécanique de la tige du *Rhododendron.*

INTRODUCTION GÉNÉRALE

Le contexte forestier québécois actuel prévoit une diminution de la possibilité forestière de même qu'une préoccupation croissante pour un aménagement forestier durable. Au Québec la baisse de la ressource en bois incite l'industrie forestière à récolter la forêt vers la limite nordique des forêts dites commerciales et dans des peuplements peu productifs. Dans la pessière noire à mousses de l'ouest du Québec, et plus particulièrement dans la ceinture d'argile, une proportion importante des volumes de coupe qui sont attribués à certaines compagnies forestières se retrouvent dans des peuplements sur sol organique des peuplements moins productifs que ceux sur sol minéral (Prévost et al. 2001). Afin de répondre à la demande en bois et ce dans un contexte d'une ressource forestière moins abondante et d'une préoccupation croissante pour un aménagement forestier durable, l'objectif de plusieurs acteurs forestiers (e.g., industries forestières, différents paliers de gouvernement, etc.) est d'augmenter la productivité de ces sites dans le cadre d'un aménagement forestier qui s'inspire de la dynamique naturelle.

La forêt boréale est la région forestière prédominante au Canada. Au Québec, la forêt boréale couvre 75% du territoire forestier et elle se compose à 79% de pessière (Parent 1994). Un des types forestiers les plus communs en forêt boréale est la pessière noire à mousses. Dans le nord-ouest du Québec, le sud-ouest de la Baie-James ainsi que sur le nord-est de l'Ontario, une partie importante de ce type de peuplement se retrouve dans la ceinture d'argile, une région naturellement encline à l'entourbement (i.e., accumulation de matière organique). De plus, cette région se caractérise par un couvert forestier dominé par l'épinette noire (*Picea mariana*) accompagné de sapin baumier (*Abies balsamea*) et de mélèze laricin (*Larix laricina*) (Lecomte et Bergeron 2005); une strate arbustive dominée par les éricacées, principalement le *Rhododendron groenlandicum* (ancien nom *Ledum groenlandicum*), le *Kalmia angustifolia* et le *Vaccinium* spp. (Fenton et al. 2005); et une strate de sous-bois dominée par les mousses hypnacées (e.g., *Pleurozium schreberi*) ou de sphaignes (surtout *Sphagnum fuscum, S. russowii, S. magellanicum*) (Boudreault et al. 2002; Fenton et Bergeron 2006).

Facteurs affectant l'entourbement

L'entourbement est un processus dynamique qui se définit par l'accumulation de matière organique directement sur le sol minéral et comporte également la succession des mousses hypnacées vers les sphaignes ainsi que l'élévation de la nappe phréatique du sol minéral vers le sol organique. La présence et le taux d'entourbement dans la ceinture d'argile sont affectés par différents facteurs internes (e.g., succession végétale, permafrost), externes (e.g., feu, climat, perturbations humaines) ou physiques (e.g., topographie, type de sol) (Figure 0.1). D'abord, la ceinture d'argile est caractérisée par des dépôts importants laissés par les lacs proglaciaires Barlow et Ojibway (Vincent et Hardy 1977). Elle a un sol minéral riche en argile et en limon (facteur géologique, Figure 0.1). De plus, le passage d'une deuxième réavancée glaciaire dans sa partie nord-ouest a eu pour conséquence de compacter le sol minéral et de le rendre difficilement perméable (appelé également Till de Cochrane). Ensuite, elle est caractérisée par un relief composé de surfaces relativement planes et de dépressions (facteur géomorphologique, Figure 0.1) (Wilde et al. 1954; Vincent 1962; Riley 1994). Cet entourbement est également favorisé par la diminution de la fréquence des feux (Gauthier et al. 2000), les conditions climatiques de la forêt boréale (facteur externe), le faible potentiel d'évapotranspiration de l'épinette noire (facteur interne), et la litière récalcitrante des conifères et éricacées (facteur interne). Enfin, l'accumulation de matière organique est affectée par la présence de perturbations naturelles (e.g., feu) ou humaines (e.g., coupe, préparation de terrain). Toutefois, contrairement aux autres types de facteurs, les perturbations comme le feu et les traitements sylvicoles ont un impact direct et immédiat sur la qualité des micro-sites pour la régénération en épinette noire.

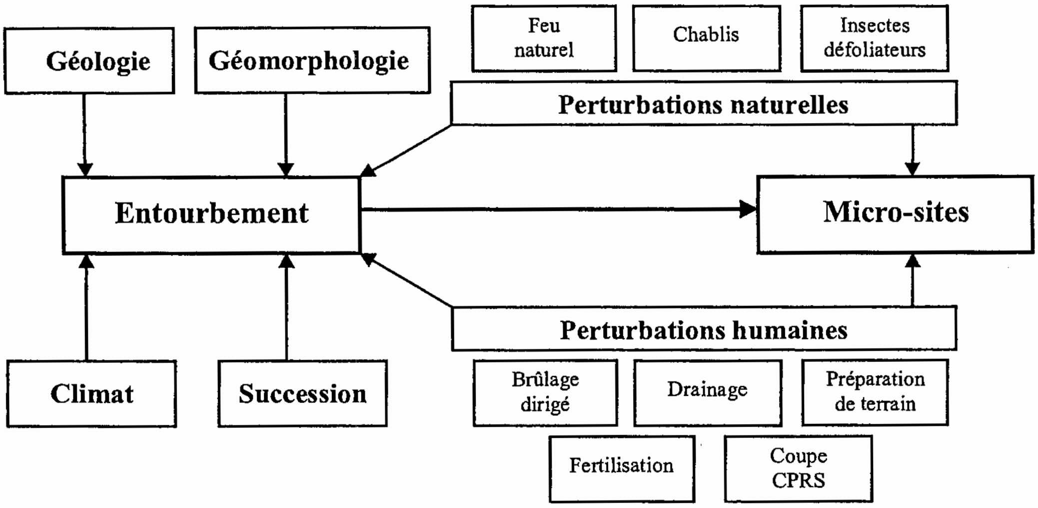

Figure 0.1. Facteurs internes, externes et physiques affectant l'entourbement.

Rôle du feu sur la régénération et les sols en forêt boréale

Comme ailleurs en forêt boréale, le feu est un des principaux agents perturbateurs. La fréquence et la sévérité du feu déterminent la structure et la composition des peuplements de la pessière à mousses de la ceinture d'argile (Lecomte et Bergeron 2005; Lecomte et al. 2006), l'accumulation de la matière organique (Fenton et al. 2005 ; Lecomte et al. sous-presse) et la composition du sous-bois (Lecomte et al. 2005; Fenton et al. 2005). En présence d'un feu sévère, une régénération abondante entraîne une fermeture rapide de la canopée et un sous-bois dominé par les mousses hypnacées (Lecomte et al. 2005). Le passage d'un feu sévère permet également de réduire l'épaisseur de l'horizon organique (Fenton et al. 2005; Lecomte et al. sous-presse), d'augmenter la fertilité des sols (Simard et al. 2001), de réduire la végétation compétitrice (Lecomte et al. 2005) et de favoriser la reproduction sexuée par semis (Lussier 1992). L'ensemble de ces effets favorise une meilleure croissance de l'épinette noire. À l'inverse, en présence d'un feu peu sévère ou d'une longue période sans feu, la canopée reste relativement ouverte (Harper et al. 2002). Cette ouverture cause des changements de compositions importants au niveau de la strate du sous-bois et arbustive avec en autre, un remplacement des mousses hypnacées par les sphaignes et une augmentation importante de la couverture du *Rhododendron* (Lecomte et al. 2005; Fenton et Bergeron 2006). Un feu peu sévère brûle partiellement la matière organique et favorise également la reproduction asexuée (i.e., marcottage). Enfin, l'accumulation constante de matière organique avec le temps depuis le dernier feu (incluant la matière organique résiduelle), associée à une élévation de la nappe phréatique et à une augmentation de la couverture de sphaignes et de *Rhododendron*, réduit la croissance des conifères (Heiselman 1963; Van Cleve et Vierek 1986; Glebov et Korzukhin 1992; Fenton et al. 2005).

Méthode de récolte à repenser ?

La forêt boréale au Québec est exploitée en très grande partie selon la méthode de coupe avec protection de la régénération et des sols (CPRS). En Ontario, une approche similaire appelée careful logging around advance growth (CLAAG) est aussi utilisée. Dans la ceinture d'argile (tant au Québec et qu'en Ontario), on récolte la matière ligneuse sur sol organique surtout en hiver afin d'assurer une protection supplémentaire des sols et de la régénération préétablie et également afin de minimiser la compaction et l'orniérage. La CPRS-CLAAG permet aussi 1) de réduire les coûts associés à la plantation, 2) de réduire le temps de révolution (Chen et Wang 2006), et 3) de conserver le pool génétique de l'épinette noire (par opposition à l'utilisation de semis plantés) (McRae et al. 2001). Lorsque la régénération préétablie avant coupe est suffisante, la CPRS-CLAGG est considérée comme un bon traitement sylvicole puisque la densité et le coefficient de distribution (i.e., stocking) de la régénération après coupe sont élevés (Harvey et Brais 2002). Bien que cette méthode de récolte procure certains avantages, on commence à remettre en question l'utilisation de cette prescription sylvicole dans certaines régions en forêt boréale, notamment dans la ceinture d'argile (Lecomte et al. 2006; Fenton et al. 2005). Contrairement à un feu sévère, la CPRS-CLAAG engendre peu d'effet sur la couche de bryophytes et la matière organique accumulée au sol (un peu comme les effets d'un feu peu sévère). Par conséquent, l'utilisation de la CPRS-CLAAG dans une région naturellement encline à l'entourbement, combinée à une réduction dans la fréquence des feux risquent d'accélérer le processus l'entourbement, de réduire la productivité de l'épinette noire, et éventuellement (long terme) de convertir ces peuplements productifs (commercialement) en tourbières non-productives.

Alternatives et aménagement forestier

Afin d'améliorer la productivité de ces sites, une approche qui s'inspire des effets d'un feu sévère a été proposée, l'utilisation de la préparation de terrain mécanique et le brûlage dirigé. Ces traitements sylvicoles semblent intéressants puisqu'ils créent des conditions favorables à la germination et améliore la croissance des semis en augmentant la disponibilité des éléments nutritifs dans le sol et en réduisant la compétition végétale (Prévost 1992, 1997; Sutherland et Foreman 1995). On l'utilise actuellement lorsque la régénération naturelle est insuffisante après une CPRS-CLAAG, et seulement lorsque l'horizon organique est relativement mince (< 25 cm). Néanmoins, avant d'utiliser ces traitements dans les sites entourbés nous devons mieux connaître cet environnement. Il est d'abord primordial de comprendre et déterminer l'origine de l'entourbement des peuplements et également d'avoir une bonne connaissance des différents micro-sites que l'on retrouve dans la ceinture d'argile (particulièrement sa partie nord). Des connaissances sur l'origine de l'entourbement permettraient de mieux déterminer les endroits où la préparation de terrain est possible et souhaitable. L'évaluation des micro-sites disponibles et de leur qualité pour la croissance de l'épinette noire permettrait de mieux connaître le potentiel de restauration de la fertilité des sites entourbées et finalement nous manquons de connaissance sur l'impact du *Rhododendron* sur la croissance de l'épinette noire puisque cet arbuste est l'espèce compétitrice la plus importante dans cette région.

Approche et objectifs

Le processus d'entourbement joue un rôle clé sur la productivité de l'épinette noire dans la ceinture d'argile. Afin d'augmenter la productivité de ces peuplements d'épinettes noires, il est essentiel de bien connaître ce processus. Dans la première partie de cette thèse, nous avons d'abord décrit et expliqué le processus d'entourbement (chapitre 1). Nous avons par la suite synthétisé les connaissances de l'impact des perturbations naturelles (particulièrement le feu) et des coupes forestières sur ce processus. Nous avons également documenté les méthodes sylvicoles actuellement employées et potentielles qui préviennent, contrôlent ou renversent l'entourbement afin de maintenir ou accroître la productivité d'un peuplement. Enfin, cette revue de littérature avait également pour objectif de définir les besoins futurs en recherche sur l'entourbement et plus particulièrement pour la région de la ceinture d'argile.

La deuxième partie de cette étude a été consacrée à déterminer l'origine de l'entourbement (topographique vs. successionnel) dans deux sites. Cette étape est nécessaire afin de bien choisir le traitement sylvicole approprié. En présence de dépressions (i.e., entourbement topographique), la matière organique qui s'accumule est souvent peu décomposée et les conditions y sont souvent très humides. Ces conditions sont peu propices à l'utilisation de la préparation de terrain mécanique ou au brûlage dirigé. À l'inverse, en absence de feu (i.e., entourbement successionnel) la matière organique accumulée est mieux décomposée et la nappe phréatique plus basse. Ces conditions sont plus favorables à la préparation de terrain. Donc, les principaux objectifs de cette étude étaient de: 1) déterminer si la croissance de l'épinette noire, l'épaisseur de matière organique et la microtopographie sont spatialement structurés (échelles fine et large); 2) déterminer si l'épaisseur de matière organique affecte la croissance à différentes échelle spatiales (fine et large); et 3) déterminer si la microtopographie influence l'accumulation de matière organique à différentes échelle spatiales (fine et large).

La troisième partie de cette étude a été consacrée à identifier les substrats de croissance propices à la croissance de l'épinette noire dans la pessière noire à mousses de la ceinture d'argile. Nous avons d'abord sur le terrain inventorié et échantillonné les micro-sites disponibles afin de bien évaluer leur potentiel pour la croissance de semis d'épinette noire dans des sites après feu et après coupe (troisième chapitre). Nous avons à nouveau testé ces substrats dans des conditions contrôlées en serre (quatrième chapitre) pour en autre, mieux contrôler les variables environnementales, déterminer la valeur nutritive de ces substrats dans un environnement plus sec, et tester des substrats de croissance sujets à l'exposition de la préparation de terrain ou d'un feu sévère.

La dernière partie de cette étude s'est attardée à l'effet du *Rhododendron groenlandicum* sur la croissance de l'épinette noire. Dans la forêt boréale de l'est du Canada, la présence d'éricacées est associée à une baisse du taux de germination et de croissance (Indergit and Mallik 1996, 1997; Thiffault et al. 2004; Fenton et al. 2005). La préparation de terrain est notamment utilisée pour enrayer la croissance de ces espèces. Au Québec, la plupart des travaux ont mesuré l'impact du *Kalmia angustifolia* sur l'épinette noire, et très peu l'impact du *Rhododendron*. Dans les stations humides et tourbeuses de la ceinture d'argile, le *Rhododendron* est l'espèce compétitrice la plus importante. Afin d'augmenter la productivité de l'épinette noire dans les stations des basses-terres, nous avons testé l'effet du contrôle mécanique du *Rhododendron* sur la croissance de l'épinette noire. Dans le cinquième chapitre, nous avons comparé la croissance et les concentrations foliaires de semis d'épinette noire dans des parcelles avec et sans contrôle du *Rhododendron* (tige seulement).

CHAPITRE 1

Paludification and management of forested peatlands in Canada: a literature review

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1.1. Abstract

The Clay Belt region of Quebec and Ontario supports a large forest resource and an important forest industry. In this region, the majority of the harvested volume allotted to forest companies is in forested peatlands and boreal forests prone to paludification. Paludification is the accumulation of organic matter over time, and is generally believed to be caused by increasing soil moisture and *Sphagnum* colonization. Paludification is influenced by external and internal factors; it reduces soil temperature, decomposition rates, microbial activity, and nutrient availability. As a result, paludification may lead to lower site productivity with time after disturbance. Therefore, in harvested stands with a thick organic matter layer, low soil disturbance (as opposed to fire) and water table rise may create favourable conditions for paludification that may ultimately be detrimental to timber production. Past experiences suggest several solutions to prevent or control the negative effects of paludification. Drainage and fertilization applied together are generally good techniques to control paludification and to improve tree productivity. On the other hand, we suggest that site preparation as well as prescribed burning, preceded or not by drainage, are avenues of research that deserve to be explored because they hold the potential to control or even reverse paludification, especially especially where peat accumulation is caused by natural succession or where lateral peat expansion has occurred.

Key words: paludification, forested peatland, productivity, wildfire, careful logging, soil disturbance.

1.2. Résumé

La ceinture d'argile située au Québec et en Ontario supporte une ressource et une industrie forestières importantes. Dans cette région, la majorité du volume de coupe alloué aux compagnies forestières se trouve dans des tourbières boisées et dans des forêts sujettes à la paludification considérées comme ayant une faible productivité. La paludification est principalement influencée par des facteurs internes et externes et peut être définie par l'accumulation de matière organique causée par une augmentation de l'humidité du sol et de la colonisation par les sphaignes. La paludification a pour effet de réduire la température du sol, le taux de décomposition, l'activité microbienne et 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. Dans des peuplements récoltés avec un horizon organique épais, une faible perturbation du sol (par opposition au feu) et une élévation de la nappe phréatique sont donc susceptibles d'être dommageables pour la production de bois. Le drainage combiné à l'utilisation de fertilisant est généralement une bonne technique pour contrôler la paludification et pour améliorer la productivité des arbres. D'un autre côté, nous suggérons que la préparation de terrain ainsi que le brûlage dirigé, précédés ou non par le drainage sont des avenues qui mériteraient d'être explorées car elles ont le potentiel de contrôler ou même 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.

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

1.3. Introduction

The Northern Clay Section of the Boreal Forest Region of Canada (Rowe 1972), also known as the Great Clay Belt of Quebec and Ontario, supports a large forest resource and an important forest industry. Strong demand for wood products, as well as increasing pressure to set land aside for conservation purposes such as forest Ontario's Living Legacy (1997-1999) and the, "Stragégie et plan d'action québécois sur la diversité biologique 2004-2005" of the Quebec government, has pushed forestry operations towards the northern limit of the commercial forest. In the James Bay Lowlands physiographic region of Quebec and Ontario (Dionne 1978), the majority of the timber volume allotted to forest companies is located in forested peatlands and forests prone to paludification with poor drainage (Robitaille and Saucier 1998, Prévost et al. 2001).

Paludification is a dynamic process that refers to peat accumulation which starts directly over a formerly dry mineral soil and which involves the formation of waterlogged conditions (Joosten and Clarke 2002). The result of paludification is a peatland (i.e., mire). It is influenced by allogenic and autogenic factors and it reduces soil temperature, organic matter decomposition rate, microbial activity, the thickness of the aerated soil zone and nutrient availability (Payette 2001; Taylor et al. 1987). As a result, paludification may lead to lower site productivity with time since disturbance (Larsen 1982; Payette 2001).

Little research has been carried out in North America on the linkage between paludification and forest management. We are aware of only one Canadian experiment, located in British Columbia, investigating this linkage (Banner and Shaw 2001*a*, *b*; Banner et al. 2002; Asada et al. 2003). Throughout this paper, we first describe and explain the initiation and development of peatlands. Later on we synthesize the knowledge of the impact of natural disturbances and forest harvesting on paludification, with particular emphasis on the Clay Belt. Finally, we review current and potential treatments to prevent, control and possibly reverse paludification in order to maintain and increase tree productivity in term of sustainable management, conservation of biodiversity, preservation of natural dynamic, and multiple uses of the forest.

1.4. The Clay Belt

The Clay Belt covers 125 000 km^2 in a broad east-west band of land on the Ontario and Quebec border (Lefort et al. 2002). It is part of the Hudson Bay – James Bay Lowlands, and forms the second largest peatland in the world (Gorham 1991). Cold climate, flat topography (plains broken by gentle undulations or ridges) and a surficial deposit that is resistant to water penetration (i.e., clay and compacted clay of the Cochrane till) make the Clay Belt highly favourable to peat formation and landscape paludification (Wilde et al. 1954; Vincent 1962; Jeglum 1991*a*; Riley 1994). Thus, any silvicultural treatment that could accelarate paludification of upland soils will have a long-term impact on tree productivity and soil fertility. Control, reduction or reversal of paludification by natural processes seem to be unlikely in a short-term perspective, while human interventions may have an impact.

1.5. Definitions and terminology

The characteristics of forest sites that are prone to paludification are not currently defined in the North American literature. In this review these sites are characterized by: 1) a cold, humid climate, soil physical and chemical properties favouring peat accumulation; 2) the presence of mosses (mainly feathermoss with an increasing cover of *Sphagnum*); and 3) an increasing organic matter layer. Upland sites surrounded by lowland sites may also be prone to paludification via the lateral expansion of *Sphagnum.*

Paludification in the boreal forest leads to the formation of fens, swamps, and bogs. Fens are peatlands with a fluctuating water table. The waters in fens are rich in dissolved minerals and are therefore minerotrophic. 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). Trees occur mostly 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 mesotrophic to eutotrophic (Vitt and Kuhry 1992). Swamp is a term that has been used in Canada and the United States in reference to forested peatlands. According to the North American definition, a swamp can be defined as a wetland dominated by trees or tall shrubs that is influenced by minerotrophic groundwater on either mineral or organic soils. The essential features of swamps are the dominance (over 30% of cover) of tall woody vegetation, and the wood-rich peat laid down by this vegetation (NWWG 1997). Bogs are isolated hydrologically from mineral soil-influenced runoff and groundwater from 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; thus, all bogs are ombrogenous (and ombrotrophic) and mostly oligotrophic. Bogs are usually covered with *Sphagnum* spp. and ericaceous shrubs (Vitt and Belland 1995; NWWG 1997).

Three terms have been frequently used in the literature to describe a peatland with a component of woody vegetation: forested, wooded and treed. To our knowledge, there are no clear distinctions made in the literature among these terms, and in discussions with different peatland ecologists, it seems that these three terms may actually have 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 (Jeglum 1985; Tim Moore, *personal communication*). For others, forested refers to a closed canopy while wooded or treed is limited to open canopy (Jeglum 1991*a*; Vitt et al.

2003*b*). 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. For the purpose of this review, forested peatlands will refer to peatlands that support commercial forest.

1.6. Paludification

1.6.1. Peatland initiation

Peatlands initiate by two main pathways: paludification and terrestrialization (Romell and Heiberg 1931; Millar 1940; Gorham 1957; Payette 2001; 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 part of the year, and peat accumulates over the previously deposited limnic sediments (Payette 2001; Charman 2002). Peat accumulation by terrestrialization is not affected directly by forest management and can hardly be reversed by silvicultural treatments. Thus this literature review will concentrate on paludification landscape where forest management can have an impact on timber productivity. Furthemore, a greater proportion of peatlands are created by paludification rather than terrestrialization (Vasander 1996; Payette 2001; Charman 2002).

Most paludified sites originate as moist or wet mineral soil sites and turn into peatlands over time, either naturally through successional processes, through external factors, or as a result of human activity. In essence, peat accumulation begins when the production of organic matter exceeds decay (Paavilainen and Päivänen 1995; Charman 2002). However, this process is not simple as there are five factors influencing peatland vegetation (mainly *Sphagnum* mosses) establishment, which triggers peat accumulation.: climate, geomorphology, geology and soils, biogeography, and human activities (Gorham 1957; Heinselman 1975; Liu 1990; Kuhry et al. 1993; Halsey et al. 1997, 1998; Charman 2002; Crawford et al. 2003): 1) Climate is probably the most important factor in determining whether there will be a surplus of water available for peatland 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 from high precipitation – low temperature conditions (Charman 2002); 2) 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 former Soviet Union. Slopes may vary from 0.1 to 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 Bay – 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 favour waterlogging (Riley 1982); 3) Geology and soils (bedrock and texture) are also very important in peatland initiation (Halsey et al. 1997), as mineral soil composed of heavy clay acts as an impermeable substrate that facilitates water accumulation. However, peatlands are also reported to form on glacial till, sand, gravelly outwash, soil formed *in situ* and rock (Rigg 1925; Gorham 1957; Hulme 1994); 4) Particular areas of the world may be more susceptible to peat accumulation because of the presence of the beaver (*Castor canadensis*), and particular plants or group of plants; 5) Lastly, human activities such as agriculture and forestry may modify the hydrological balance of the peatland and it may also change peatland development (Franzen 1983). Consequently, these five main factors can create conditions promoting excess water and the establishment of peat-forming vegetation, especially *Sphagnum* spp.

1.6.2. Development of forested peatlands

Paludification often occurs in wet basins and depressions (Payette 2001). As the thickness of the organic matter increases, the peat surface is isolated from the mineral soil and the conversion to bog occurs. As the peat accumulates, it may eventually expand beyond the deepest parts of the depression onto the surrounding landscape (Korhola 1994, 1996).

Paludification also occurs outside of basins on flat or even sloping (up to 20% (Gorham 1957; Payette 2001; Charman 2002)) terrain. In such situations, as the peat deposit 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 *Sphagnum* moss may grow where the ground is saturated. Also, 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 *Sphagnum* mosses and unsuitable conditions for the rapid breakdown of their dead residues (Gorham 1957).

It is often assumed that the initiation of peat accumulation requires an external factor such as climate change, but it may also be just a result of natural succession (Rigg 1925; Zack 1950; Heilman 1966, 1968; Viereck 1970; Engstrom and Hansen 1985; Mäkilä et al. 2001). In the absence of fire, there is an accumulation of organic matter and an increase in *Sphagnum* cover in a black spruce-feathermoss community (i.e., the main forest community in the eastern boreal forest in Canada (Bergeron et al. 1999)). By promoting cold soil temperatures and, in some areas, permafrost, *Sphagnum* spp. reduces 1) organic matter decomposition rates, 2) microbial activity, and 3) nutrient availability (Taylor et al. 1987; Bonan and Shugart 1989; Payette 2001). 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 secondary metabolites (*e.g.* sphagnol) produced by living *Sphagnum* plants (Weber and Van Cleve 1984; Verhoeven et al. 1990; Johnson and Damman 1991). Thus, with time, a black spruce-feathermoss community may develop into a peatland black spruce forest. Once *Sphagnum* is established, it is unlikely to disappear as long as climate and hydrological conditions remain stable (van Breemen 1995; Charman 2002). However, in the absence of a severe fire, if it does not reach a state where it is very thick, it can be reversed if it is burnt to the mineral soil. Ultimately, it remains very difficult to determine if paludification of these black spruce stands originated from a chronosequence (i.e., accumulation due to time since the last fire) or a toposequence (i.e., accumulation due to a depression or basin). Thus, it is not always possible to distinguish paludification by natural succession produced by lateral expansion from surrounding peatlands or depressions. Peat stratigraphy and an understanding of local and surrounding topography are essential to discriminate between these two causes (Korhola 1994). Because appropriate forest management strategies differ between the two situations, understanding the origin of peat formation is important.

1.6.3. Peat height development and peat accumulation

Height development of peat deposits range from 0.06 to 3.8 mm yr^{-1} (Table 3 in Lavoie et al. *submitted*) according to factors such as peatland type, age, topography, and geography, although these long-term estimates of peat height growth may not take into account repeated peat fires, which could remove surface layers, thereby underestimating actual peat accumulation rates. Peat height growth is the difference between the production of living plants atop the acrotelm and decomposition, compaction (Malmer and Holm 1984) and subsidence in both the acrotelm and the catotelm. The acrotelm is the biologically active layer and is characterized by variable water content, variable soil aeration, high microbial activity and high hydraulic conductivity (Ingram 1978). Between the acrotelm and the catotelm there is a transition zone where the water level fluctuates and water moves laterally. Below this we find the catotelm, which is permanently saturated with water, is anaerobic, has low hydraulic conductivity and, as a result, has little biological activity (Ingram 1978). 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.

1.6.4. Primary production

One might expect that areas with high productivity of total biomass would also have high rates of peat accumulation, but because decay rates are often 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 thinner than in northern peatlands. Although production is difficult to estimate precisely, there are numerous studies reporting the primary production of mineral wetlands and peatlands (Charman 2002). For marshes and swamps, aboveground net primary productivity ranges from 125 to 2590 g $m^{-2}yr^{-1}$, while belowground productivity ranges from 150 to 1800 g $m^{-2}yr^{-1}$ (Bradbury and Grace 1983; Mitsch and Gosselink 2000; Charman 2002). In peat bogs and wet tundra, aboveground productivity ranges from 40 to 1400 g $m^{-2}yr^{-1}$, while belowground productivity ranges from 70 to 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; Charman 2002; O'Connell et al. 2003). 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 to 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.

Among bryophytes, *Sphagnum* spp. have a key role in controlling peat accumulation. *Sphagnum* spp. production and growth rates are highly variable across the northern hemisphere (Rochefort et al. 1990; Lavoie et al. *submitted*). *Sphagnum spp.* height growth can vary from less than 1 to 160 mm yr^{-1}, while production ranges from 3 to 865 g C m^{-2} yr^{-1} in Canada and Scandinavia (Rochefort et al. 1990; Lavoie et al. *submitted*). *Sphagnum* is known as a paludifier in cool humid areas because of the expansion of carpets from peatlands into the surrounding forest (Andrus 1986). The cover area of *Sphagnum girgensohnii* has been observed to invade grounds by 2% (Noble et al. 1984) and 20% (Asada et al. 2003) per year after clear-cutting. This variability in growth and productivity is explained in part by the different niches occupied by different *Sphagnum* spp. (Vitt and Slack 1984). *Sphagnum* productivity and distribution are influenced by mean temperature, water table level (Noble et al. 1984; Moore 1989; Gerdol 1995; Grosvernier et al. 1997; Gignac et al. 2000), light availability (Bisbee et al. 2001) and peat characteristics (Grosvernier et al. 1997).

1.6.5. Organic matter decomposition

Decomposition rate of organic matter in peatlands is controlled by climate, soil temperature, soil moisture, soil aeration, soil pH, chemical and physical characteristics of litter and peat, 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). As newly produced litter and new peat in the acrotelm are exposed to oxygen and varying water levels, they are subject to relatively high decay rate. Once in the catotelm, the decay rate declines sharply and becomes independent of minor climatic fluctuations. Organic matter 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 the catotelm, or the acrotelm residence time, therefore largely determines net peat accumulation (Yu et al. 2001). Several authors have suggested that peat accumulation is controlled by slow organic matter decomposition rates rather than rapid net primary production rates (Clymo 1965; Damman 1979, 1986; Malmer 1986; Farrish and Grigal 1988). However, peat accumulation may also occur in rich fens because of greater production. The equilibrium point, when addition from the acrotelm to the catotelm equals material lost from the catotelm due to decomposition (Clymo 1984; Clymo et al. 1998; Thormann et al. 1999), is reached earlier in fens than in bogs (Thormann et al. 1999).

1.6.6. Paludification and tree productivity

Paludification has been associated with forest disappearance (Klinger 1996; Crawford et al. 2003) and is also 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). In North America, paludification has been associated with reduced timber production in black spruce forests (Rigg 1917; Heilman 1966; Larsen 1982; Van Cleve et al. 1983; Munson and Timmer 1989; Paré and Bergeron 1995; Harper et al. 2002, 2003). In a short-term perspective, black spruce growth is affected by paludification in three ways: 1) accumulation of organic matter, 2) rise of the water table level, and 3) colonization of mosses and *Sphagnum* spp. However, these factors can be explained in terms of soil aeration and nutrient availability. Thick peat layer 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 (Gorham 1957; Heinselman 1963; Tilton 1978). The existence of occasional good stands on thick peat illustrates that a thick peat layer is not necessarily growth limiting (Heinselman 1957, 1963). Similarly, edaphic factors such as site wetness, distance to the 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.

Thus, forest management aimed at controlling or reversing paludification in forested peatland will need not only to control *Sphagnum* but also to stop the decline in nutrient availability and poor root growth conditions found under the natural forest succession.

1.6.7. Knowledge gaps about paludification in the Clay Belt

The primary productivity of peatlands, and more specifically of *Sphagnum*, has seldom been evaluated on the Clay Belt. Fundamental research on peatland history with respect to topography, disturbance and climate using approaches such as paleoecological reconstructions would help to increase knowledge about productivity. 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 versus toposequence. Furthermore, a better knowledge of the topography, thickness and degree of decomposition of the peat layer will help to understand the location of small depressions, as well as primary peat growth and lateral expansion. This information is essential to facilitate forest management.

1.7. Disturbances: wildfire and logging

Although wildfires have played a major role in boreal forest dynamics since the last glaciation, logging has become one of the main disturbances in the eastern Canadian 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) (Keenan and Kimmins 1993; 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 forest floor of the boreal forest.

First, the level of soil disturbance differs between fires and clearcuts. While soil disturbance is relatively even across the stand in clearcuts, after a fire soil disturbance, severity is heterogeneous. Second, logging may also increase soil compaction and rutting (Brais and Camiré 1998; Harvey and Brais 2002) and, as a consequence, reduce soil hydraulic conductivity. Third, 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 organic matter 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 C and microbial biomass (Dyrness and Norum 1983; Fritze et al. 1993; Pietikäinen and Fritze 1993; Simard et al. 2001). Harvesting also has a significant influence on nutrient cycling, but unlike wildfire, logging also removes the 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). Lastly, several studies suggest that the deposition of charcoal after a fire may also be favourable to tree growth. Charcoal has the ability to absorb phenolic compounds and Zackrisson et al. (1996) and Wardle et al. (1998) concluded that charcoal might catalyze important ecological soil processes in early successional boreal forests. This effect diminishes as succession proceeds, and may ultimately 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. 2002).

Johnson (1992) mentioned that the mineral soil exposed by fire results in greater recruitment for most boreal trees than does a duff-covered surface. However, 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 broad concept that includes 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 (pers. observ. 2002, 2003). These conditions may lead to high black spruce seedling mortality. On the other hand, we also observed that after fire, charred (scorched or lightly burned) humus may be a highly unfavourable microsite; 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 also prevent black spruce germination (Zasada et al. 1983; Engstrom and Hansen 1985; McRae 1985; pers. observ. 2002, 2003).

1.8. Can forest harvesting affect paludification rates?

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

1.8.1. Watering-up

One of the major changes following clearcutting is the rise of the water table up to 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, 1991*a*; Haavisto et al. 1988; Roy et al. 1997; Jutras et al. 2002; Asada et al. 2003; Pothier et al. 2003). The rise of the water table ranges from 4 to 22 cm (Berry and Jeglum 1991*a*; Dubé et al. 1995; Roy et al. 1997, 2000*a*). 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 distance to the original water table (Heikurainen 1967; Päivänen 1980), and the percentage of the stand volume removed (Heikurainen and Päivänen 1970; Päivänen 1980; Roy et al. 2000*a;* Pothier et al. 2003). Watering-up is also negatively correlated to soil porosity, as soils with higher porosity will have more space to store the excess water. Therefore, the average water table rise after clearcutting is greater on sites covered with a thin organic layer than on sites covered with a thick organic layer, and is greater on fine textured soils than on coarse texture soils (Dubé et al. 1995; Roy et al. 2000a).

The general conclusion is that watering-up is caused by a reduction in interception and evapotranspiration rates (Heikurainen 1967; Dubé and Plamondon 1995). Silvicultural treatments that maintain interception and transpiration by leaving logging debris, small trees and advance regeneration should limit water table rise. Careful logging and partial harvesting, as opposed to clearcutting, have been considered efficient in: 1) reducing water table rise after the first cut; and 2) promoting vigorous regeneration stratum that should also mitigate water table rise following the final cut (Heikurainen 1967; Heikurainen and Päivänen 1970; 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).

It should be noted that wildfire may also cause: 1) water table rise (Wilde et al. 1954; Kubiw et al. 1989; Crawford et al. 2003) favoured by lower evapotranspiration (Walter 1977; Gorham 1991); 2) deposition of ash particles and C into the soil profile (Crawford et al. 2003), and 3) the establishment of *Sphagnum sp.* on the newly burned surfaces. Thus, fire may also be a factor leading to paludification.

1.8.2. Sphagnum and feathearmoss covers

In the boreal forest, where the soil temperature is low and the moisture content is high, ericaceous shrubs and mosses are the dominating constituents of the forest floor vegetation. These soil conditions are in turn promoted by moss growth (Oechel and Van Cleve 1986). Feathermosses grow best in heavy shade, and often dry out after exposure by clearcutting and may even die (Groot 1996). In contrast, some *Sphagnum* mosses, which prefer open areas, thrive after clearcutting (Wilde et al. 1954; Heinselman 1959; Groot 1996). While feathermoss and *Sphagnum* both act as black spruce seedbeds, they also compete for nutrients with the growing seedlings (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* mosses, as opposed to feathermosses, make the local environment more acidic by the release of 1) polyuronic acid, which decreases the CEC, and 2) humic and fulvics acids during organic matter 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).

The abundance of *Sphagnum* spp. versus feathermoss on the forest floor, and therefore the magnitude of the effect of *Sphagnum*, may be partly dictated by competition. 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). Although growth in both feathermoss and *Sphagnum* is controlled by light and water availability, and temperature, they have different physiological and structural features that determine their physiological niche (Heinselman 1963; Bisbee et al. 2001). However, the processes that allow *Sphagnum* establishment and expansion over feathermoss are still not well understood.

In general, the more open conditions, watering-up and soil disturbance following forest harvesting favour the establishment and growth of *Sphagnum* mosses over feathermosses.

1.8.3. Soil disturbance

Careful logging was initiated to protect advance regeneration and to reduce soil disturbance, but site damage has not been completely eliminated (Groot and Haig 1991; Groot 1996). It has been demonstrated in British Columbia that rutting promotes paludification because *Sphagnum* is able to establish itself in the ruts (Asada et al. 2004). Site disturbances may also vary according to site types. For example, compaction, rutting and erosion may be more frequent in mineral wetlands, while in peatlands, rutting is the dominant disturbance. In a forested peatland located on the Clay Belt, Groot (1998) however did not find evidence of disruption of surface drainage immediately after site disturbance. Nevertheless, these site disturbances could be further reduced. An experimental trial in the UK showed that the use of slash roads provided an effective means of limiting soil disturbance on sensitive thick peat and peaty gley soils, despite high trafficking intensities (Wood et al. 2003).

1.8.4. Cover of ericaceous shrubs

Ericaceous shrubs have been reported to increase in cover following harvesting (Groot 1996; 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 combined with an increase in light availability may favour ericaceous growth. Ericaceous shrubs compete for light, soil water and nutrient availability with black spruce. Shrub cover also limits soil temperature and consequently soil organic matter decomposition and soil nutrient availability. On the Clay Belt, competition with ericaceous species occurs mainly with *Kalmia angustifolia* (Inderjit and Mallik 1996*a*, 2002; Wallstedt et al. 2002; Yamasaki et al. 2002) and *Ledum groenlandicum* (Inderjit and Mallik 1996*b*, 1997; Zackrisson et al. 1997; Prégent and Végiard 2002). Based on various field and greenhouse trials, it has been suggested that *Kalmia* and *Ledum* may impede black spruce growth by a number of mechanisms (Inderjit and Mallik 1996*a*, *b*, 1997, 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* or *Ledum* 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).

1.8.5. Consequences of thick organic matter

The preservation of a thick organic layer after harvest has several consequences for the growth and establishment of the regenerating stand. The progressive accumulation of a thick 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 total quantities of P, K and Mg in available and exchangeable forms (Heilman 1966, 1968). Moreover, peat accumulation results in a distribution of N in the soil that is unfavorable for its mineralization. Instead of being concentrated in the surface horizons of the soil, the bulk of the N becomes located in deeper and colder layers (Heilman 1966). Damman (1988) reports that periods of fast *Sphagnum* growth produce poorly decomposed peat with a low N content, whereas periods of slow growth increase decay and raise the N concentration of the peat.

1.8.6. Summary of the effect of harvesting on paludification

In conclusion, clearcutting, careful logging (CPRS-CLAAG), HARP (harvesting with regeneration protection in Ontario), CPPTM (cutting with protection of small merchantable trees in Quebec), and partial harvesting may lead to an increase in paludification and to a reduction in tree growth in some boreal stands. In contrast with careful logging and clearcutting, paludification should be less problematic following partial harvesting and shelterwood harvesting since the percentage of trees removed and the amount of light available to *Sphagnum* should be lower, while the amount of rainfall interception and evapotranspiration 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. The amount of canopy retained and the amount of disturbance to the soil are key factors in limitating paludification.

1.9. Control of paludification

Current harvesting techniques, combined with fire suppression and the expected reduction in fire frequency (due to climate change and CO_2 increase), may create conditions favourable to increase paludification. It should be noted that the options available to forest managers are 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 and increase site productivity. In the following section, current techniques such as drainage, fertilization and mechanical site preparation will be first discussed in lenght. The use of prescribed burning alone or in combination with drainage and promotion of mixed stands will be then discussed as new options to reduce or reverse paludification.

1.9.1. Peatland drainage

Drainage with the purpose of increasing tree productivity on peatland has been used extensively as a silvicultural technique in Russia, Finland and Sweden, starting in the early part of the 20th century (Heikurainen 1964). Because of this long history, the consequences of drainage are well documented. Following positive results in Finland, this forest technology was imported to Canada and was experimentally applied in Newfoundland (Päivänen and Wells 1977), Quebec (Trottier 1984; Bolghari 1986), northeastern Ontario (Stanek 1968; Payendeh 1973*a*; Haavisto 1984; Rosen 1989; Jeglum 1991*b*), and 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 though Canada possesses large areas of peatland. Currently, about 14 to 15 Mha (million hectares) of wetlands globally have been drained for forestry in the boreal and temperate zones, mainly in Finland (6 Mha) and the Former Soviet Union (5.5 Mha) (Päivänen 1997; Prévost et al. 2001).

1.9.1.1. Effects of drainage

Tree growth improvement following drainage has been reported in the literature for premature and mature stands (Stanek 1977; Payandeh 1973*a*; Dang and Lieffers 1989; Hillman 1991; Sundström 1992; Macdonald and Yin 1999) as well as in regenerating stands (Roy et al. 1999; Jutras et al. 2002).

By lowering 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. 2000*b*), and increases soil temperature and soil organic matter decomposition (Lieffers and Rothwell 1987*a*; Lieffers 1988; Rothwell et al. 1993; Prévost et al. 1997). It should be noted, that in some particular cases such as in the cold and humid climatic conditions found in Finland, can occurr considerable cooling of peat due to intensive drainage (Hökkä et al. 1997). The improved aeration created by drainage is related to the water holding capacity and capillarity connection to the surface, which may change considerably after drainage due to peat subsidence (Rothwell et al. 1996). Drainage also initiates subsidence on the soil 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; Price and Schlotzhauer 1999). 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. Drainage may also influence ground frost. Ground frost can penetrate deeper in peat aerated by dewatering than in water-saturated peat with high specific heat. However, a low thermal conductivity of unsaturated peat delays thawing in spring. In light of this, 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*a*; Tóth and Gillard 1988). Finally, by lowering the water table level, specifically during severe drought, drainage may increase the fire index and possibly fire severity. We suggest that drainage combined with prescribed burning will be an effective means of reversing paludification on sites with moderately thick organic layers.

Following drainage, Minkkinen et al. (1999) and Korpela (1999) measured a drastic change in the species composition of the sites, especially at the minerotrophic sites, where almost all *Sphagnum* mosses had been replaced by forest mosses. Near-surface soil temperature increases and accelerated organic matter decomposition lead to enhanced nutrient uptake and water absorption (Lieffers 1988; Lieffers and Macdonald 1990; Mugasha et al. 1993; Laiho and Laine 1994; Wells and Williams 1996; McLaren and Jeglum 1998). Trees in drained plots are also 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 N content (Macdonald and Lieffers 1990). Finally, in Alberta, Lieffers and Rothwell (1987*a, b*) reported that drainage increased fine root biomass and the maximum rooting depth of black spruce and tamarack.

1.9.1.2. Factors affecting growth response to drainage

Because drainage involves a number of interacting physical and biological processes, tree growth response can be highly variable.

1) *Water level*: Drainage frequently lowers the water table, but it does not always limit water table rise after cutting on mineral (Dubé et al. 1995) and organic soils (Berry and Jeglum 1988, 1991*a*).

2) *Nutrient status and peatland types*: Numerous studies, principally conducted in Fennoscandia but also in Canada, have demonstrated that tree growth can be improved by forest drainage without fertilization, with generally better results on more fertile sites (Paavilainen and Päivänen 1995). Drainage may not be sufficient to increase nutrient uptake on every site. Drainage response may also be related to peatland type, since nutrient status differs among site types (Stanek 1977; Hånell 1988; Hillman 1991; Paavilainen and Päivänen 1995; Nykänen et al. 1996). On productive sites (mesotrophic to eutrophic sites), organic matter decomposition may exceed organic matter input to the soil. On poorer sites (oligotrophic sites), net organic matter accumulation in the soil will continue after drainage. Consequently, on less productive sites, nutrient supplies may become insufficient for continued forest growth over time (Westman and Laiho 2003). Thus, the alternative is to supplement drainage with fertilization. Ombrotrophic bogs are evidently so poor with nutrients that forest drainage even with fertilization will turn to be uneconomised.

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

al. 2003). There also differencies between tree species in their response to drainage (Macdonald and Yin 1999).

4) *Time since drainage*: Generally, stem growth does not increase immediately following drainage because the limited resources are initially allocated to the development of the root system and leaf area. Black spruce stem growth may respond 3 to 10 years after drainage (Dang and Lieffers 1989; Sundström 1992; Sundström and Jeglum 1992; Dumais et al. 1998; McLaren and Jeglum 1998).

5) *Physical site characteristics*: The level of the water table is affected by characteristics such as peat thickness, peat hydraulic conductivity, quality of microsites, microtopography and water stress. Thus, these physical site characteristics may influence drainage growth responses although the original site type is the same (Lieffers and Rothwell 1987*a*; Rothwell et al. 1993; Macdonald and Yin 1999; Roy et al. 1999).

6) *Ditch spacing and tree distance to the ditch*: Soil bulk density and soil nutrient content, soil water content, organic matter decomposition as well as soil temperature all vary with ditch spacing (Wells and Williams 1996; Prévost et al. 1997). Numerous studies show that the tree response to drainage is related to ditch spacing (Berry and Jeglum 1988, 1991*a*; Prévost et al. 1997; Roy et al. 1999, 2000*b*), and the lowering of the water table may be inversely proportional to ditch spacing (Braekke 1983; Belleau et al. 1992). Tree response to drainage is also related to the tree distance to the ditch with greater growth response with trees closer to the ditch (McLaren and Jeglum 1998; Roy et al. 1999, 2000*c*; Jutras et al. 2002).

1.9.1.3. Environmental impacts of forest drainage

The main negative effects of drainage are: change in biodiversity composition, increase in runoff, increase in down-stream flooding risk in some cases, increase in suspended sediments transport in aquatic ecosystem, and modification in the quality of surface water, which influences stream beds and aquatic ecosystem (mainly temperature and oxygen concentration) (Laine et al. 1995; Korpela 1999; Prévost et al. 2001). Forest drainage usually results in an increase in suspended sediments, mainly during the digging of ditches and high water flows in the following weeks or months (Ahtiainen 1992; Åström et al. 2001; Prévost et al. 2001). Changes in water pH are also reported (Berry and Jeglum 1991*b*; Laine et al. 1995). In the literature, nutrient losses by leaching have been reported frequently (Berry and Jeglum 1991*b*; Laine et al. 1995; Paavilainen and Päivänen 1995; Laiho et al. 1999; Åström et al. 2001; Klove 2001; Prévost et al. 2001). 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; Korpela 1999; Klove 2001). The effect of drainage on peatland hydrology may decrease with time since drainage or remain high (Päivänen 1997).

1.9.1.4. Recommendations

Drainage in the eastern Canadian boreal forest should be limited to the first cohort stand following logging since the improvement in tree growth may be relatively low in premature and mature stands without additional fertilization, as show by Jutras et al. (2002) who showed the effectivness of drainage in post-harvested stands. It remains that there have been few published experimental peatland drainage studies in the eastern forested wetland in Canada, and more research into the short- and long-term responses of black spruce to drainage according to stand age, ecological and vegetation types should be completed.

In general, drainage increases soil nutrient availability, suggesting that the nutrient pool will suffice for the production of at least one post-drainage tree crop according to the peatland type. But, as noted previously, fertilization is sometimes needed in conjunction with drainage. Thus, the use of foliar analysis may be required to detect changes in nutritional status. 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.

Technological issues are not the only limiting factor, however. Peatlands are known to be very sensitive to disturbance and the environmental impacts (short- and long-term) of management practices on peatlands must be considered before forest drainage is employed more extensively. In addition to practical and biodiversity concerns, economic balance between investment cost and return needs to be considered. In 1973, Payandeh (1973*b*) completed this exercise and suggested that the annual rate of return on investment for draining black spruce stands of northeastern Ontario would range from –2.7% to 10%. However, the current situation is different and logging in remote areas is more frequent.

Costs will also vary if drainage occurs in uncut versus harvested peatlands. Additional costs should be added for proper ditch maintenance and if fertilizer is necessary.

1.9.2. Peatland fertilization

The growth of tamarack and black spruce in natural forested peatlands in Canada is limited by N and P more often than by any other nutrient element (Macdonald and Lieffers 1990; Mugasha et al. 1991, 1993), suggesting that fertilization could be an essential tool in order to improve tree productivity.

Fertilization has been shown to have a positive effect on tree growth in the boreal forest (Weetman 1968, 1975; Morrison and Foster 1979; Morrison et al. 1976; van Nostrand 1979; Alban and Watt 1981; Foster et al. 1986; Wells and Warren 1997; Gale et al. 1998; McLaren and Jeglum 1998; Turkinton et al. 1998). Growth response is induced by both changes in tree physiology and changes in soil nutrient status. For example, needle nutrient and water status were improved in short- and long-term experiments by increased foliar nutrient concentrations and increased water use efficiency. These growth responses to fertilization can be translated into increased net photosynthesis and photosynthetic capacity (Mugasha et al. 1999; Paquin et al. 1998, 2000). The addition of fertilizers also results in i) an increase in nutrients turnover, ii) a change in nutrient retranslocation, and iii) an increase in organic matter decomposition and microbial activity (Weetman 1962*a*, *b*; Alban and Watt 1981; Munson and Timmer 1990, 1991, Mugasha et al. 1991, 1993; Wells and Williams 1996). It should be noted that even with nutrient status improvement following fertilization, trees may still be under deficient levels (van Nostrand 1979; McLaren and Jeglum 1998). Fertilization may increase biological drainage by increasing tree leaf area and thereby increase interception loss and transpiration (Päivänen 1972; Paavilainen and Päivänen 1995), leading to a further lowering of the groundwater level. Lastly, in many situations fertilization alone will be necessary to increase tree productivity. However, it should be noted that for some forest stands drainage will also be required in order to get an effect from nutrient supplement.

Few studies on the effect of fertilization on the understory exist. First, an increase in growth, biomass and nutrient content for *Ledum groenlandicum*, *Chamaedaphne calyculata*, and *Kalmia angustifolia* is reported (Alban and Watt 1981; Bartsch 1994; Mallik 1996).

Enhanced growth of ericaceous shrubs likely increases competition with alleopathic interference with conifer regeneration (Mallik 1996). Second, *Sphagnum* growth increases (Rochefort et al. 1990; Bartsch 1994; Vitt et al. 2003*a*), decreases (Alban and Watt 1981) or remains unchanged (Aerts et al. 2001) in response to fertilization. It seems that moderate fertilization may increase *Sphagnum* growth but an excessive nutrient supply can be detrimental (Gunnarsson and Rydin 2000; Malmer et al. 1997; Vitt et al. 2003*a*).

1.9.2.1. Factors affecting growth response to fertilization

Several factors influence the efficiency of an applied fertilizer. This includes site and stand characteristics and on the other hand the techniques used.

A) Site and stand characteristics:

1) *Peatland types*: As previously indicated, nutrient status and the defiency of nutrient in question differs between peatland types. Thus, response to fertilization may vary according to peatland types (Tilton 1978; Munson and Timmer 1991; Sundström 1992).

2) *Climate*: Tree growth response to fertilization is lesser in the northern part of Finland due to the lower temperature (Paavilainen and Päivänen 1995). Similarly, the amount of available nutrients, especially N and P, in northern Finland was smaller than in the corresponding peatland site types in southern Finland (Starr and Westman 1978).

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

4) *Water regime of soil*: If excess water limits the tree growth, hardly any response on tree growth with fertilization alone.

B) Techniques used:

1) *Drainage*: On sites with high water table, drainage combined with fertilization improves the effect of the fertilizers (Sundström 1992; McLaren and Jeglum 1998).

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

3) *Fertilization techniques*: Possible reasons to explain low response to fertilization include application rate and nutrient used (Morrison et al. 1976) and application date, winter not being recommended because of the greater risk for leaching of nutrients (Paavilainen and Päivänen 1995). Besides application rate and date, types of fertilizers and spreading methods (by air or by hand) are other choices to be made. It is also highly recommended, before any fertilization, to proceed with a soil and foliar analysis in order to have a nutritional diagnosis and be able to indicate which nutrients and amounts are needed to increase tree growth.

1.9.2.2. Environmental impacts of fertilization

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

1.9.2.3. Recommendations

Fertilization is effective in increasing tree productivity and organic matter decomposition . However, more long-term experiments are needed to study fertilization responses specific to vegetation types found on the Clay Belt. Environmental impacts (water quality and biodiversity) of this management practice on peatlands should be considered before fertilization of forested peatlands is utilized more extensively. Further work on the effects of fertilization on growth substrates and seedbeds is required. Lastly, economic models that consider timing and amount of fertilizers as well as growth responses and environmental aspects should also be developed for future investment decisions.

1.9.3. Site preparation

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, by prescribed burning or by a combination of these techniques (OMNR 1997). The OMNR (1997) formulates a difference between site preparation and scarification, the latter referring specifically to the mechanical preparation of a site for natural regeneration. But for the purpose of this review, site preparation will be used to define both techniques. In disturbing the forest floor and upper soil horizons (and/or vegetation), the 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 competiting vegetation and insect hazard; iv) reduce fire hazard and slash on the site; v) remove or reduce the soil organic matter, *Sphagnum* and/or feathermoss layers; vi) manipulate wildlife habitat; vii) increase soil temperature, soil oxygen and availability of soil nutrients; viii) decrease frost risk; ix) establish seedlings quickly; and x) maximize seedling growth and survival rates (Chrosciewicz 1976; Weber and Taylor 1992; Sutherland and Foreman 1995, 2000; OMNR 1997; Berger and Gilmore 2003; Frey et al. 2003; Lieffers et al. 2003; Prévost and Dumais 2003).

1.9.3.1. Mechanical site preparation

Site preparation is not widely used in forested peatlands. In black spruce peatland forests, the most often used type of site preparation is winter shearblading, which is carried out when the soil is frozen. A sharpened blade mounted on a tractor is used 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 jack pine and balsam fir. However, some forest companies (e.g., Abitibi-Consolidated) have occasionally used shearblading in lowland sites (R. Gemmell, pers. comm., 2002), 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 (e.g., soil temperature increase) but also by indirect effects on the composition and the dynamics of the plants colonizing the site (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, organic matter decomposition rate, nutrient availability, and the cover of competiting vegetation (Prévost 1992; Johansson 1994; Sutherland and Foreman 1995, 2000; Trettin et al. 1996; Lundmark-Thelin and Johansson 1997; Prévost et al. 1997; McLaughlin et al. 2000; Alcázar 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 colonisation of plants that stimulate soil fertility, in particular deciduous trees and herbaceous species with broad leaves. Site preparation may also contribute to a reduction in evapotranspiration and an increase in the water table level. However, contrary to logging, site preparation allows the creation of elevated microsites and improves local drainage and aeration while controlling the competing vegetation (Prévost 1992).

The creation of microsites favourable to planted seedlings (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 up to mid-rotation, when the nutritive needs for black spruce stands are at their maximum (Burgess et al. 1995; Piatek and Allen 1999). Nutrient losses and a reduction in site productivity have been observed at 7 and 27 years after site preparation (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 the beneficial effects due to stimulation of nutrient cycling. In short, for an optimal site preparation, a compromise must be made between adequate production of microsites for planted and seeded seedlings and reduction of competing vegetation and the maintenance of soil fertility.

There are five broad categories of mechanical site preparation, varying 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, jack pine 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 (see above). Little experimentation on mechanical site preparation on peatland has been carried out, and it has been suggested that mechanical site preparation should not be used in wet sites since *Sphagnum* is already an excellent receptive seedbed (Frisque and Vézina 1977; Jeglum 1987). Sutherland and Foreman (1995) have experimented with trenching and screefing/trenching on peat soils. 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, mounding and trenching increased soil temperature, soil organic matter decomposition and N mineralization (Trettin et al. 1996; McLaughlin et al. 2000). These increases were positively related to soil disturbance, and greatest decomposition occurred on the mounding treatment, followed by the trenched treatment and the control. Prévost et al. (1997), found that after trenching in a mineral wetland in Quebec, ericaceous shrub cover significantly decreased (but paper birch establishment was promoted), and that stocking of black spruce seedlings slightly increased over advance regeneration. Finally, a premature black spruce–feathermoss stand on mineral soil showed an increase in the initial growth of black spruce regeneration (planted and natural seedlings and layer) and nutrient status (Prévost 1996; Prévost and Dumais 2003) after mechanical site preparation.

Exposing the mineral soil, as has been 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, desiccation, 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 Shaw 2001*b*; Asada et al. 2004).

In summer 2003, in the northeastern part of the Clay Belt, an experimental trial was initiated in a black spruce stand prone to paludification (Cormier 2004). Three intensities of mechanical site preparation and a 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 were planted during the summer of 2004. The initial results from these tests with regard to growth performance should be available in 3 years but for now, results show that all methods are applicable in this area in terms of producing planting spots for black spruce seedlings. The scarifier-crusher was the more efficient in producing planting spots (1600-2400 ha^{-1}), followed by the scarifying rake mounted on a bulldozer (1608-1624 ha^{-1}) and mounding (945-1058 ha^{-1}) (Cormier 2004). However, mounding produced better planting spots and it would become very expensive to get higher planting spot density (Cormier 2004).

1.9.3.2. 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 prescribed burning poses a health risk and a traffic hazard on highways, and there is also a fear of loss of control of burning that may result in loss of forest, property or life (Lieffers et al. 2003). Prescribed burning is also time consuming and expensive, and is ultimately dependent on the required fire index rating. There is also, unfortunately, a positive correlation 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).

Experimental burns in peatlands in general (Johnston 1971, 1977; Chrosciewicz 1976, 1990; Aksamit and Irving 1984) or especially on the Clay Belt (McRae 1979, 1985) are rather rare. In most cases, experimental prescribed burning studies looked at short-term results, i.e., the effect on germination rate, slash removal, or reduction of competition. However, 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 or mechanical site preparation should be compared. As noted earlier, in forests prone to paludification, seedling establishment is not a problem, although 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 evaluated in the boreal forest. This technique may be particularly suited to the Clay Belt, where a large area of forested peatland is generally quite far from local villages.

The position of the water table 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 fire severity (Zoltai et al. 1998). Three types of peat fires can be distinguished according to the amount of organic matter burned: surface, shallow and deep peat fires. Deep peat fires, which can burn down to the underlying peat, are very rare and require very dry conditions. Thus, most peatlands are subjected to surface fires with only a small area expected to be affected by shallow peat fires. Surface peat fires can only slow down paludification and do not influence the long-term vegetation development of *Sphagnum*-dominated boreal peatlands, as the *Sphagnum* resprouts from the remains (Kuhry 1994; Charman 2002).

Based on these observations and in order to improve the efficiency of prescribed burning, we suggest that in situations where paludification is at an advanced stage, prescribed burning should be tested in combination with drainage. Fires that can burn deep into the peat have mostly been observed after very dry years or after drainage (Zoltai et al. 1998). By reducing the water table level, especially during severe drought, drainage could increase fire index and thereby fire severity.

1.9.3.3. Environmental impacts of mechanical site preparation and prescribed burning

Few studies have examined the environmental impacts of site preparation in forested peatland. The effects of site preparation may be similar to those of harvesting, i.e., reduction in soil organic matter, nutrient loss, soil erosion, soil compaction, rutting and changes in biodiversity (Ahtiainen 1992; Sutherland and Foreman 1995; Alcázar et al. 2002; Haeussler et al. 2002). The severity of these negative effects is related to the severity of site preparation. Lastly, although prescribed burning results in environmental impacts (e.g., nutrient losses by volatilization), it, to a considerable extent, imitates soil disturbance associated with natural fire.

1.9.3.4. Recommendations

Long-term studies of the effects of mechanical site preparation 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. It would be interesting to estimate if a certain amount of time (e.g., 2 to 4 years) between a severe mechanical site preparation and plantation is desirable to allow the water accumulated in small depressions to dry out. Finally, a combination of drainage with either site preparation or prescribed burning should be experimentally tested in forested stands where paludification is in an advance stage. This method could be the best solution to reverse paludification because it could control water table rise following harvesting and could provide a substrate richer in nutrients as observed following wildfire.

As we previously noted, prescribed burning is risky and could potentially result in health problem for the local population. Thus, as a second alternative to a combination of prescribed burning and drainage, we also suggest that a combination of drainage and mechanical site preparation should be tested in order to control paludification in forested stands close to inhabited areas. Using drainage in combination with site preparation would also increase the efficiency of site preparation in very wet stands.

1.9.4. Promotion of mixed stands

Watt and Heinselman (1965) suggested that higher levels of N on fertile sites may be attributed to N fixation by speckled alder, more rapid decomposition of litter (indicated by less peat accumulation), movement of enriched water, and proximity 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 for black spruce component on some sites would likely result in small losses in total volume, but would definitely result in an increase in commercial volume (Whynot and Penner 2000). In addition, Paré et al. (1993) report that, with the exception of N, the availability of all nutrients declines with time since fire in the southern boreal forest in Abitibi. They suggest that the maintenance of high N mineralization rates could be explained by the persistence of *Betula papyrifera* in late successional stages. They also propose that the presence of deciduous trees may limit the development of moss cover. Moreover, in the same area, Légaré et al. (2004, 2005*a*) have shown that the presence of aspen (between 0-41% basal area) also had a positive effect on black spruce growth (e.g., dbh and height). They suggested that the presence of aspen enhanced soil fertility by its influence on nutrient availability (Légaré et al. 2005*b*).

1.10. Concluding remarks

In this review, we have demonstrated that paludification is a very complex process with a number of factors affecting peatland initiation, accumulation of organic matter and lateral expansion of peatland. In the eastern boreal forest in Canada, 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 maintains evapotranspiration, but may also 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 emphasize methods 1) that will prevent or inhibit *Sphagnum* growth and expansion, and 2) that will increase organic matter decomposition.

However, a priority for the eastern Canadian boreal forest in terms of advancing forest management is paleoecological reconstructions (peat stratigraphy) and studies examining topography at different scales (micro to macro). We think it is essential to know the history of these forested peatlands not only in order to be able to predict, with modelling, 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, and this information will facilitate forest management. Drainage and fertilization applied together is generally a good technique to control paludification and to improve tree productivity. On the other hand, we suggest site preparation as well as burning, preceded or not by drainage, as avenues of research to control and reverse paludification, especially where peat accumulation is caused by natural succession or where lateral peat expansion has occurred. Lastly, important environmental and economic issues should be considered and investigated. Another aspect not treated in this review is the role of these ecosystems in the global carbon cycling. The use of management techniques previously discussed that could enhance tree growth and therefore carbon sequestration in the tree component may also reduce soil carbon pools. The assessment of the net effect of these techniques on carbon storage would be pertinent to international agreements on carbon emissions.

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CHAPITRE 2

The effects of microtopography and organic layer thickness on seedling height growth of regenerating trees in black spruce stands prone to paludification

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2.1. Abstract

Questions: Are *Picea mariana* height growth, thickness of the organic layer and microtopography spatially structured at coarse and fine scales? Does organic layer thickness affect height growth and does microtopography influence the accumulation of organic matter at coarse and fine spatial scales?

Locations: Black spruce (*Picea mariana*) forests, northwestern Quebec, Canada.

Methods: We assessed the spatial pattern of each variable in one wildfire site and one harvest site using semivariograms and correlograms. We measured the cross-correlation between relative elevation and organic layer thickness, and between organic layer thickness and growth using cross-correlograms.

Results: *Picea mariana* height growth was autocorrelated to a greater extent in the wildfire site (103 m) than in the harvest site (43 m). The spatial structure of organic layer thickness was similar in both sites. Deeper depressions in the harvest site, as illustrated by spatial variance in relative elevation at short distances (approx. 50 m) and by high autocorrelation values, increased the accumulation of organic matter within 20 m.

Conclusions: The accumulation of organic matter in depressions with low relative elevation created poor conditions for *Picea mariana* growth indicating paludification developed in undulating terrain in the harvest site. In contrast, paludification likely occurred during stand development in the wildfire site where the landscape was relatively flat.

Keywords: forested peatland, forest management, geostatistics, harvest, *Picea mariana,* spatial analysis, wildfire.

2.2. Résumé

Questions: Est-ce que la croissance en hauteur de *Picea mariana* (épinette noire), l'épaisseur de matière organique et la microtopographie sont spatialement structurées à une échelle fine et large. Est-ce que l'épaisseur de matière organique affecte la croissance en hauteur de l'épinette noire et si la microtopographie influence l'accumulation de matière organique à une échelle fine et large.

Locations: Forêts d'épinettes noires (*Picea mariana*), nord-ouest du Québec, Canada.

Méthodes: Nous avons estimé 1) les patrons spatiaux de chaque variable dans un site issu d'un feu et un site issu d'une coupe en utilisant les semivariogrammes et corrélogrammes, ainsi que 2) la corrélation avec retard entre l'élévation relative et l'épaisseur de l'horizon organique et entre l'épaisseur de l'horizon organique et la croissance en utilisant les corrélogrammes avec retard.

Résults: La croissance en hauteur de *Picea mariana* était autocorrélée sur une plus grande distance dans le site feu (103 m) que dans le site coupe (43 m). La structure spatiale de l'épaisseur de l'horizon organique était similaire dans les deux sites. La présence de dépressions plus profondes dans le site coupe, illustrée par une variance spatiale sur courte distance (approx. 50 m) pour l'élévation relative, a affecté négativement l'accumulation de matière organique sur une distance de moins de 20 m.

Conclusions: Dans le site coupe, l'accumulation de matière organique dans les dépressions, illustrée par une élévation relative plus petite, crée des conditions pauvres permanentes pour la croissance de *Picea mariana* signifiant que l'entourbement est probablement d'origine topographique. À l'inverse dans le site feu où la microtopographie était relativement plate, la matière organique accumulée est probablement due à un entourbement successionnel.

Mots clés: aménagement forestier, analyse spatiale, coupe, feu, géostatistiques, *Picea mariana,* tourbière boisée.

2.3. Introduction

Microtopography and productivity are amongst several factors that can control the spatial structure in soil and vegetation (Jenny 1941). Studies in agricultural systems have shown that topography or depth to bedrock can affect the spatial pattern of soybean nutrient concentration (Kravchenko & Bullock 2002), *Quercus rubra* growth (Meredieu et al. 1996) and soil phosphorus concentration (Kozar et al. 2002). In black spruce (*Picea mariana*) boreal forest, the spatial structure of forest stands varies on sites with different productivity (Harper et al. in press).

In black spruce forests, tree productivity is reduced by paludification, the process of an accumulation of organic matter accompanied by an increase in the cover of *Sphagnum* moss leading to the formation of waterlogged conditions (Lavoie et al. 2005). By promoting a cold, wet and acidic environment, *Sphagnum* reduces organic matter decomposition rates, microbial activity and nutrient availability (Taylor et al. 1987; Payette, 2001; Turetsky 2003; Fenton et al. 2005). In addition, *Sphagnum* also affects decomposition rates through the rapid production of biomass, which has a high C : N ratio and is resistant to decomposition (Hobbie 1996; Turetsky 2003).

Due to the low decomposition rate of *Sphagnum*, organic matter can accumulate during the later stages of stand development. Paludification can also develop in an undulating terrain. In this process, organic matter accumulates in deep hollows independent of stand development. Water collects in these hollows and slows decomposition thereby allowing organic matter to accumulate. Under these conditions, fire can only reduce the depth of accumulated organic matter slightly (Lavoie et al. 2005).

An analysis of spatial structure of the microtopography and organic matter thickness can help distinguish between the two types of paludification. Relative elevation that is autocorrelated only at short distances indicates undulating terrain. Combined with the presence of a strong negative correlation between relative elevation and organic layer thickness, this suggests that paludification was caused by topography. In contrast, weak or absent spatial structure in microtopography and a lack of a strong correlation between microtopography and organic layer thickness suggest that paludification occurred during stand development. The ability to differentiate between these two causes of paludification can help managers select the appropriate management strategy to increase tree productivity.

The overall goal of this study was to investigate the origin of paludification and its effect on *Picea mariana* growth in a 6-year old harvest site and in a 6-year old wildfire site. The specific objectives were: 1) to determine the spatial pattern of *Picea mariana* growth, organic layer thickness and relative elevation of the mineral soil (i.e., microtopography) at coarse and fine spatial scales; and 2) to assess the relationships between the spatial structures of (a) *Picea mariana* growth and organic layer thickness and (b) organic layer thickness and relative elevation.

2.4. Materials and Methods

2.4.1. Study area

The study was located in the black spruce forest in the southwestern James Bay Lowlands physiographic region of Quebec (Fig. 1). This area is typical of the Clay Belt region in Quebec and Ontario which is characterised by lacustrine deposits left by the glacial lakes Barlow and Ojibway (Vincent & Hardy 1977). The study area is part of the Lake Matagami Lowland ecological region within the western black spruce-feathermoss bioclimatic domain (Saucier et al. 1998). Forest stands within the study area belong to the black spruce community with *Sphagnum* on mineral deposits (Bergeron et al. 1999). The stands were dominated by *Picea mariana* with some *Abies balsamea* and *Larix laricina. Rhododendron groenlandicum* dominated the shrub cover with *Kalmia angustifolia* and *Vaccinium* spp., *Sphagnum* moss and feathermosses (mainly *Pleurozium schreberi*) covered the forest floor which consisted of hummocks and hollows.

The study area consisted of two sites: a wildfire site and a harvest site (Fig. 1). We selected the youngest wildfire available with easy access, a large 540 km^2 wildfire that burned in 1997. Our wildfire site was located in an area that was salvage cut in 1997 and planted with *Picea mariana* in 1998. There was no field preparation before planting. A harvest site was located close to the wildfire site (to minimize differences in climatic conditions) with similar age, soil and stand characteristics prior to disturbance. In the harvest site, forest stands were harvested by CPRS ("Cut with Protection of Regeneration and Soils", careful logging) in 1997. There was no field preparation or planting after harvesting. These sites were considered to be representative of post-disturbed sites of the Clay Belt. Prior to disturbance, forest stands on both sites were older than 175 years with a maximum tree height less than 17 m and canopy cover less than 60% (Ministère des Ressources naturelles du Québec 1999; Bergeron et al. 2004). Both sites were relatively flat with clay deposits.

2.4.2. Sampling design

Three plots were located in each of the wildfire and harvest sites for a total of six plots (Fig. 1). Plots were at least 500 m apart in the wildfire site and at least 1.5 km apart in the harvest site. Because wildfire is an unplanned natural event, we were restricted to a pseudoreplication design (Hulbert 1984). Such case studies of natural disturbance events can still provide valuable information about disturbance effects but their results must be interpreted cautiously (e.g., Turner et al. 1997; Larson & Franklin 2005). The area covered by each plot varied and was determined by the size of the cut (for harvest plots), the size of the salvage cut in the wildfire (for wildfire plots) and external limitations (i.e., plots were at least 50 m from any road, forest edge, lake or river). Plots ranged in size from 8750 m^2 to 29 000 m^2. There were four randomly located 40 x 10 m sub-plots within each plot for a total of 24 (see Fig. 2 for an example of one plot).

In each sub-plot, thirty regenerating trees < 1.3 m were randomly sampled. Regenerating trees in the harvest site included seedlings or saplings produced by layering and originated from either before or after the disturbance. In the wildfire site, regenerating trees included only seedlings planted after the fire. For each tree, we measured its height and the cumulative growth for the past three years (i.e., 3-year annual increment (AI)).
Relative elevation, a measure of the microtopography of the mineral soil, was measured using an additional uniform sampling grid within each sub-plot. This regular sampling grid consisted of 30 points at the intersections of 3 rows (3 m apart) and 10 columns (4 m apart) as well as four additional points at three corners and at position [1 m 1 m] for a total of 34 points. Relative elevation was defined as the difference in height of the mineral substrate between the sampling point and the height at the base of the theodolite (Theodolite Leica Wild T-2; initial level of 0 cm). Afterwards, a zero value was given to the lowest value within each sub-plot or plot. Long distances between sampling points made relative elevation measurements difficult among sub-plots. Thus, measurement at the plot level (i.e., all 4 sub-plots combined) was possible only in one wildfire plot and two harvest plots. Organic layer thickness was measured with a soil auger next to each tree and at each of the 34 systematic sampling points for a total of 64 samples. Sampling was conducted in 2003.

2.4.3. Statistical analysis

Three-year annual increment, organic layer thickness and relative elevation were compared among the six plots using analysis of variance. Relationships between 3-year annual increment and organic layer thickness as well as between relative elevation and organic layer thickness were analysed with linear regression analysis. All statistical analyses were computed using SAS 8.02 (SAS Institute Inc. 1999). Data were checked for normality and equality of variance prior to statistical analyses.

2.4.4. Spatial pattern analysis

The spatial structure of 3-year annual increment, organic layer thickness and relative elevation was examined within each sub-plot using semivariance and autocorrelation analysis. Each method provides unique information about the spatial pattern. The semivariogram and the correlogram are used in conjunction to evaluate both the range of spatial dependence and the significance of any spatial dependence measured. Moreover, semivariograms measure the portion of the total variance explained by structural variance, while correlograms can determine if autocorrelation is positive or negative. Both tests require the condition of second-order stationarity, meaning that the expected value (mean) and spatial covariance of the variable are the same over the entire study area (Legendre & Legendre 1998). Therefore, all variables were checked for the presence of a broad spatial trend by fitting a first-degree regression equation for each variable as a function of the geographic coordinates. The only variable with a significant geographic trend was relative elevation in wildfire plot 1. In this case, we removed the trend by computing residuals from a trend-surface analysis; we used the residuals for subsequent spatial pattern analyses (Legendre & Legendre 1998). For organic layer thickness, spatial analyses were performed for all sampling points combined (n=64). In order to evaluate spatial pattern at a coarser scale, semivariograms and correlograms for 3-year annual increment and organic layer thickness were also performed at the site level (i.e., for all sub-plots combined within each site), and for relative elevation at the plot level (for the four sub-plots combined within each plot).

Semivariograms were used to determine the spatial variance of each variable at different scales using the following estimator (Legendre & Fortin 1989):

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z_i(x_i) - z_i(x_i + h)]^2 \qquad [1]$$

where γ (h) is the semivariance at distance interval h; $z(x_i)$ and $z(x_i + h)$ are the values of each variable at locations x_i and $x_i + h$, respectively, and N (h) is number of point-pairs separated by distance h. The results of the semivariogram for each subplot, plot or site were fitted to one of five models: Nugget, Linear, Gaussian, Spherical and Exponential (formulae in Appendix 1). These fitted models can be classified as exhibiting one of three types of spatial structure. (1) The Nugget model indicated random spatial structure or lack of spatial dependence; the variance is independent of the geographical distance between paired sampling locations. (2) A linear spatial structure (Linear model), in which the variance increases proportionally with lag distance, indicates that the spatial structure may extend beyond the scale sampled. (3) The remaining models (Gaussian, Spherical, Exponential) exhibit asymptotic spatial structure in which the variance becomes constant after a certain lag distance (Nansen et al. 2003). Where possible, various parameters were estimated from the fitted models: a) the range or the distance at which sample values are no longer correlated (i.e., when a plateau is reached), b) the sill ($C + C_o$) or the error variance when samples are no longer correlated, and c) the nugget (C_o) which is the γ intercept. Structural variance, calculated as a proportion of the total model variance [$C / (C + C_o)$], was used as a measure of spatial dependence (Klironomos et al. 1999). This value approaches one in a strongly spatially structured system with no nugget semivariance. Alternatively, in a system that has little structure or is structured at scales larger or smaller than those measured, the proportion of the total model variance represented by structural variance will approach zero (a pure nugget model).

Each semivariogram was calculated with a minimum of 30 data pairs per distance and with a maximum of half the total distance measured in any direction over the sampling space (Rossi et al. 1992). Directionality in the semivariogram analysis was not considered because of the rectangular shape of the sampling area which would have resulted in distances that were too small in one direction (Fortin 1999; Wu et al. 2002). Semivariograms were performed using GS+ version 7.0 (Gamma Design Software 2005).

For univariate autocorrelation analyses, we used Moran's I (Moran 1950) coefficient:

$$I = n\frac{\sum_{ij} w_{ij}\left(y_i - \bar{y}\right)\left(y_j - \bar{y}\right)}{W\sum_{i=1}^{n}\left(y_i - \bar{y}\right)^2} \qquad [2]$$

where y_i is the value of organic layer thickness, 3-year annual increment, or relative elevation at the i^{th} location, n is the number of points, w_{ij} are the weights in the weight matrix which were allocated with the inverse of the distance between points i and j, and $W = \sum_{ij} W_{ij}$, the sum of the values in the weight matrix. Moran's I is related to Pearson's correlation coefficient and is the most commonly used one in correlogram analysis. Values of Moran's I usually range between −1 and +1, but can exceed these limits when outliers are present. Positive and negative values of Moran's I indicates that points at a given lag are, on average, more similar or different, respectively, to each other than to the overall mean.

Autocorrelations were only computed for distance classes with a minimum of 30 pairs of points (Legendre & Fortin 1989) and only pairs of points separated by less than half the maximum distance observed were considered for the analysis (Rossi et al. 1992). Moran's I coefficient statistics were calculated for each distance class using the program PASSAGE (Rosenberg 2001). Auto-correlograms were tested for significance following Sokal and Oden (1978 a, b). A global test was made by checking whether the correlogram contains at least one value which is significant at the significance level according to the Bonferroni method of correcting for multiple tests (Oden 1984).

Cross-correlations (Rossi et al. 1992) were calculated between 3-year annual increment and organic layer thickness and between organic layer thickness and relative elevation. A cross-correlogram describes the correlation between two different variables as a function of the distance between samples. When the distance between samples is zero (both variables are sampled at the same location), the cross-correlogram yields the ordinary (non spatial) Pearson correlation coefficient. Cross-correlograms were performed using Variowin 2.2 (Pannetier 1997). For more information on semivariograms, correlograms and cross-correlograms, readers are invited to consult Legendre & Legendre (1998).

We expected that topographic paludification would be evident from 1) a peak in autocorrelation for relative elevation within the scales measured indicating a smaller spatial dependence combined with 2) a negative correlation between *Picea mariana* 3-year annual increment and organic layer thickness and between organic layer thickness and the microtopography in the mineral soil. In contrast, if paludification was caused by stand development (prior to the recent disturbance), we expected to find 1) a weak or absent autocorrelation for relative elevation within the scales measured and 2) little or no correlation between regenerating tree growth and organic layer thickness. A lack of influence of organic layer thickness on tree growth would indicate more homogenous environmental conditions created by a relatively flat microtopography of the mineral soil.

2.5. Results

2.5.1. Univariate spatial trends

Three-year annual increment and organic layer thickness varied significantly among plots, even within each site (Fig. 3a, b). Three-year annual increment was greater in the wildfire plots while the organic layer was thicker in the harvest plots. For relative elevation, microtopography was more variable in harvest plot 2 than in harvest plot 1 or wildfire plot 1 (Fig. 3c).

At a broad scale within each site, the proportion of the total model variance attributable to spatial structure (structural variance) for regenerating tree growth was higher in the harvest site than the wildfire site (Table 1). However, the spatial range (i.e., the distance at which sample values are no longer correlated) was greater in the wildfire than the harvest site (Fig. 4a, b; Table 1). Correlogram results were similar; regenerating tree growth was positively autocorrelated up to 20 m in the harvest site and up to 50 m in the wildfire site (Fig. 4c, d). Thus, regenerating trees closer than these distances were more similar in height than trees farther apart.

Spatial structure was similar on both sites for organic layer thickness as shown by a similar range of spatial dependence (Fig. 4e, f; Table 1). However, in the wildfire site, the semivariogram for organic layer thickness shows a hole effect which typically reflects pseudo-periodic or cyclic phenomena. Here, the hole effect relates to the existence of two variance peaks 30 m apart (Fig. 4f). This spatial pattern is also confirmed by the form of the correlogram which shows a distance of autocorrelation of ca. 30 m but with alternating peaks and troughs (i.e., regions of thick and thin organic layer) about 30 m apart (Fig. 4h). In contrast, the form of the correlogram in the harvest site is a single peak suggesting the site contains a single region with a thick organic layer (Fig. 4g). Structural variance for organic layer thickness was slightly higher in the harvest site (Table 1).

For relative elevation, spatial analysis was possible only for one plot in the wildfire site and two plots in the harvest site. In the wildfire plot, the semivariogram shows a range of spatial dependence of ca. 20 m (Table 1; Fig. 5a) and the form of the correlogram indicates a spatial pattern composed of small peaks and troughs (i.e., high and low relative elevation) separated by 20m (Fig. 5d). In both harvest plots variance peaks in the semivariogram indicate a range of spatial dependence at scales of ca. 40 m (Table 1; Fig. 5b, c). The correlograms show positive autocorrelation in relative elevation up to ca. 20 m for both harvest plots with subsequent negative autocorrelation in plot 2 at greater distances (Fig. 5e, f). However, the form of both correlograms (plots 1 and 2) suggest the presence of a deep depression in the landscape (i.e., single peak) with a range of influence of ca. 40m (Fig 5e, f). Structural variance for relative elevation was higher in the harvest site than in the wildfire site (Table 1).

At the fine scale (i.e., sub-plot), regenerating tree growth was randomly distributed (Nugget model) on ca. 60% of the sub-plots and showed a significant spatial structure (i.e., significant correlogram) on only one third of the sub-plots (Table 2). For organic layer thickness, more sub-plots showed a random spatial distribution in the harvest site (i.e., 50%) than in the wildfire site (i.e., 17%). Moreover, less than 60% of the correlograms for organic layer thickness had significant spatial structure in the harvest site, and 75% of the correlograms had significant spatial structure in the wildfire site. Relative elevation had significant spatial structure in most of the sub-plots, half of which were best fit to linear models which suggests spatial dependence often extended beyond the scales sampled.

2.5.2. Bivariate spatial trends

There was a significant but weak negative linear relationship between organic layer thickness and regenerating tree growth in the wildfire ($r^2 = 0.0530, p < 0.0001$, n = 360; Fig 6a) and the harvest ($r^2 = 0.0712, p < 0.0001$, n = 360; Fig 6a) sites. Although an exponential decay relationship between the thickness of the organic layer and black spruce growth is intuitive, we found that exponential curves were barely indistinguishable from the linear curves in both sites (results not shown). We expect that there is an exponential relationship which was approximately linear over the range of organic layer thickness that we studied. The cross-correlograms indicate that this negative correlation between regenerating tree growth and organic layer thickness persisted up to distances of ca. 20 m for the harvest site (Fig. 7a). At greater distances, the correlation was generally positive. In the wildfire, there was no relationship between regenerating tree growth and organic layer thickness (Fig. 7b).

Relative elevation and organic layer thickness were not significantly related in the wildfire plot (Fig 6b). However, there was a significant negative linear relationship between organic layer thickness and relative elevation in harvest plot 1 ($r^2 = 0.1007, p < 0.0001$, n = 139 ; Fig 6c) and in harvest plot 2 ($r^2 = 0.4134, p < 0.0001$, n = 139; Fig 6d). Thus, in the harvest site, organic layer accumulation was reduced on mounds where relative elevation was higher. The results from the cross-correlogram show that in the wildfire plot, the correlation between relative elevation and organic layer thickness oscillates between negative and positive at different distances (Fig. 7c). In the harvest plots, the correlation also switches from negative to positive and remains positive up to 50 m in plot 1 (Fig. 7d) and up to at least 70 m in plot 2 (Fig. 7e).

2.6. Discussion

The results suggest that in our study area organic matter accumulated in microtopographic depressions on the harvest site and during stand development on the wildfire site. However, the origin of the paludification cannot necessarily be attributed to the type of disturbance since the mineral soil layer (which is not affected by disturbance) at the harvest site was more undulating than at the wildfire site. Although the surface topography on the harvest site appeared relatively flat, spatial analysis revealed that the relative elevation of the mineral soil was variable. A negative relationship between relative elevation and organic layer thickness also indicates that organic matter accumulated in hollows of low relative elevation. In contrast, in the wildfire plot where analysis was possible, microtopography was less variable and the relationship between relative elevation and organic layer thickness was weaker. Therefore, it appears as if organic matter accumulated during stand development prior to the fire and was most likely reduced following the recent fire.

Differences in spatial structure between the harvest and wildfire sites could have been due to the different origin of paludification or disturbance type. Although the extent of autocorrelation of *Picea mariana* growth was greater in the wildfire site than the harvest site, the spatial pattern of organic layer thickness was similar in both sites. The difference for regenerating tree growth may be due to the different types of regeneration: regularly spaced planted seedlings in the wildfire site vs. a more clumped distribution of layers in the harvest site. Although we did not find any evidence several years after planting, the spatial pattern in the wildfire site might also have been affected by the remains of stored nutrients around the planted seedlings. It is possible that even though the soil transported with them was no longer distinguishable from the surrounding soil, nutrients from the transported soil may have affected past growth and created more uniform growth conditions resulting in a more homogenous spatial pattern of tree growth. In Finland, greater homogeneity in stand structure caused by extensive management was also considered an important factor in explaining greater autocorrelation in tree size in managed sites compared to primeval spruce forests (Kuuluvainen et al. 1996). The range of spatial dependence of the thickness of the organic layer in the wildfire site was comparable to that observed in a boreal Scots Pine stand (35 m, Hokkanen et al. 1995). The range of spatial dependence of the organic layer thickness was slightly shorter in the harvest than in the wildfire sites and this difference might have been the result of different microtopography.

The results suggest that the variation in the microtopography affects *Picea mariana* growth in the harvest site up to distances of 20-25 m where organic matter accumulated at lower elevations which then led to decreased *Picea mariana* growth. Deep depressions combined with the hard clay soil favoured the accumulation of water and the establishment of *Sphagnum* thereby facilitating the accumulation of low quality organic matter (i.e., fibric peat according to the Von Post decomposition scale, Lavoie et al. 2005). Therefore, poor growth conditions prevailed in deep depression, creating a more fine-grained spatial structure of *Picea mariana* growth (Giroux et al. 2001). In contrast, we attribute the near absence of a correlation between regenerating tree growth and organic layer thickness in the wildfire site to more homogenous environmental conditions created by a relatively flat microtopography of the mineral soil. The recent wildfire may also have created conditions more favorable to *Picea mariana* growth. Following fire there is a thinner humus layer, drier soil, higher pH, higher concentration of total and available nutrients, and better growth substrates (i.e., material made of feathermosses) as compared to following harvest (Nguyen-Xuan et al. 2000; Simard et al. 2001; Kasischke & Johnstone, 2005; Lavoie et al. in press). The type of regeneration (planted seedlings vs. layers) may also explain greater *Picea mariana* growth in the wildfire site than in the harvest site (Prévost and Dumais 2003).

Forest management strategies differ according to the origin of paludification because of its effect on soil substrate quality. On sites where paludification develops in the depressions of an undulating terrain, the presence of a poorly decomposed organic matter layer combined with wet conditions limits the use of equipment for mechanical site preparation and reduces the success of prescribed burning. In contrast, on sites where paludification occurred during stand development, the accumulated organic matter is well-decomposed. These conditions are more appropriate to prescribed burning and mechanical site preparation. Our method of determining the origin of paludification using spatial pattern analysis of relative elevation and organic layer thickness can facilitate forest management decisions.

2.7. Acknowledgements

We thank Mike Austin, H. Asselin and an anonymous reviewer for valuable comments on an earlier version of the manuscript. We thank Benoit Lafleur and Gabriel Diab for technical assistance in the field and Alain Leduc for statistical assistance. The study was funded by the NSERC-UQAT-UQAM Industrial Research Chair in Sustainable Forest Management, the Lake Abitibi Forest Model, Tembec, and the Canadian Forest Service. The senior author received a scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC) and from the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT).

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Table 2.1. Semivariogram model parameters for cumulative growth over the past 3 years (3-year annual increment (AI)) of regenerating spruce trees, thickness of the organic layer (OL) and elevation in wildfire and harvest sites.

	Plots	**Number of sampling points**[a]	**Sill** $(C + C_0)$	**Nugget** (C_o)	**Range** (m)	**Structural variance** $C/(C + C_o)$	**Model**[b]
Wildfire							
3-year AI	1,2,3	90	5.4	2.4	102.6	0.551	SPH
OL	1,2,3	192	143.2	52.8	33.8	0.631	EXP
Elevation	1	34	262.2	87.4	21.0	0.667	SPH
Harvest							
3-year AI	1,2,3	90	3.66	0.7	43.0	0.809	SPH
OL	1,2,3	192	538.2	165.6	30.3	0.692	SPH
Elevation	1	34	3582.0	10.0	32.2	0.997	GAU
Elevation	2	34	20270.0	0.0	49.4	1.000	GAU

[a] Three-year AI based on 30 points per sub-plot; elevation based on 34 points per sub-plot; thickness of the organic layer based on 64 points per sub-plot.

[b] Model: SPH = Spherical, EXP = Exponential, GAU = Gaussian.

Table 2.2. Number of sub-plots (max. 12) with nugget, linear and asymptotic models, as well as the number of significant correlograms (Moran's I) for cumulative growth over the past 3 years (3-year annual increment (AI)), thickness of the organic layer (OL) and elevation for wildfire and harvest sites. See Appendix 2 for detailed results.

	3-year AI[a]	**OL thickness**[a]	**Elevation**[a]
Wildfire			
Nugget model	7	2	1
Linear model	0	1	5
Asymptotic model[b]	5	9	6
Moran's *I*	6	9	10
Harvest			
Nugget model	8	6	0
Linear model	0	2	7
Asymptotic model[b]	4	4	5
Moran's *I*	2	7	11

[a] Three-year AI based on 30 points per sub-plot; elevation based on 34 points per sub-plot; thickness of the organic layer based on 64 points per sub-plot.

[b] Asymptotic models include Gaussian, Spherical and Exponential.

2.9. Figure captions

Figure 2.1. Location of the study area in Quebec (inset) and locations (circles) of the wildfire (W 1, 2, 3) and harvest (H 1, 2, 3) plots.

Figure 2.2. Sampling design for one plot. Each plot varied in size and included four 10 x 40 m sub-plots. Each sub-plot contained 64 points. Thirty four of these points were located on a regular sampling grid composed of 30 points at the intersections of 3 rows (3 m apart) and 10 columns (4 m apart) as well as four additional points at three corners and position [1 m 1 m]. The remaining thirty points were randomly selected.

Figure 2.3. Means with standard error bars in wildfire (F; white bars) and harvest (H; black bars) plots for: a) cumulative growth over the past three years (3-year annual increment (AI)) of regenerating spruce trees, b) organic layer (OL) thickness and c) relative elevation. Different letters indicate means that are significantly different from one another.

Figure 2.4. Auto-semivariograms and auto-correlograms (Moran's *I* coefficient) for: a and c) cumulative growth over the past three years (3-year annual increment (AI)) of regenerating spruce trees in harvest sites; e and g) organic layer (OL) thickness in harvest sites; b and d) cumulative growth over the past three years (3-year annual increment (AI)) of regenerating spruce trees in wildfire sites; f and h) organic layer (OL) thickness in wildfire sites. The results for the organic layer thickness are based on all 64 sampling points. In the auto-semivariograms, circles represent the semivariance at each distance and black lines represent the fitted semivariograms models. In the auto-correlograms, black circles indicate autocorrelation statistics that were significant after progressive Bonferroni correction ($\alpha =$ 5%) and white circles are non-significant values.

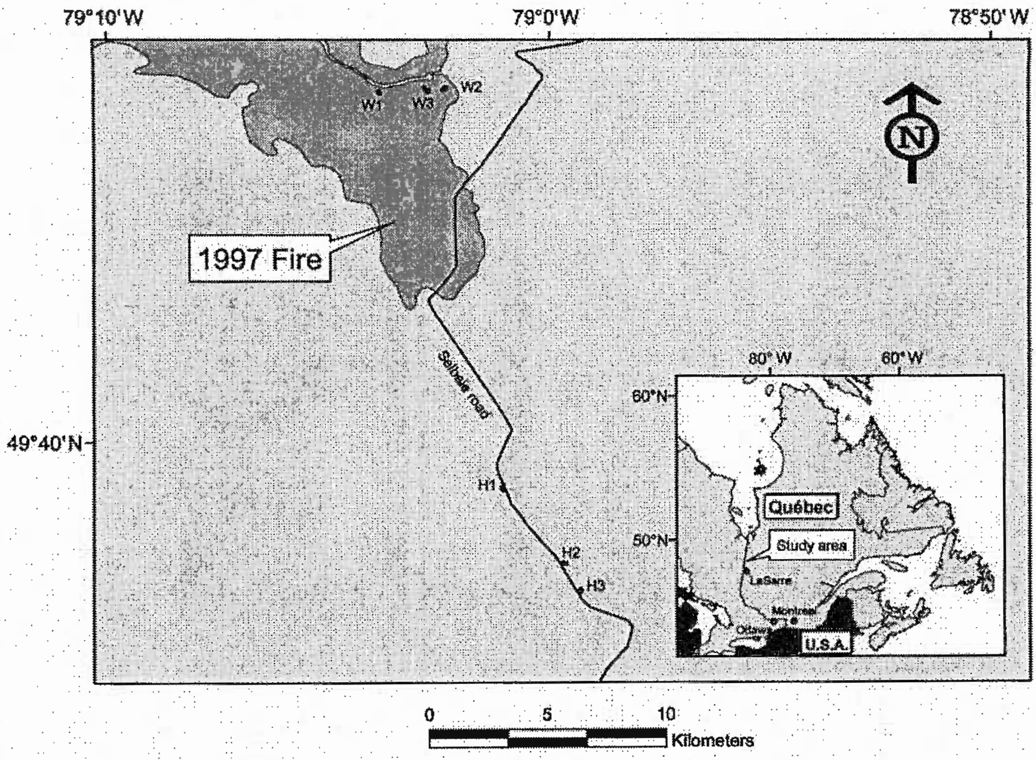
Figure 2.5. Spatial statistics for relative elevation in wildfire plot 1 and harvest plots 1 and 2: a-c) auto-semivariograms and d-f) auto-correlograms (Moran's *I* coefficient). In the auto-semivariograms, circles represent the semivariance at each distance and black lines represent the fitted semivariograms models. In the auto-correlograms, black circles indicate

autocorrelation statistics that were significant after progressive Bonferroni correction (α = 5%) and white circles are non-significant values.

Figure 2.6. Non-spatial relationships between variables: cumulative growth over the past three years (3-year annual increment (AI)) of regenerating spruce trees in relation to organic layer (OL) thickness (a) and and OL thickness in relation to relative elevation in the wildfire plot 1 (b), harvest plot 1 (c) and harvest plot 2 (d). In (a), white and black circles represent sampling points in the wildfire and harvest sites, respectively. Lines represent significant linear regressions ($R^2 = 0.0530$ and 0.0712 for the wildfire (solid line) and harvest (short dash line) sites in a, $R^2 = 0.1007$ and 0.3849 for c and d, respectively).

Figure 2.7. Cross-correlograms for: cumulative growth over the past three years (3-year annual increment (AI)) of regenerating spruce trees and organic layer (OL) thickness in the harvest (a) and wildfire (b) plots; and for relative elevation and OL thickness in wildfire plot 1 (c) and harvest plots 1 (d) and 2 (e).

Figure 2.1.


79°10'W
79°0'W
78°50'W
49°40'N
W1
W3
W2
1997 Fire
N
Selbaie road
H1
H2
H3
80°W
60°W
60°N
50°N
Québec
Study area
LaSarre
Montreal
Ottawa
U.S.A.
0
5
10
Kilometers

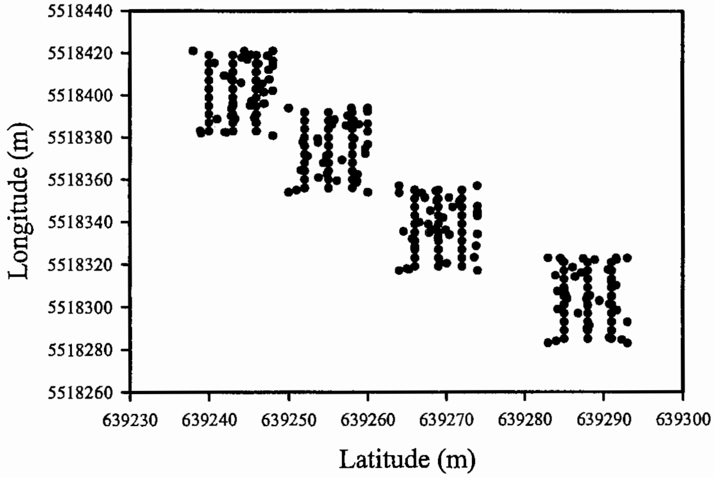

5518440
5518420
5518400
5518380
5518360
5518340
5518320
5518300
5518280
5518260
Longitude (m)
639230
639240
639250
639260
639270
639280
639290
639300
Latitude (m)

Figure 2.2.

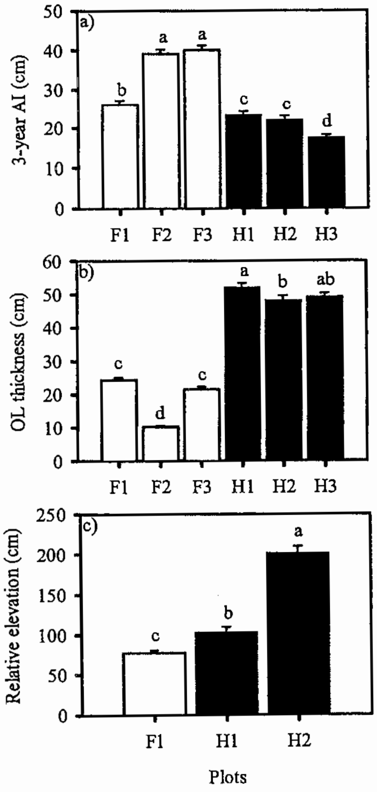

a)
3-year AI (cm)
0
10
20
30
40
50
b
a
a
c
c
d
F1
F2
F3
H1
H2
H3
b)
OL thickness (cm)
0
10
20
30
40
50
60
c
d
c
a
b
ab
F1
F2
F3
H1
H2
H3
c)
Relative elevation (cm)
0
50
100
150
200
250
c
b
a
F1
H1
H2
Plots

Figure 2.3.

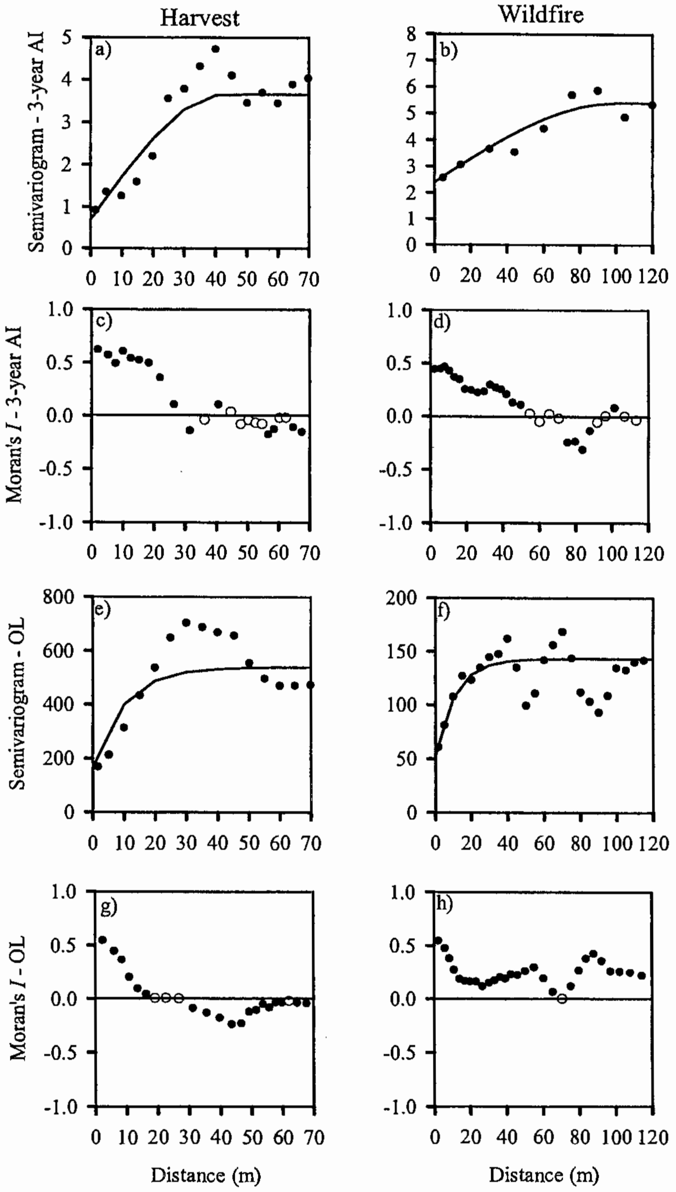

Harvest
Wildfire
Semivariogram - 3-year AI
Moran's I - 3-year AI
Semivariogram - OL
Moran's I - OL
a)
b)
c)
d)
e)
f)
g)
h)
0 10 20 30 40 50 60 70
0 20 40 60 80 100 120
Distance (m)
Distance (m)
5
4
3
2
1
0
8
7
6
1.0
0.5
0.0
-0.5
-1.0
800
600
400
200
200
150
100
50

Figure 2.4.

Figure 2.5.

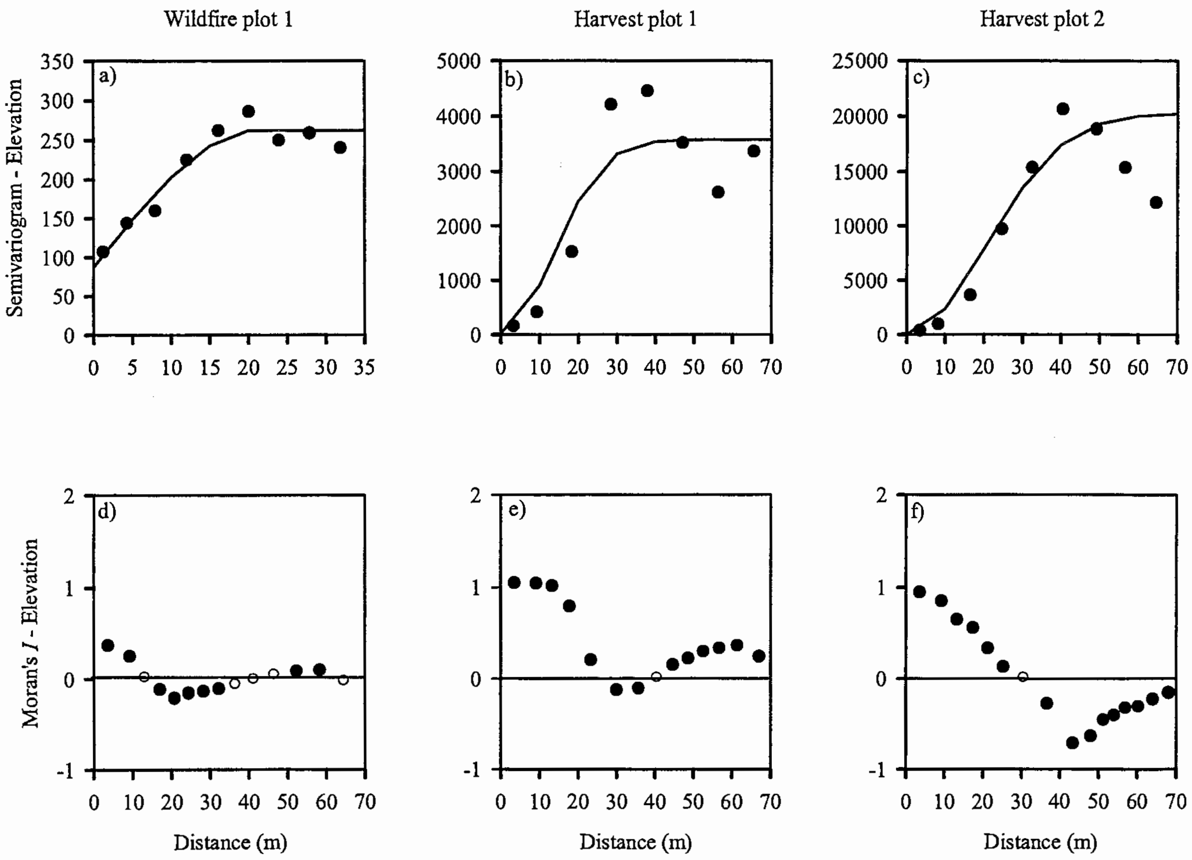

Wildfire plot 1
Harvest plot 1
Harvest plot 2
Semivariogram - Elevation
a)
b)
c)
350
300
250
200
150
100
50
0
0 5 10 15 20 25 30 35
5000
4000
3000
2000
1000
0
0 10 20 30 40 50 60 70
25000
20000
15000
10000
5000
0
0 10 20 30 40 50 60 70
Moran's I - Elevation
d)
e)
f)
2
1
0
-1
0 10 20 30 40 50 60 70
Distance (m)
Distance (m)
Distance (m)

Figure 2.6.

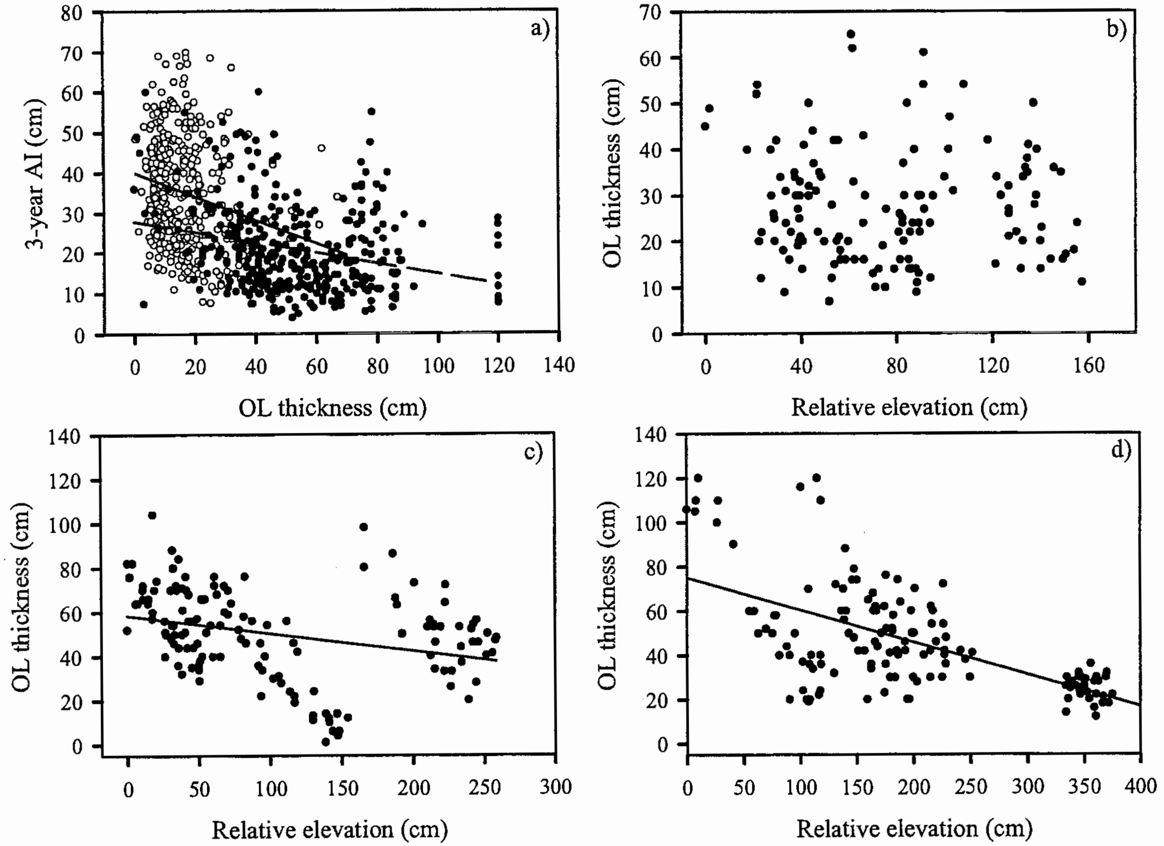
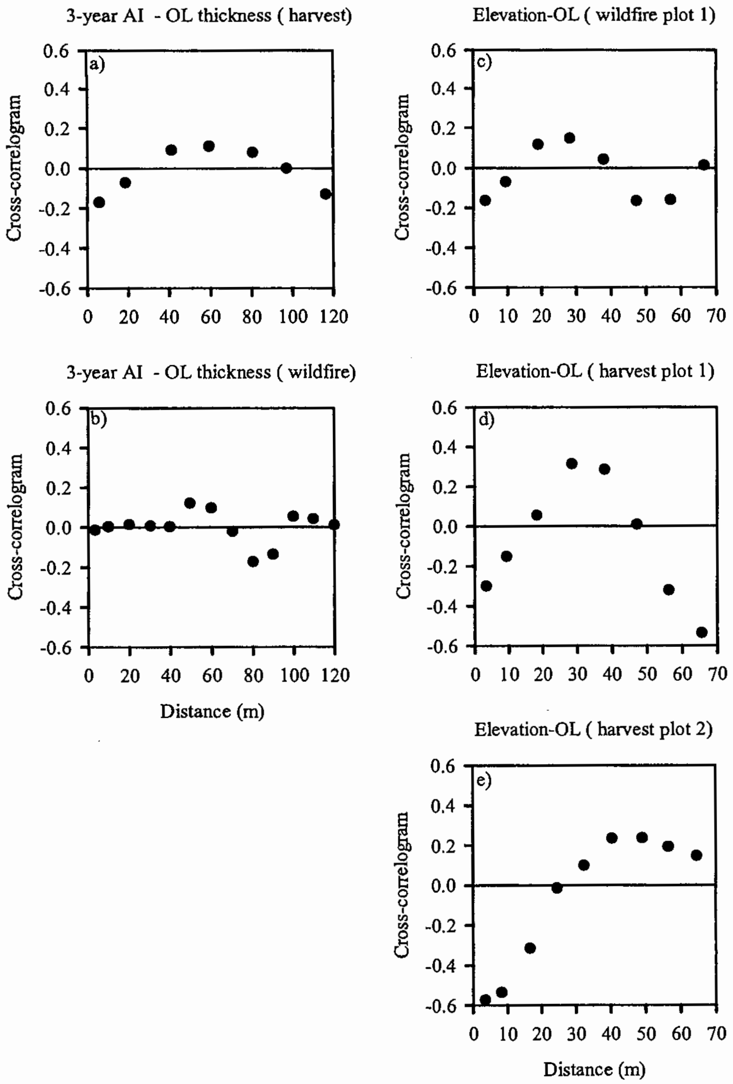

a)
3-year AI (cm)
0
10
20
30
40
50
60
70
80
OL thickness (cm)
0
20
40
60
80
100
120
140
b)
OL thickness (cm)
0
10
20
30
40
50
60
70
Relative elevation (cm)
0
40
80
120
160
c)
OL thickness (cm)
0
20
40
60
80
100
120
140
Relative elevation (cm)
0
50
100
150
200
250
300
d)
OL thickness (cm)
0
20
40
60
80
100
120
140
Relative elevation (cm)
0
50
100
150
200
250
300
350
400

Figure 2.7.


3-year AI - OL thickness (harvest)
a)
3-year AI - OL thickness (wildfire)
b)
Elevation-OL (wildfire plot 1)
c)
Elevation-OL (harvest plot 1)
d)
Elevation-OL (harvest plot 2)
e)
Cross-correlogram
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0
20
40
60
80
100
120
0
10
20
30
40
50
60
70
Distance (m)

Appendix 2.1. Formula used to fit the semivariograms to the spherical, gaussian, exponential and linear models.

Spherical semivariogram model :

$$\gamma_{12}(h) = \begin{cases} 0 & h = 0 \\ C_0 + C\left[\frac{3}{2}\left(\frac{h}{a}\right) - \frac{1}{2}\left(\frac{h}{a}\right)^3\right] & 0 < h < a \\ C_0 + C & h \geq a \end{cases}$$

Gaussian semivariogram model :

$$\gamma_{12}(h) = \begin{cases} 0 & h = 0 \\ C_0 + C\left[1 - \exp(-\left(\frac{3h^2}{a^2}\right)\right] & h > 0 \end{cases}$$

Exponential semivariogram model

$$\gamma_{12}(h) = \begin{cases} 0 & h = 0 \\ C_0 + C\left[1 - \exp(-\left(\frac{3h}{a}\right)\right] & h > 0 \end{cases}$$

Linear semivariogram model :

$$\gamma_{12}(h) = C_0 + b(C/a)$$

For all these models: (C_o) represents the variance due to sampling error and/or spatial dependence at scales not explicitly sampled; ($C + C_o$) represents the error variance when samples are no longer correlated (i.e., sill); (C) represents the spatially structured component; (a) represents the distance when sample values are no longer correlated (i.e., range); (h) is the effective range; and (b) is the slope.

Appendix 2.2. Semivariogram model parameters at the sub-plot (s) level for cumulative growth for the past three years (i.e., 3-year annual increment (AI)), organic layer (OL) thickness and elevation (elev) in wildfire and harvest sites.

				Semivariogram parameters					
	Variable	Grid	Points	Sill ($C+C_o$)	Nugget (C_o)	Range (m)	Q $C/(C+C_o)$	Model	R^2
Wildfire									
Plot 1 s 1	AI	R	30	3.3	3.3	-	0.000	NUG	0.054
Plot 1 s 2	AI	R	30	4.3	0.8	27.18	0.826	EXP	0.513
Plot 1 s 3	AI	R	30	3.8	3.8	-	0.000	NUG	0.030
Plot 1 s 4	AI	R	30	2.8	1.1	9.98	0.599	GAU	0.425
Plot 2 s 1	AI	R	30	3.3	3.3	-	0.000	NUG	0.054
Plot 2 s 2	AI	R	30	2.2	2.2	-	0.000	NUG	0.114
Plot 2 s 3	AI	R	30	3.1	3.1	-	0.000	NUG	0.168
Plot 2 s 4	AI	R	30	3.1	0.0	18.5	1.000	GAU	0.557
Plot 3 s 1	AI	R	30	31.4	31.4	-	0.000	NUG	0.000
Plot 3 s 2	AI	R	30	3.8	3.8	-	0.000	NUG	0.126
Plot 3 s 3	AI	R	30	2.6	0.0	17.8	1.000	GAU	0.477
Plot 3 s 4	AI	R	30	3.5	0.0	9.0	1.000	GAU	0.598
Harvesting									
Plot 1 s 1	AI	R	30	2.39	0.16	6.1	0.932	SPH	0.179
Plot 1 s 2	AI	R	30	2.1	1.0	15.1	0.500	SPH	0.909

Plot 1 s 3	AI	R	30	1.1	1.1	-	0.000	NUG	0.002
Plot 1 s 4	AI	R	30	0.76	0.38	6.5	0.501	SPH	0.063
Plot 2 s 1	AI	R	30	2.9	2.9	-	0.000	NUG	0.216
Plot 2 s 2	AI	R	30	3.0	3.0	-	0.000	NUG	0.235
Plot 2 s 3	AI	R	30	0.4	0.0	10.0	1.000	EXP	0.006
Plot 2 s 4	AI	R	30	0.9	0.9	-	0.000	NUG	0.320
Plot 3 s 1	AI	R	30	0.3	0.3	-	0.000	NUG	0.028
Plot 3 s 2	AI	R	30	0.1	0.1	-	0.000	NUG	0.061
Plot 3 s 3	AI	R	30	0.8	0.8	0.75	0.000	NUG	0.000
Plot 3 s 4	AI	R	30	0.8	0.8	1.2	0.000	NUG	0.011
Wildfire									
Plot 1 s 1	Elev	S	34	188.4	39.3	31.5	0.788	GAU	0.874
Plot 1 s 2	Elev	S	34	830.9	160.0	31.3	0.807	GAU	0.818
Plot 1 s 3	Elev	S	34	142.6	16.5	12.8	0.885	SPH	NA
Plot 1 s 4	Elev	S	34	205.0	205.0	-	0.000	NUG	0.145
Plot 2 s 1	Elev	S	34	290.0	0.0	25.0	1.000	EXP	0.531
Plot 2 s 2	Elev	S	34	1704.0	93.0	31.5	0.945	EXP	0.953
Plot 2 s 3	Elev	S	34	487.2	26.0	25.7	0.947	GAU	0.913
Plot 2 s 4	Elev	S	34	-	111.0	-	0.000	LIN	NA
Plot 3 s 1	Elev	S	34	-	51.0	-	0.000	LIN	NA
Plot 3 s 2	Elev	S	34	-	10	-	0.000	LIN	NA
Plot 3 s 3	Elev	S	34	-	130.0	-	0.000	LIN	NA
Plot 3 s 4	Elev	S	34	-	80.0	-	0.000	LIN	NA
Harvesting									

Plot 1 s 1	Elev	S	34	-	109.0	-	0.000	LIN	NA
Plot 1 s 2	Elev	S	34	813.9	5.0	23.3	0.994	SPH	0.672
Plot 1 s 3	Elev	S	34	920.0	270.0	21.0	0.710	GAU	0.556
Plot 1 s 4	Elev	S	34	499.2	96.0	26.8	0.808	GAU	0.924
Plot 2 s 1	Elev	S	34	-	650.0	-	0.000	LIN	NA
Plot 2 s 2	Elev	S	34	-	420.0	-	0.000	LIN	NA
Plot 2 s 3	Elev	S	34	-	350.0	-	0.000	LIN	NA
Plot 2 s 4	Elev	S	34	878.0	1.0	14.3	0.999	SPH	0.664
Plot 3 s 1	Elev	S	34	-	71.0	-	0.000	LIN	NA
Plot 3 s 2	Elev	S	34	1400.0	0.0	23.0	1.000	SPH	0.870
Plot 3 s 3	Elev	S	34	-	200.0	-	0.000	LIN	NA
Plot 3 s 4	Elev	S	34	-	204.0	-	0.000	LIN	NA
Wildfire									
Plot 1 s 1	OL	S + R	64	86.7	0.0	3.6	1.000	SPH	0.780
Plot 1 s 2	OL	S + R	64	166.5	80.2	35.0	0.518	SPH	0.559
Plot 1 s 3	OL	S + R	64	206.5	35.4	14.4	0.829	EXP	0.691
Plot 1 s 4	OL	S + R	64	-	92.3	-	0.000	LIN	NA
Plot 2 s 1	OL	S + R	64	35.0	0.0	22.0	1.000	EXP	0.023
Plot 2 s 2	OL	S + R	64	25.0	25.0	-	-	NUG	0.129
Plot 2 s 3	OL	S + R	64	104.7	44.2	28.5	0.578	GAU	0.747
Plot 2 s 4	OL	S + R	64	15.0	15.0	-	0.000	NUG	NA
Plot 3 s 1	OL	S + R	64	52.7	26.3	10.0	0.500	SPH	0.574
Plot 3 s 2	OL	S + R	64	447.6	42.2	15.7	0.906	GAU	0.905
Plot 3 s 3	OL	S + R	64	190.0	110.0	30.0	0.395	SPH	0.527

Plot 3 s 4	OL	S + R	64	277.8	77.4	33.0	0.721	GAU	0.734
Harvesting									
Plot 1 s 1	OL	S + R	64	187.1	187.1	-	0.000	NUG	0.063
Plot 1 s 2	OL	S + R	64	1100.0	0.0	27.0	1.000	SPH	0.743
Plot 1 s 3	OL	S + R	64	-	16.1	-	0.000	LIN	NA
Plot 1 s 4	OL	S + R	64	173.9	74.5	3.0	0.573	GAU	0.508
Plot 2 s 1	OL	S + R	64	57.1	57.1	-	0.000	NUG	0.016
Plot 2 s 2	OL	S + R	64	-	135.0	-	0.000	LIN	NA
Plot 2 s 3	OL	S + R	64	460.0	164.0	22.4	0.643	GAU	0.784
Plot 2 s 4	OL	S + R	64	240.0	240.0	-	0.000	NUG	0.016
Plot 3 s 1	OL	S + R	64	230.0	230.0	-	0.000	NUG	0.276
Plot 3 s 2	OL	S + R	64	862.0	156.0	14.7	0.819	GAU	0.800
Plot 3 s 3	OL	S + R	64	205.8	205.8	-	0.000	NUG	0.033
Plot 3 s 4	OL	S + R	64	130.3	130.3	-	0.000	NUG	0.002

Note: R = random; S = systematic; Model: SPH = Spherical, EXP = Exponential, LIN = Linear; GAU = Gaussian, NUG = Nugget; Q= structural variance; Sill: $(C+C_o)$ = C indicates the spatially structure variance and C_o represents the variance due to sampling error and/or spatial dependence at scales not explicitly sampled; NA = not available.

CHAPITRE 3

Relationships between micro-site type and the growth and nutrition of young black spruce on post-disturbed lowland black spruce sites in Eastern Canada

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3.1. Abstract

The soil surface of recently harvest or burned lowland black spruce sites is composed of a fine mosaic of different bryophytes (mostly *Sphagnum* and feathermosses) of disturbed organic material originating mostly from mosses at different stages of decay, and of exposed mineral soil. Growth substrates were compared in lowland black spruce stands regenerating after either careful logging or wildfire. Black spruce seedling annual increment was greatest with substrates of *Pleurozium*, fibric material of *Pleurozium* origin, and a mixture of fibric *Pleurozium* and humic materials; it was least with fibric *Sphagnum*, mineral soil and decaying wood substrates. The most favourable substrates for growth were characterized by better spruce N and P foliar status. Our results also suggest that categories of growth substrates in the rooting zone reflect nutritional quality better than categories of growth substrates on the soil surface. To maintain or increase black spruce growth following careful logging of sites prone to paludification, we recommend fill-planting of seedlings in substrates originating from *Pleurozium*; management techniques that promote *Pleurozium* to the detriment of *Sphagnum* mosses should also be developed.

3.2. Résumé

La surface du sol de sites récemment récoltés ou brûlés dans des peuplements d'épinettes noires de basses terres est composée d'une fine mosaïque de différents types de bryophytes, principalement les sphaignes et les mousses hypnacées, de matière organique perturbée composée de différents types de mousses à différents degrés de décomposition et de sol minéral exposé. Les substrats de croissance qu'on retrouve dans des peuplements d'épinettes noires de basses terres provenant de sites régénérés suite à la coupe avec protection de la régénération et des sols (CPRS) ou suite à un feu ont été comparés. Les résultats suggèrent que la croissance en hauteur des semis d'épinette noire est plus élevée avec les substrats de *Pleurozium schreberi*, de matériel fibrique composées de *Pleurozium* et d'un mélange de matériels fibrique (composé de *Pleurozium*) et humique qu'avec la sphaigne fibrique, le sol minéral et le bois mort. Les substrats de croissance les plus favorables à la croissance sont caractérisés par une meilleure nutrition en azote et phosphore. Nos résultats suggèrent également que la classification des substrats de croissance au niveau des racines est plus indicative de leur valeur nutritive que la classification des substrats de croissance localisés en surface. Basé sur ces résultats, pour maintenir ou augmenter la croissance en hauteur de l'épinette noire après coupe sur des sites susceptibles à la paludification, nous recommandons que la plantation dans des substrats formés de *Pleurozium* et un aménagement qui favorise la présence de *Pleurozium* au détriment des sphaignes soient favorisés.

3.3. Introduction

In Canada, the Clay Belt region of Quebec and Ontario supports a large forest resource that is important to the forest industry. Because of the strong demand for wood products as well as the increasing pressure to set land aside for conservation purposes, forestry operations in this area are being pushed towards the northern limit of the commercial forest. In lowland James Bay in Quebec and in northeastern Ontario, most of the harvesting volumes allotted to forest companies are located in low productivity peatlands (Prévost et al. 2001). These stands originate from stand replacing wildfire (Bergeron et al. 2004) but in the absence of subsequent fires, developed an irregular structure (Lecomte et al. in press). Wildfire severity and time since fire have been identified as important factors contributing to forest floor thickness, moss cover type, and stand structure and productivity (Lecomte et al. 2006).

In Quebec, the boreal forest is generally harvested with the cutting with protection of regeneration and soils or CPRS (i.e., coupe avec protection de la régénération et des sols) system (Messier et al. 2004). CPRS is used in all conifer stands irrespective of characteristics (e.g., organic matter thickness, topography, etc.) or soil properties (e.g., drainage, nutrient pools). In Ontario, this harvesting system is called careful logging of around advanced growth (CLAAG) and is applied to very specific ecosites. In the Clay Belt, CLAAG is mostly used in lowland stands (i.e., ecosites 11 and 12; Kim Taylor, NESI, Terrestrial Ecologist and Dean Cedarwall, NE Region FMP Specialist, personal communication February 3, 2006).

As the aim of careful logging systems such as CPRS and CLAAG is to minimize soil disturbance and protect advanced regeneration, harvesting in forested peatlands is often carried out during winter for added protection. Currently, when the stocking and density of advance regeneration are good before harvesting, Careful logging systems are regarded as good harvesting methods given that regeneration density and stocking after logging are high

(Harvey and Brais 2002). Nevertheless, in spite of its general application, careful logging may not be the best harvesting method in certain areas, notably in northern black spruce forests located on the Till of Cochrane in the Clay Belt (Lecomte and Bergeron 2005). In this area the mineral soil is generally heavily compacted, which facilitates paludification, and growth problems in post-harvest stands have been observed (see review in Lavoie et al. 2005).

The soil surface of black spruce lowlands is composed of a large number of micro-site types that vary over short distances; one single type does not usually cover more than a few square meters, and often less than a single square meter. These micro-sites are the result of site drainage, disturbance history and especially the type and severity of the last disturbance. They are mainly composed of disturbed and undisturbed layers of mosses at different stages of humification. Exposed mineral soil can also be found, as well as organic debris.

Black spruce seedbeds are relatively well understood and differences between the effects of fire and logging on spruce germination are described in the literature (Pothier 2000; Greene et al. 2004; Jayen et al. 2006). Very little information, however, is currently available that describes the best substrates (i.e., micro-sites) for black spruce growth in lowland stands once seedlings are established through either natural or artificial means. To our knowledge, only two studies had been conducted on the quality of *Sphagnum* vs. *Pleurozium* for black spruce seedling growth, and these are mostly for advance regeneration in mature forests (Arnott 1968; Jeglum 1981) However, the quality of the great variety of substrates that are found after disturbance (including mineral soil, burned substrates, other living bryophytes (e.g., *Polytrichum* spp.), exposed organic substrates at different stages of decomposition and woody debris) have not been evaluated under field conditions. It is important that this be done because as the use of emulation silviculture (i.e., inspired from natural disturbances) increases in Canada (McRae et al. 2001), soil conditions following forestry operations are being compared with those found following wildfire (Keenan and Kimmins 1993). The information on substrate quality will also be valuable in forestry operations because it will help to evaluate the relevance of exposing soil layers during harvest or site preparation operations or to determine what substrates should be favoured during plantation.

The objective of this study was to identify and characterize the soil substrates that are found on post-disturbed sites of the Clay Belt region and to determine how black spruce growth and nutrition are related to soil substrate (micro-site) types.

3.4. Materials and Methods

3.4.1. Study area

The study area was located in northwestern Quebec (49°48' N; 79°01' W) and northeastern Ontario (49°45' N; 80°40' W). The field work was conducted in two areas that both included sites affected by large wildfires that occurred in June 1997. In Quebec, the studied area included a 540 km^2 wildfire and adjacent logged sites (CPRS), and in Ontario it included a 24.5 km^2 wildfire site and adjacent cutblocks (CLAAG). In Quebec, the study area is part of the ecological area of the plain of the Lake Matagami bioclimatic domain, which is part of the western black spruce-feathermoss community (Bergeron et al. 1999). According to Quebec's classification system, stands within this study belong to two ecological types: 1) black spruce (*Picea mariana* (Mill.) BSP) stand with *Sphagnum* on mineral deposit, and 2) black spruce stand with *Sphagnum* on thick organic deposit with hydrous drainage (i.e., forested peatland) (Bergeron et al. 1999). In Ontario, the study sites are located in the Lake Abitibi Model Forest (LAMF) which belongs to site region 3e (Jones et al. 1983). The study sites, according to Ontario's classification system, are located in ecosites ES 11–Ledum and ES 8–Feathermoss-*Sphagnum* (Taylor et al. 2000). These sites are dominated by black spruce accompanied by balsam fir (*Abies balsamea* (L.) Mill.) and tamarack (*Larix laricina* (Du Roi) K. Koch). Labrador tea (*Rhododendron groenlandicum* Oeder) dominates the shrub cover, with blueberries (*Vaccinium* spp.) and sheep laurel (*Kalmia angustifolia* L.) also present. *Sphagnum angustifolium, S. capillifolium, S. rubellum, S. russowii, S. fuscum, S. magellanicum* and feathermosses (mainly *Pleurozium schreberi*) cover the forest floor across a landscape of hummocks and hollows. The study area is typical of the Clay Belt, a territory characterized by important glacial lacustrine deposits left by the glacial lakes Barlow and Ojibway (Vincent and Hardy 1977).

According to nearby weather stations, the mean annual temperature is 0.1 to 0.9 °C, annual precipitation is 776 to 892 mm, and there are 64 to 90 frost-free days (Joutel, Quebec, and Iroquois Falls, Ontario weather stations respectively) (Environment Canada 2004).

3.4.2. Plot layout

Two plots were established in the Ontario post-wildfire site and two others in the adjacent cut. In Quebec, three plots were established on each disturbance type, for a total of 10 plots. Plots were at least 500 m apart and each plot was composed of four 400 m^2 sub-plots, for a total of 40 sub-plots. All plots were located on sites with a relatively flat topography, with clay deposits, and with poor drainage. Based on forest and fire maps, all sites were older than 120 years before disturbance, with a maximum tree height lower than 17 m and with canopy cover of less than 60% (Ministry of Natural Resources of Ontario 1993; Ministère des Ressources naturelles du Québec 1999; Bergeron et al. 2004).

3.4.3. Regeneration survey

Micro-site sampling was completed during summer 2003. Thirty regenerating trees, regardless of their origin, were studied in each of the 40 sub-plots. Regenerating trees are defined by height rather than by age. The great majority of trees on this site were short (less than 1.3 m in height). The site also contained taller trees that were presumably all remnants. Those trees were not considered because we wanted to limit the study to trees that achieved most of their growth following the disturbance. The micro-site around each regenerating black spruce tree was determined by a radius equivalent to the total height of the plant. For each tree (<1.30 m), we determined type of regeneration (layer-origin, planted seedlings, and seed-origin), total height, the cumulative growth for the past three years (i.e., 3-year annual increment; years 2000, 2001 and 2002), root collar diameter (RCD), mean length of three side branches (LSB), and the position of regeneration (micro-topography: hummock, slope, depression and flat). The percent cover of ericaceous shrubs (mainly *Rhododendron groenlandicum*) was also determined by ocular evaluation for each regenerating tree. Growth substrates were sampled at the soil surface and in the rooting zone. In order to evaluate the appropriate root depth in each sub-plot, 30 regenerating black spruce trees were dug out randomly in different substrates to measure root depth. The results showed that the average root depth was 9.8 cm (SD = 4.38; n = 356). Therefore, the rooting zone was determined to be 10-15 cm, on average. We distinguished 16 growth substrates, 11 at the surface and 5 in the rooting zone (see Table 1). We separated the decomposed material coming from mosses into two major classes: 1) *Pleurozium schreberi* as fibric *Pleurozium* after harvesting and as burned *Pleurozium* after wildfire; and 2) *Sphagnum* as fibric *Sphagnum* after harvesting and as burned *Sphagnum* after wildfire. This classification was based on the assumption that feathermoss-based substrates (mainly *Pleurozium schreberi* in our sites) were more favourable than *Sphagnum* to black spruce growth (Arnott 1968; Jeglum 1981; Klenk 2001).

3.4.4 Soil and foliar analyses

The nutritional value of all micro-sites was evaluated in three ways: 1) by substrate analysis (C and total N, CEC and pH), 2) by seedling foliar analysis (N, P, K, Ca and Mg), and 3) by seedling growth measurements. Growth substrates and needles were sampled in a way to include all types of substrates found at the sub-plot level. Due to logistics and budget limitations, and also because regenerating trees often had more than one type of substrate (soil surface and rooting zone), substrate sampling was reduced to 658 samples. Our objective was to sample a minimum of 50 samples of each dominant substrate type, but we were unable to achieve this for those substrates that were less abundant. Substrate samples were immediately placed in coolers, returned to the laboratory and frozen. Immediately prior to analysis, all substrate samples were air-dried at 30 °C for 48 h and ground to pass through 6-mm sieves. Substrate pH was analyzed in distilled water and $CaCl_2$ (Carter 1993). Total C and N were determined by wet digestion and analyzed with a LECO CNS-2000 analyzer (LECO Corporation). Exchangeable cations were extracted using unbuffered 0.1 M $BaCl_2$ and determined by atomic absorption (Hendershot et al. 1993). Cation exchange capacity (CEC) was defined as the sum of exchangeable cations (Na_e, K_e, Mg_e, Ca_e, Mn_e, Fe_e and Al_e). Mineral soil texture was determined by granulometric analyses (Carter 1993).

Needle samples were collected in late September 2003 when the growing season had ended. Needle samples were collected from seven randomly selected regenerating trees per sub-plot, thus yielding a total of 280 samples of which 265 were kept for the analysis (134 samples in the harvest plots and 131 samples in the wildfire plots), as the discarded ones were found on multiple substrate types. Needle samples were selected from the current year's growth and were sampled from various positions in the crown (mid, top 1/3, and leader) and mixed. For the same reasons mentioned above, needle sampling was restricted. We also randomly selected all needle samples in each plot and type of disturbance. Samples for needle and substrate analysis were not necessarily located at the same tree locations. These samples were oven-dried at 70 °C for 48 h. After drying, needles were separated from twigs and ground. Total C and N were determined as for the substrates on a CNS analyzer while total cations and phosphorus were determined following calcination at 500 °C and dilution with hydrochloric acid (Miller 1988). Cations were analyzed by atomic absorption, and P by colorimetry (Lachat Instruments, Milwaukee, WI).

3.4.5. Data analysis

The preliminary redundancy analysis (RDA) (ter Braak and Smilauer 1998) explained very little of the variation (less than 26%) in black spruce growth. The RDA also showed that the type of regeneration greatly contributed to black spruce growth variability, and that there was a close relationship between the type of regeneration and substrate availability. For example, we found more planted trees and *Polytrichum* spp. after wildfire, while layers and *Pleurozium* were more abundant after harvesting. Therefore, to control the effect of regeneration type and substrate availability, subsequent analyses were performed only with planted seedlings. We used planted seedlings because it was the only type of regeneration that was found on the various substrates. Moreover, to test more effectively the effect of substrate on black spruce growth, we have decided to use only planted trees with pure substrates (i.e., substrates dominated by a single substrate type by more than 70%) for subsequent analyses. This step was necessary since trees were often growing in more than one type of substrates. Thus, this reduced the initial database of 1200 regenerating trees down to 454/401 (rooting zone/soil surface) planted seedlings, and several substrate types (decaying wood, mixture of fibric *Pleurozium* and humic materials, and mineral soil) could not be considered anymore and were discarded from further analysis.

Box plots were used to compare the properties of substrates as well as foliar nutrient concentrations of regenerating black spruce trees growing on different substrates. The relationship between 3-year annual increment (AI), foliar nutrient concentration and needle weight was determined using stepwise regression (holding p to enter = 0.1 and p to remove =

0.05) with a subset of 265 regenerating trees (i.e., each regenerating tree used for needle sampling).

Canonical discriminant analysis can be used to classify a category-dependent variable that has more than two categories, based on a number of interval-independent variables. We used it to investigate the differences among growth substrates (testing rooting zone and soil surface separately) and to find both the combination of substrate nutrient concentrations, and the combination of foliar nutrient concentrations that can be used to best distinguish these substrates.

A mixed linear model was used to assess the effect on black spruce growth (3-year AI) of the two most abundant substrates that were present in all plots (*Pleurozium* and *Sphagnum*, which covered over 90% of the soil surface), the type of disturbance (wildfire and careful logging), and the interaction of these two factors while taking randomization restrictions into account. The use of a mixed linear model was possible only with *Pleurozium* and *Sphagnum* categories due to the low number of samples and the poor distribution of the other growth substrates. Inverse transformation was used to correct non-normally distributed data. Two (one highest and one lowest) outliers also had to be taken out of the database in order to correct for normality. A second mixed linear model was used to control the effect of the type of regeneration on black spruce growth, with growth substrate as the fixed effect. Square root transformation was used to achieve normality. All statistics were conducted with SAS 8.02 (SAS Institute Inc. 2001).

3.5. Results

3.5.1. Growth substrates

Overall, *Sphagnum* followed by *Pleurozium schreberi* and burned *Pleurozium* constituted the most abundant soil surface substrates, while fibric *Sphagnum* followed by fibric *Pleurozium* were the most abundant in the rooting zone. In wildfire plots, burned substrates (*Pleurozium* = 43%; *Sphagnum* = 16%) and *Polytrichum* spp .(26%) were the most abundant substrates at the soil surface while fibric *Pleurozium* (55%) and fibric *Sphagnum* (38%) were the most important substrates in the rooting zone (Fig. 1). Following careful logging, *Sphagnum* spp. (50%) and *Pleurozium* (33%) were the most abundant substrates at the soil surface, while fibric *Sphagnum* (64%) and fibric *Pleurozium* (34%) were the most abundant substrates available in the rooting zone (Fig. 1). A chi square test showed that at both depths (soil surface and rooting zone) the substrate distribution differs significantly (p = 0.001) between wildfire and careful logging.

3.5.2. Cumulative growth for the past 3-year

Planted seedlings exhibit a considerable variation in the growth response depending on growth substrates (Fig. 2). At the soil surface, all substrates, except for the mixture of organic and mineral soils and burned *Sphagnum*, had a normal distribution (data not shown). Black spruce 3-year AI was significantly less when growing on burned *Sphagnum* (only 23 cm) than on any other surface substrate ($p < 0.0001$). For the rooting zone, only mineral soil and the mixture of fibric *Pleurozium* and humic materials resulted in a normal distribution. Box plot results showed that the last 3-year AI was significantly ($p < 0.0001$) higher with the mixture of fibric *Pleurozium* and humic materials (46 cm), than fibric *Pleurozium* (36 cm), mineral soil (28 cm), and fibric *Sphagnum* (25 cm); however all substrates exhibited a wide range of values.

The properties of each substrate are presented in Figure 3. At the soil surface, pH in water and in $CaCl_2$ was significantly lower in decaying wood. CEC was similar in all substrates except for significant lower values in mineral soil ($p < 0.0001$). For soil surface substrates, the C/N ratio was significantly higher in decaying wood and lower in mineral soil ($p < 0.0001$). For the rooting zone, soil pH was significantly higher in mineral soil (in water and in $CaCl_2$) and lower in decaying wood (in water and in $CaCl_2$) ($p < 0.0001$). As for CEC, decaying wood and mineral soil showed significant lower average concentrations than the other substrates. Carbon and nitrogen ratios was significantly higher in decaying wood followed by fibric *Sphagnum*, fibric *Pleurozium*, mixtures of fibric *Pleurozium* and humic materials, and mineral soil ($p < 0.0001$) (Fig. 3).

3.5.3. Tree nutrition

All needle nutrient concentrations (except Mg) showed a significant positive correlation with 3-year AI (Fig. 4), with N and P having the highest level of correlation with 3-year AI. However, r-values were low (< 0.37). Needle samples were randomly collected on each regenerating tree growing in the different micro-sites. Some trees were growing in micro-sites composed of pure substrate (i.e., > 70% cover of one substrate), and others were growing in micro-sites composed of several substrates. In order to retain the greatest number of samples in the analysis, we created substrate classes that were either pure or a mixture of two substrates in relatively equivalent proportions (ranging from 40 to 60%). At the soil surface (i.e., 10 substrate classes) and for the rooting zone (i.e., 6 substrate classes), the effect of growth substrates on foliar nutrient concentration were very variable within each substrate (Table 2). High variability in foliar concentration was found within substrate types and values ranged from deficiency to optimal levels, according to Stewart and Swan (1970) and Lowry (1975). Although average nutrient concentration values were at a sufficiency level for N, P and K, they expressed deficiency for Mg and excess of consumption levels for Ca. Suggested standard foliar concentrations for black spruce reported by Stewart and Swan (1970) for the range "transition zone from deficiency to sufficiency" are: N (1.20-1.50 %); P (1.4-1.8 mg g^{-1}); K (3.0-4.0 mg g^{-1}); Mg (0.9-1.2 mg g^{-1}); and Ca (1.0-1.5 mg g^{-1}). The statistics for multiple linear regression models are shown in Table 3. The variables that performed the best in predicting 3-year AI for black spruce were developed from needle P concentrations ($R^2 = 0.171$). Adding needle N concentration and needle weight increased the fit between the measured and predicted 3-year AI of regenerating black spruce trees ($R^2 = 0.227$).

Discriminant analysis indicated that the seven main growth substrates at the soil surface were significantly separated by the first four of the six canonical functions. Of the nine variables included in the canonical discriminant analysis to evaluate differences among growth substrates at the surface, Na_e, K_e and pH had the greatest discriminatory importance for the first two canonical functions (Table 4) and explained 73% of the total variance. The first canonical axis represents the direction of the greatest variance (58%) between growth substrates at the soil surface. Na_e, K_e and pH were the variables with the highest correlation to the first axis. The second canonical axis represents 15% of the variance between growth substrates for the soil surface. An overall classification accuracy of 50% was obtained for growth substrates at the soil surface (Table 5). Classification accuracy (i.e., the analysis evaluates the performance of a discriminant criterion by estimating error rates in the classification of future observations) was reduced by a high statistical misclassification (i.e., poor performance) for the following growth substrates: fibric *Pleurozium*, burned *Sphagnum* and fibric *Sphagnum*.

For the rooting zone, the discriminant analysis indicated that the four main growth substrates were significantly separated by the three canonical functions. Of the nine variables included in the canonical discriminant analysis to evaluate differences among growth substrates, N_t, pH and Fe_e had the greatest discriminatory importance for the first two canonical functions (Table 4) and explained 94% of the total variance. The first canonical axis represents the direction of the greatest variance (83%) between growth substrates for the rooting zone. N_t, pH and Fe_e were the variables with the highest correlation to the first axis. The second canonical axis represents 11% of the variance between growth substrates for the rooting zone. The same variables influencing axis 1 had the most influence on axis 2, but the direction of the correlation differed for pH and Fe_e. The overall success of classifying samples into the four growth substrates correctly was 74%. Group membership was predicted well for three of the four growth substrates (Table 5).

Discriminant analysis was also used to classify growth substrates at the soil surface and for the rooting zone, this time based on the foliage nutrient concentration (N, P, Ca, Mg, K) of trees growing in these substrates. Classification accuracy was very low (25% and 46% for the soil surface and rooting zone, respectively; results not shown). This low accuracy might be explained in part by substrate classes created from a mixture of two substrates (40 to 60% of each). Three of the ten growth substrates were a mixture of two substrates at the soil surface, and three of six growth substrates were a mixture of two growth substrates in the rooting zone.

As shown in Figure 1, growth substrates at the soil surface are mainly *Pleurozium* and *Sphagnum* after harvesting and, burned *Pleurozium* and burned *Sphagnum* after wildfire, and these types are present in almost all harvest or burned subplots, respectively. Thus, a mixed linear model was used to test the effect of the two main substrates (i.e., *Pleurozium* vs. *Sphagnum*), the type of disturbance (wildfire and careful logging) and the interaction of these two factors on 3-year AI. Since we used only planted seedlings for analysis, the type of disturbance and the interaction between substrate and disturbance could not be tested because many plots in harvest sites did not have planted trees. The random effects selected in the model were zone (Quebec or Ontario), the interaction "zone and type of disturbance", and sub-plots nested in the interaction "zone, type of disturbance and plot". The decision to remove error terms was based on the Akaike information criterion (AIC). There was a significant effect of substrates ($p = 0.0009$) on growth, with higher growth observed on *Pleurozium* substrates.

3.6. Discussion

Initially, we were hoping to include in our analysis all types of regeneration (i.e., seeds, planted seedlings and layers) to measure the effect of growth susbstrates on black spruce growth. However, our preliminary results (i.e., RDA) showed differences in growth rates between the types of regeneration, as well as a close relationship between the type of regeneration and substrate availability. Thus, in order to determine as clearly as possible the effect of growth substrates on black spruce growth, we have only retained planted seedlings for our analysis. Therefore, the following discussion will be only on planted and not naturally-regenerated seedlings.

Our results show that black spruce height growth tends to be higher on material made of feathermosses and fibric material than on any other type of substrate. This is consistent with the pioneer greenhouse work of Arnott (1968) which indicated a tendency for black spruce growing on *Pleurozium* to have a higher shoot weight and better foliar levels of P and lower levels of K than when growing on *S. capillifolium*. In a greenhouse study, Jeglum (1981) also found greater growth with *Pleurozium* than with *S. angustifolium* and *S. fuscum* substrates, but only when there was daily watering (Jeglum 1979). Our results from the field experiment were also recently confirmed by those from a greenhouse experiment (Lavoie et al. accepted). Our results also show poor growth on mineral soil, which is less consistent with the literature. Some field experiments have reported a tendency for black spruce to have a more rapid height growth on soil covered with either moss or a thin organic layer than on bare mineral soil (Linteau 1957; Fleming and Mossa 1995), while some report the opposite (Vincent 1965). Our results are nevertheless consistent with a greenhouse experiment (Lavoie et al. accepted) that indicated very poor growth on mineral soil of the same sites. The mineral soil in the Clay Belt is generally heavily compacted due to a high silt and clay content and, in our area, to a second glacial readvance that left a very hard argillaceous till (i.e., Till of Cochrane). Regenerating trees on bare mineral soil micro-sites have a tendency to suffer drought stress under dry conditions, whereas trees located in depressions can become waterlogged under prolonged wet conditions (Bergsten et al. 2001; de Chantal et al. 2003). Even though the depth of accumulation of organic matter is generally important in our study area, our results suggest that mineral soil exposed by heavy disturbances such as severe wildfires or site preparation could reduce black spruce growth.

Our study also confirmed that the micro-sites suitable for black spruce seedling establishment are not necessarily the best substrates for subsequent black spruce seedling growth. It is well known that *Sphagnum* mosses and peat provide better conditions for black spruce germination and seedling survival than feathermosses, mainly due to a better moisture and water supply (Roe 1949; Heinselman 1957; Arnott 1968; Wood and Jeglum 1984; Groot and Adams 1994). However, as the root system of seedlings becomes established, nutrient supply may become more important to seedling growth than water availability. Seedling growth may also be affected on *Sphagnum* moss substrates because seedlings can be smothered due to the faster growth rate of these mosses (Roe 1949; Arnott 1968; Jeglum 1981; van Breemen 1995). Even though our results show that soil surface growth substrates generally (80% of the samples) correspond to growth substrates for the rooting zone, data obtained from the rooting zone sampling generated better relationships between substrate type and seedling growth.

Foliar analysis provided little explanation for the differences in height growth between the growth substrates. We have also tried vector analysis but the results were not conclusive. Black spruce is a conservative species and this sometimes makes it difficult to use vector analysis (see Thiffault et al. 2006). However, the nutritional value of growth substrates was more informative. The discriminant analysis suggests the importance of total N concentration, pH (negative with the first axis) and exchangeable Fe (negative with the second axis) in the rooting zone. This did not come as a surprise since total soil N is usually correlated with available N (Binkley and Hart 1989; Côté et al. 2000), especially in organic soils where it reflects the soil CN ratio. A positive correlation between tree growth and soil pH is a general feature of mineral soils as acidic conditions increase soluble Al and decrease P availability, but this relationship has also been reported in boreal peatlands (Jeglum 1981). Lower soil pH in organic soil also affects soil microorganism activities such as N and P mineralization (Persson and Wirén 1995; Davidsson and Stahl 2000). On the other hand, at the soil surface, the separation between substrates was different. For the first axis, the three highest correlations (all positive) were with exchangeable Na, K and pH, while exchangeable Na, Fe and Mn were the three highest correlations (all positive) with the second axis. These results are more surprising. Although Na, Fe and Mn are micronutrients. Our results may indicate that the classification of growth substrates from the soil surface is more indicative of the soil physico-chemical conditions than nutrient quality because Fe and Mn solubility is directly linked to reducing conditions. However, Mn can play an important role in lignin degradation by white rot fungi (Kirk and Farrell 1987) and by accelerating N mineralization (Berg 2000). A closer look at the nutritional value of each substrate showed that fibric material and the mixture of fibric and humic materials in the rooting zone had lower C/N ratios than fibric *Sphagnum*. Previous work has shown greater rates of decomposition of organic matter and N mineralization under feathermosses than under *Sphagnum* mosses (Klenk 2001; O'Connell et al. 2003). Finally, DeLuca et al. (2002) reported that *Pleurozium schreberi* was a host for an associative or symbiotic *Nostoc* spp. that has an N fixation potential of 1.5-2.0 N $ha^{-1}yr^{-1}$, which could partially explain the better spruce growth we observed on the *Pleurozium* substrate. Nitrogen deficiencies are quite common in all types of forests in Canada, while phosphorus deficiencies also appear to be a feature of some temperate forests (Gradowski and Thomas 2006), forested wetlands (Arnott 1968; Alban and Watt 1981; Roy et al. 1999; Banner et al. 2005) and boreal forests (Prévost and Dumais 2003). Our results suggest that P availability is potentially an important limiting factor for black spruce growth and there is certainly a need for more information on P cycles in black spruce ecosystems, especially after wildfire (Dyrness and Norum 1983; Certini 2005).

Besides substrate quality, black spruce growth could also have been influenced by the presence of ericaceous shrubs, variation in the water table and the thickness of the organic layer. We did not observe a significant correlation between *Rhododendron* cover (the main ericaceous shrub present on these sites) and black spruce height growth for planted seedlings. These results are in contradiction with the literature on *Rhododendron groenlandicum* (Inderjit and Mallik 1996, 1997), but in agreement with the detrimental effect of the mechanical removal of aboveground *Rhododendron* on black spruce growth observed by Lavoie et al. (2006) as well as the absence of the effect of *Rhododendron* on black spruce germination found by Titus et al. (1995).

High water table levels can have a negative effect on tree growth (Lavoie et al. 2005), but we do not believe that this was an issue for our sites. Water table depth was only measured once on the Quebec sites, and was not measured in Ontario (data not presented). When the water table was found above the mineral soil surface (17% and 60% of regenerating trees on the burned and the harvest sites respectively), its depth from the surface was on average 24 cm with a standard deviation of 12 cm, which is below the average rooting depth of 10 to 15 cm. Moreover, the low percentage cover of *Sphagnum* (living, burned or fibric) in the wildfire (see Fig. 1) combined with the thin organic layer (< 25 cm on average) in the wildfire sites (Lavoie, unpublished data) suggest the absence of the water table near the soil surface. Therefore, we are confident that most roots of planted trees were above the water table.

Lastly, we observed a negative correlation between organic matter thickness and 3-year AI but the correlation was relatively weak (planted seedlings: $r = -0.351$; $p = 0.001$). This suggests that organic matter thickness has a negative impact but that organic matter composition (i.e., fibric *Pleurozium* vs. fibric *Sphagnum*) and its properties are also important. In fact, the literature generally reports a good productivity on well-decomposed organic soils (see review in Lavoie et al. 2005).

3.7. Conclusion and management implications

There is little information available on the quality for black spruce growth of the different substrates that are found in lowland forests. Most of this information is based on studies on the susbtrates of mature forests. Our study provided new information on the quality for tree growth of the substrates that are found on after disturbance (harvest and wildfire) on lowland sites. This study shows that black spruce height growth is highly variable (i.e., RDA) and that environmental variables such as organic matter thickness and percentage cover of *Rhododendron* explained very little of this variability. On the other hand, our results show that black spruce seedlings growing on soil surface substrates made of *Pleurozium* and fibric *Pleurozium* or rooting zone substrates made of either fibric *Pleurozium* or a mixture of fibric *Pleurozium* and humic materials performed better than seedlings growing on *Sphagnum* materials (fresh, decomposed or burned), decaying wood or mineral soil. It is noteworthy that these growth substrates were always located on the same sites and were often very close to each other. Usually, most regenerating trees grew in more than one type of substrate (soil surface and rooting zone).

Our study also confirms that micro-sites suitable for black spruce seedling establishment are not identical to those suitable for black spruce seedling growth. Thus, relying mostly on layers and favourable seedbeds (i.e., *Sphagnum*) to regenerate black spruce stands may not provide a tree distribution that is optimal for initial tree growth. This may explain in part the better growth of planted vs naturally regenerated black spruce on some sites (Prévost and Dumais 2003; Thiffault et al. 2004). Targeted planting (i.e., infill planting on high-quality substrates) of black spruce seedlings after harvesting should be considered to improve stocking and increase the number of regenerating trees on the best growth substrates (i.e., *Pleurozium* and fibric material originated from *Pleurozium*) available.

At the young stage that was considered in this study, the regenerating tree roots were in the top 20 cm of the profile and did not reach the mesic (i.e., Nos. 5-6 on the Von Post decomposition scale) and humic (i.e., Nos. 7-10 on the Von Post decomposition scale) peat soil layers, nor the mineral soil in undisturbed substrate. As the trees grow, the root systems may reach these layers. The mesic and humic peat layers and the mineral soil may also be exposed by site preparation (e.g., mounding) or intense disturbance (e.g., wildfire). Thus, the impact of the physical and chemical properties of these layers on black spruce growth requires further investigation. Finally, to maintain or increase black spruce growth in these low productivity stands with regard to sustainable forest management, we recommend: 1) plantation in substrates originating from *Pleurozium*; and 2) the development of a management techniques that can promote forest mosses to the detriment of *Sphagnum* mosses (Lavoie et al. 2005). For example, following harvesting, stand should be re-established at high density to limit light availability in order to restrain *Sphagnum* and *Rhododendron* growth (Fenton et al. 2005).

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