UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

IMPACTS DE LA PERTURBATION MÉCANIQUE DES SOLS SUR LES PROPRIÉTÉS PHYSICO-CHIMIQUES DES SOLS ET LA CROISSANCE DE L'ÉPINETTE NOIRE DANS LES TOURBIÈRES FORESTIÈRES DE LA CEINTURE D'ARGILE

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À Géraldine et à Charlotte

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AVANT-PROPOS

Cette thèse est composée de quatre articles scientifiques rédigés en anglais, et comporte un résumé, une introduction et une conclusion générale rédigés en français. Conformément aux exigences du programme de Doctorat en Sciences de l'Environnement, j'ai procédé à la récolte des données, à l'analyse des résultats et à la rédaction des articles à titre de premier auteur. Le premier chapitre, intitulé « **Do harvest methods and soil type impact on the regeneration and growth of black spruce stands in northwestern Quebec?** », a été écrit en collaboration avec David Paré, Nicole J. Fenton et Yves Bergeron. Ce chapitre a été publié dans *Canadian Journal of Forest Research* en septembre 2010. Le deuxième chapitre, « **Contrasting effects of season and method of harvest on soil properties and the growth of black spruce regeneration in the boreal forested peatlands of eastern Canada** », a été écrit avec la collaboration de Nicole J. Fenton, David Paré, Martin Simard et Yves Bergeron. Ce chapitre a été accepté pour publication dans *Silva Fennica* en novembre 2010. Le troisième chapitre, intitulé « **Growth and nutrition of black spruce seedlings in response to disruption of *Pleurozium* and *Sphagnum* moss carpets** », a été soumis à *Plant and Soil* en juillet 2010. Ce chapitre a été écrit en collaboration avec David Paré, Nicole J. Fenton et Yves Bergeron. Enfin, le quatrième chapitre, « **Efficiency of different mechanical site preparation techniques in stimulating tree growth in black spruce peatlands with variable organic layer thickness** », sera soumis à *Scandinavian Journal of Forest Research.* Ce chapitre a été écrit avec la collaboration de David Paré, Nicole J. Fenton et Yves Bergeron.

Enfin, j'ai joint en annexe un article adapté de ma synthèse environnementale. Cet article, intitulé « **Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration?** », a été écrit conjointement avec David Paré, Alison D. Munson et Yves Bergeron. Il a été publié dans *Environmental Reviews* en août 2010.

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ANNEXE I

RÉSUMÉ DE LA THÈSE

En écologie, la notion de résilience se définit comme la capacité d'un système naturel à se réorganiser suite à une perturbation. Dans le cas d'un écosystème forestier, par exemple, la résilience pourra être évoquée pour décrire sa capacité à se reconstituer à la suite d'un feu sans subir de transformations importantes de composition ou de structure. La différence entre la persistance d'un système (i.e. sa résilience) ou sa transformation (i.e. un changement d'état) dépend de l'équilibre entre des rétroactions négatives qui tendent à maintenir le système dans son état actuel et des rétroactions positives qui tendent à le faire basculer dans un nouvel état. Cette définition de la résilience suppose donc, pour un écosystème donné, la possibilité que celui-ci se trouve dans des états stables alternatifs. Du point de vue des sociétés humaines, tous les états stables alternatifs d'un écosystème ne sont pas désirables. La valeur qu'on accordera à un état stable dépendra, entre autres, de son utilité sociale ou économique, et du contexte dans lequel se fait la gestion des ressources tirées de cet écosystème.

Une vaste région du nord-ouest québécois est constituée de peuplements d'épinette noire susceptibles à la paludification, i.e. à la transformation graduelle de forêt productive en tourbière forestière. Dans cette région, les feux constituent un des plus importants agents de perturbation et dynamisation des forêts et exercent un contrôle important sur le processus de paludification. Selon la sévérité de la perturbation des sols lors d'un incendie de forêt, les pessières à mousses de la ceinture d'argile sont susceptibles d'osciller entre deux états stables alternatifs, soit entre un peuplement productif et une tourbière forestière. Des études récentes menées dans la région ont par ailleurs suggéré que les pratiques sylvicoles visant à protéger les sols pourraient contribuer au déclin à long terme de la productivité forestière en favorisant ou en accélérant le processus de paludification. Dans le contexte de l'aménagement forestier, il importe donc de bien comprendre comment les interventions en forêts peuvent contribuer à maintenir les écosystèmes forestiers dans leur état actuel ou de les faire basculer dans un autre état.

Dans ce contexte, il s'avère donc nécessaire d'améliorer nos connaissances des effets des pratiques sylvicoles sur la paludification et la productivité des peuplements *postrécolte* et d'identifier non seulement celles qui sont les plus susceptibles de maintenir ou de restaurer la productivité forestière, mais aussi de préserver la diversité biologique, structurelle et fonctionnelle du paysage forestier régional et d'assurer sa résilience. L'objectif général de cette thèse est de raffiner nos connaissances des effets de diverses pratiques sylvicoles sur les propriétés des sols et sur la croissance de l'épinette noire dans des peuplements susceptibles à la paludification. Plus spécifiquement, nous chercherons à déterminer (*i*) les effets à l'échelle du paysage de deux méthodes de récolte (coupe avec protection de la régénération et des sols [CPRS] et coupe totale) et de cinq types de dépôts-drainage

sur la régénération et la croissance de peuplements d'épinette noire, (*ii*) comment, 10 à 30 ans après la récolte, la perturbation des sols créée par diverses méthodes et saisons de récolte influence la productivité forestière, (*iii*) comment la perturbation de l'humus forestier influence la température, l'humidité, la décomposition et la disponibilité des éléments nutritifs dans des tapis de *Pleurozium schreberi* et de *Sphagnum* spp. et comment ces modifications influencent la nutrition et la croissance de semis plantés d'épinette noire et (*iv*) si l'épaisseur de la couche organique peut influencer la capacité de la préparation de terrain à créer des microsites favorables à la croissance de semis d'épinette noire plantés.

Nos résultats montrent qu'en forêt paludifiée, la perturbation des sols permet d'augmenter la croissance et la productivité forestière, du moins à court terme, et que cet accroissement est fortement influencé par les propriétés physico-chimiques des sols. Ensuite, nos résultats soutiennent l'hypothèse qu'en forêt boréale paludifiée la régénération et la croissance des arbres suivant la récolte sont influencées par la sévérité de la perturbation de la couche organique à l'échelle du peuplement, ces résultats s'appliquant à une vaste gamme de dépôts de surface. De plus, nos résultats montrent qu'une perturbation mécanique suffisamment sévère (p. ex., une coupe totale effectuée l'été) de la couche organique est capable de régénérer des peuplements dont la croissance et la productivité est similaire à celle produite par des feux qui brûlent sévèrement la couche organique. Enfin, nos résultats montrent que l'épaisseur de la couche organique avant la récolte a peu d'influence sur la capacité de la préparation mécanique de terrain à créer des microsites favorables à la croissance de semis d'épinette noire.

Depuis peu, le concept d'aménagement durable des forêts se trouve au cœur de la politique forestière québécoise. Le maintien de la biodiversité et des processus écologiques fait donc désormais partie des éléments qui doivent être pris en compte lors de la préparation des plans d'aménagement forestier. Parallèlement, il s'est développé au cours des dernières années un intérêt grandissant pour le développement d'approches d'aménagement forestier basées sur la dynamique des perturbations naturelles. Afin de parvenir à créer des paysages aménagés ayant les mêmes caractéristiques que les paysages naturels, les aménagistes forestiers devront non seulement raffiner leurs connaissances de la dynamique des perturbations naturelles et de leurs effets sur les écosystèmes forestiers, mais également diversifier et adapter les traitements sylvicoles en fonctions des caractéristiques, parfois particulières, des territoires aménagés. Les résultats de cette thèse suggèrent donc que l'utilisation adéquate et simultanée de méthodes de récolte visant à protéger les sols et de la coupe totale, ainsi que celle d'autres méthodes de récolte et de traitements sylvicoles (par ex. la coupe partielle, coupe à rétention variable et la préparation de terrain), pourrait permettre d'élargir le gradient des effets des opérations forestières à l'échelle du paysage et ainsi aider à maintenir la diversité biologique, structurelle et fonctionnelle des paysages forestiers.

INTRODUCTION GÉNÉRALE

0.1. Introduction

Au cours des derniers siècles, les activités humaines ont fortement altéré la structure et la composition des écosystèmes terrestres. Ces modifications ont été causées par des phénomènes se déroulant à l'échelle globale, tels que la modification des cycles biogéochimiques, les changements climatiques et l'introduction d'espèces animales et végétales (Newman, 1995; Vitousek et al., 1997; Simberloff, 2000; Dale et al., 2001; Honnay et al., 2002; Steffen et al., 2005; IPCC, 2007), ainsi que par des activités ayant eu des impacts régionaux et locaux, par exemple l'exploitation minière et gazière, l'agriculture, le développement urbain et la récolte de la matière ligneuse (Forman, 2000; Trombulak et Frissell, 2000; World Resources Institute, 2000; Schneider et al., 2003; Steffen et al., 2005). Ainsi, les écosystèmes terrestres ont subi d'importantes modifications qui, dans de nombreux cas, ont mené à une altération ou à une diminution de leur diversité biologique, structurale et fonctionnelle (Liebhold et al., 1995; Laurance, 1999; Simberloff, 2000; Hoekstra et al., 2005; Steffen et al., 2005), ainsi qu'à une diminution de leur capacité à fournir les biens et services écosystémiques à un même niveau de qualité et au même rythme (Toman et Ashton, 1996; Costanza et al., 2000; Steffan et al., 2005).

En réponse aux inquiétudes posées par la diminution de la capacité des écosystèmes à fournir les biens et services nécessaires au maintien et au développement des sociétés humaines, plusieurs scientifiques ont soutenu que la gestion des ressources naturelles devait se faire en tenant compte de la résilience et de la résistance des écosystèmes (Holling, 1973, 1986; Peterson et al., 1998; Gunderson, 2000; Groffman et al., 2006). En écologie, la notion de résilience se définit comme la capacité d'un système naturel à se réorganiser suite à une perturbation, alors que la notion de résistance réfère à la capacité d'un système à absorber les effets d'une perturbation sans subir de modification d'état, c'est-à-dire sans subir de changement important en regard des variables et processus qui gouvernent son fonctionnement (Holling, 1973, 1986; Gunderson, 2000; Groffman et al., 2006). Dans le cas d'un écosystème forestier, par exemple, la résilience pourra être évoquée pour décrire sa capacité à se reconstituer à la suite d'un feu sans subir de transformations importantes de composition ou de structure (Figure 0.1). La différence entre la persistance d'un système (i.e. sa résilience) ou sa transformation (i.e. un changement d'état) dépend de l'équilibre entre des rétroactions négatives qui tendent à maintenir le système dans son état actuel et des rétroactions positives qui tendent à le faire basculer dans un nouvel état (Chapin et al., 2009, 2010). Cette définition de la résilience suppose donc, pour un écosystème donné, la possibilité que celui-ci puisse se trouver dans des états stables alternatifs. Rietkerk et al. (2004) et Groffman et al. (2006) utilisent les termes bistabilité et multistabilité pour évoquer la possibilité qu'un écosystème puisse se trouver dans deux ou plusieurs états stables alternatifs. Par exemple, en forêt boréale, Payette et al. (2000) ont montré que la résilience de la pessière à mousses peut être estimée par la fréquence et l'action combinée de diverses perturbations (dans ce cas-ci une épidémie d'insectes suivie d'un feu) et qu'au-delà d'un certain seuil la pessière à mousses change d'état et se transforme progressivement en pessière à lichens (Figure 0.1). Lorsqu'un système se trouve dans un de ses états stables alternatifs (p. ex., la pessière à mousses), ses attributs, tels que sa productivité ou ses structures verticale et horizontale, peuvent fluctuer, mais à l'intérieur de certaines limites maintenues par des contraintes internes ou externes au système (Connell et Sousa, 1983; Scheffer et al., 2001), par exemple par la disponibilité des éléments nutritifs ou le régime des perturbations.

Du point de vue des sociétés humaines, tous les états stables alternatifs d'un écosystème ne sont pas désirables. La valeur qu'on accordera à un état stable dépendra, entre autres, de son utilité sociale ou économique, et du contexte dans lequel se fait la gestion des ressources tirées de l'écosystème (Holling, 1973; Ludwig et al., 1997; Drever et al., 2006), peu importe que ce système soit résilient ou non. Par exemple, un paysage forestier composé principalement d'espèces introduites ayant peu d'utilité peut être considéré comme étant indésirable, mais être hautement résilient, alors qu'une monoculture d'arbre peut être économiquement désirable, mais posséder une faible résilience aux perturbations (Drever et al., 2006).

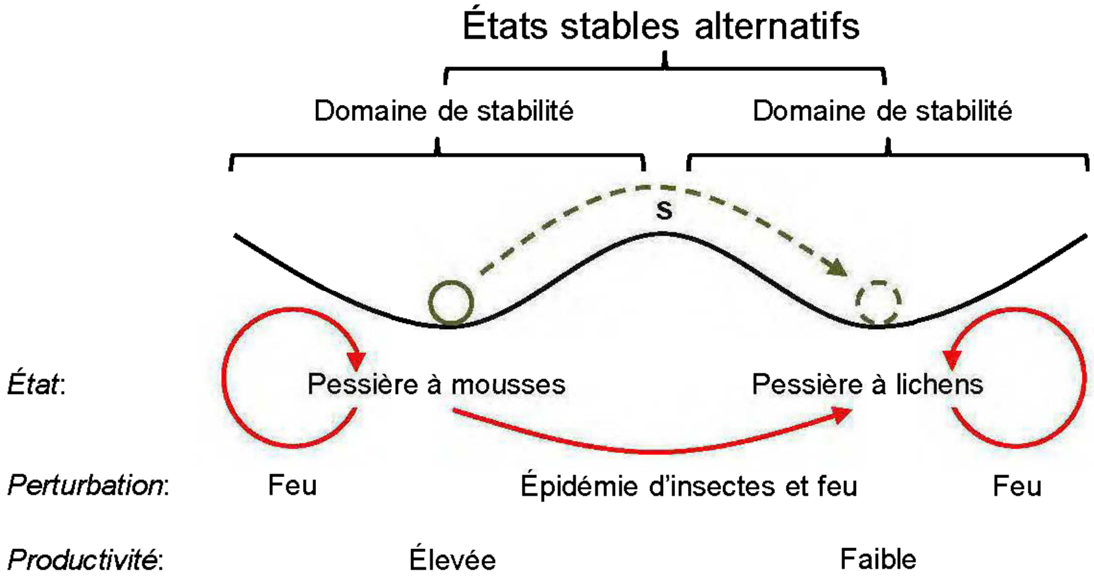

Figure 0.1. Modèle illustrant les concepts de résilience et d'états stables alternatifs en utilisant pour exemple la pessière à mousses et la pessière à lichens. Dans les limites de son domaine de stabilité, la pessière à mousses est résiliente face aux perturbations par le feu (boucle de gauche). Toutefois, des perturbations en rafale (p. ex., une épidémie d'insecte suivie de près par un feu) sont susceptibles de faire basculer la pessière à mousses au-delà du seuil (S) à partir duquel elle change d'état, i.e. à partir duquel elle se transforme en pessière à lichens. Dans les limites de son domaine de stabilité, la pessière à lichens peut elle aussi être résiliente face aux perturbations (boucle de droite)

Dans le contexte de l’aménagement forestier, il importe de bien comprendre comment les interventions en forêts peuvent contribuer à maintenir les écosystèmes forestiers dans leur état actuel ou de les faire basculer dans un autre état. La décision de maintenir un écosystème forestier dans son état actuel ou de le faire basculer d’état dépendra, entre autres, des objectifs d’aménagement à l’échelle du paysage. Par exemple, un plan d’aménagement pourrait avoir comme objectif de maintenir la représentativité des divers types de peuplements forestiers composant actuellement le paysage, d’accroître la productivité du territoire en augmentant la productivité des peuplements considérés improductifs ou encore d’accroître la proportion de vieilles forêts dans le but de maintenir la biodiversité qui y est associée.

0.2. Résilience et états stables alternatifs dans le nord-ouest québécois : pessières productives ou tourbières forestières?

Une vaste région du nord-ouest québécois se situe dans la province naturelle des Basses-terres de l’Abitibi et de la Baie James (Li et Ducruc, 1999). Cette province naturelle constitue une plaine légèrement inclinée vers la baie James. Au cours de la dernière période glaciaire qui s’est terminée il y a environ 10 000 ans, divers processus glaciaires et périglaciaires (i.e. glaciation, réavancées glaciaires régionales, invasions marine et lacustre) ont laissé sur ce territoire d’épais dépôts d’argile, de limon et de graviers relativement mal drainés sur lesquels se sont développées de grandes tourbières forestières (Veillette, 1994). La partie sud de ce territoire, communément appelée la ceinture d’argile, est recouverte d’un épais (>10 m) dépôt glaciolacustre constitué d’argile et de limon mis en place par les lacs proglaciaires Barlow et Ojibway suivant la dernière glaciation (Veillette, 1994). La partie nord du territoire quant à elle est recouverte d’un till très compact (le till de Cochrane) constitué d’un mélange d’argile, de graviers et de galets, et mis en place par une avancée glaciaire tardive il y a environ 8 000 ans (Veillette, 1994).

L'ensemble du territoire fait partie du domaine bioclimatique de la pessière à mousses de l'ouest (Robitaille et Saucier, 1998) et est dominé par des peuplements d'épinette noire (*Picea mariana*) montrant une grande variabilité de densité et de hauteur. Le pin gris (*Pinus banksiana*) et le peuplier faux-tremble (*Populus tremuloides*), bien que moins fréquents, forment des peuplements purs ou mélangés avec l'épinette noire (Harper et al., 2002). Les éricacées (p. ex., *Rhododendron groenlandicum*, *Kalmia angustifolia* et *Vaccinium* spp.) dominent la strate arbustive, alors que la strate muscinale est dominée par les sphaignes (*Sphagnum* spp.*)* et les mousses hypnacées, principalement par l'hypne de Schreber (*Pleurozium schreberi*).

En raison des interactions complexes entre le climat régional (relativement froid et humide), la nature et le drainage des dépôts de surfaces, la topographie généralement plane, la présence d'espèces récalcitrantes à la décomposition (p. ex., les éricacées et sphaignes) et le régime des perturbations naturelles (Lavoie et al., 2005; Lecomte et al., 2006a, 2006b; Simard et al., 2009), les pessières à mousses de la région sont particulièrement susceptibles à la paludification, c'est-à-dire à la transformation graduelle de forêt productive en tourbière forestière. En raison de cette susceptibilité, le paysage régional prend l'aspect d'une mosaïque complexe où alternent des peuplements productifs et des tourbières forestières (Figure 0.2).

Comme ailleurs dans la forêt boréale nord-américaine, les feux constituent un des plus importants agents de perturbation et dynamisation des forêts couvrant la ceinture d'argile et le till de Cochrane (Bergeron et al. 2004). Ces feux exercent un contrôle important sur le processus de paludification (Fenton et al., 2005; Simard et al, 2007). Pour l'ensemble de la région, Bergeron et al. (2004) ont calculé que la fréquence des feux est passée d'un cycle d'environ 100 ans avant 1850 à un cycle d'environ 400 ans depuis. Toutefois, une étude récente indique que bien qu'on observe depuis environ 5000 ans un allongement du cycle de feu, l'augmentation projetée des températures pourrait raccourcir ce cycle si les températures accrues ne sont pas compensées par une augmentation des précipitations (Hély et al., 2010). Dans un cadre d'aménagement forestier où l'on voudrait calquer la fréquence et les superficies de récolte sur le régime des perturbations naturelles par le feu, une augmentation de la fréquence des feux pourrait conséquemment soustraire une partie du territoire à la récolte (Gauthier et al., 2008a).

Figure 0.2. Image satellitaire du paysage forestier des Basses-terres de l'Abitibi et de la baie James. Les peuplements productifs (vert foncé) et les tourbières forestières (vert pâle) s'assemblent en une mosaïque complexe. Sur cette image, on aperçoit en haut à gauche la mine Selbaie (rose) et un feu survenu en 1997 (brun), et en bas à gauche une coupe forestière (gris) (Source: Google Earth, 2010; échelle approximative, 1: 180 000).

Par ailleurs, d'autres travaux menés dans les pessières de la ceinture d'argile et du till de Cochrane ont montré que les feux sévères, c'est-à-dire ceux consumant presque entièrement la couche organique, laissent en place une couche résiduelle de moins de 5 cm d'épaisseur et permettent l'établissement de peuplements *post* incendie dont les arbres parviennent à s'enraciner dans le sol minéral (Lecomte et al, 2006a, 2006b; Simard et al., 2007). Ces peuplements sont généralement denses et sont considérés comme étant productifs. À l'inverse, les feux peu sévères, c'est-à-dire ceux ne consumant le sol qu'en surface, laissent en place une couche organique résiduelle de plus de 5 cm d'épaisseur au travers de laquelle les arbres sont peu susceptibles de pouvoir s'enraciner dans le sol minéral (Lecomte et al, 2006a, 2006b; Simard et al. 2007). Ces feux sont susceptibles de favoriser la paludification et, par conséquent, de régénérer des peuplements *post* incendie ouverts et peu productifs, i.e. des tourbières forestières (Fenton, et al., 2005; Simard et al, 2007).

Ainsi, selon la sévérité de la perturbation des sols lors d'un incendie de forêt, les pessières à mousses de la ceinture d'argile sont susceptibles d'osciller entre deux états stables alternatifs, soit entre un peuplement productif et une tourbière forestière (Figure 0.3).

Enfin, des études récentes menées dans ce territoire suggèrent que les pratiques sylvicoles actuelles, entre autres la coupe avec protection de la régénération et des sols (CPRS), pourraient contribuer au déclin à long terme de la productivité forestière en favorisant ou en accélérant le processus de paludification (Fenton et al., 2005; Lavoie et al., 2005). Ces auteurs suggèrent que la CPRS, à l'instar des feux peu sévères, ne perturberait pas les sols suffisamment sévèrement et forcerait conséquemment la régénération d'un peuplement sur une couche organique épaisse peu favorable à la croissance des arbres et servant d'amorce à la conversion d'un peuplement productif en une tourbière forestière. Par conséquent, dans la ceinture d'argile la productivité des peuplements *post* récolte pourrait être plus faible que celle des peuplements récoltés.

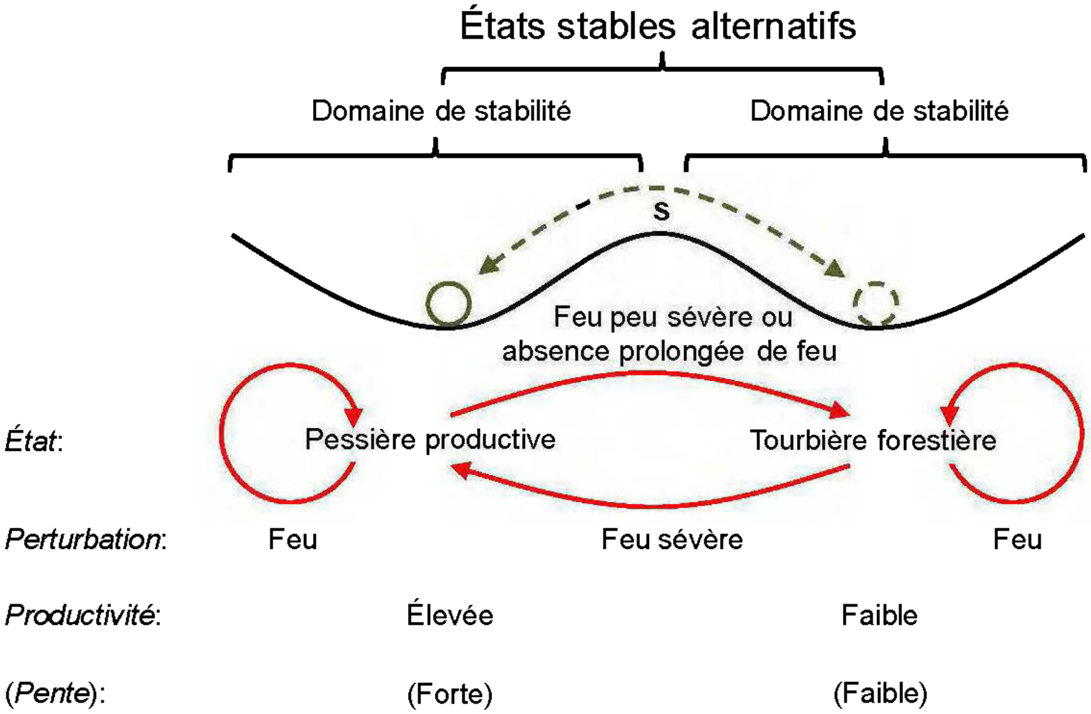

Figure 0.3. Effet de la sévérité de la perturbation du sol lors d'un feu sur la résilience ou le changement d'état des pessières à mousses de la ceinture d'argile. La résilience de la pessière productive est conditionnée, entre autres, par une pente forte (p. ex., >3 % à 7 %), alors qu'une pente faible (p. ex., <3 %) est susceptible de la faire basculer vers la tourbière forestière (Simard et al., 2009). Ainsi, une pente faible favorise le développement de la tourbière forestière. Outre la pente, il est à noter que d'autres facteurs, tels que le climat, la perméabilité des sols et la présence d'espèces récalcitrantes à la décomposition, facilitent également la transition de la pessière productive vers la tourbière forestière.

Dans le contexte physiographique et bioclimatique particulier de la ceinture d'argile et du till de Cochrane, les pratiques sylvicoles actuellement en cours sont donc susceptibles d'homogénéiser le paysage régional en favorisant la transformation de peuplements productifs en tourbières forestières. Cette homogénéisation de la structure et de la composition du paysage pourrait avoir comme effet de diminuer la résilience du paysage forestier régional face aux perturbations (Peterson et al., 1998). Afin de maintenir la composition, la structure et les fonctions du paysage forestier de la région et en même temps répondre aux objectifs d'approvisionnement en matière ligneuse, les aménagistes forestiers devraient par conséquent faire usage de stratégies d'aménagement, tant à l'échelle du peuplement que du paysage, leur permettant l'atteinte de ces objectifs. Ceux-ci devront toutefois avoir une idée claire des caractéristiques de paysage qu'ils souhaitent maintenir en place ou obtenir par l'aménagement (p. ex., proportion de peuplements productifs, de tourbières ou de vieilles forêts, connectivité entre les milieux…). Les aménagistes devront par conséquent être en mesure de comprendre comment, en utilisant diverses stratégies d'aménagement et méthodes de récolte, ils peuvent favoriser le maintien des paysages forestiers dans leur état actuel ou faciliter leur transition dans un autre état.

0.3. L'aménagement forestier basé sur les perturbations naturelles

Il s'est développé au cours des dernières années un intérêt grandissant pour l'aménagement forestier basé sur la dynamique des perturbations naturelles (Attiwill, 1994; Bergeron et Harvey, 1997). Cette approche d'aménagement réfère à l'ensemble des pratiques et des stratégies sylvicoles dont l'objectif est de reproduire les effets des perturbations naturelles sur la structure et la composition des peuplements et des paysages forestiers (Hansen et al., 1991; Hunter, 1993; Attiwill, 1994; Bergeron et Harvey, 1997; Angelstam, 1998). Le principal argument en faveur de cette approche veut qu'un aménagement des forêts qui favorise le développement de peuplements et de paysages ayant une composition et une structure semblables à celles des écosystèmes naturels devrait également favoriser le maintien de leur diversité biologique et de leurs fonctions (Franklin, 1993; Hunter, 1999; Gauthier et al., 2008b).

L'aménagement forestier basé sur la dynamique des perturbations naturelles s'applique aussi bien à l'échelle du peuplement qu'à l'échelle du paysage. À l'échelle du peuplement, cette approche s'articule, entre autres, autour du concept de rétention variable dont l'objectif est de préserver dans les peuplements récoltés des éléments structuraux tels que des arbres d'espèces et de diamètres variés, des bouquets d'arbres, des chicots de tailles variées et des débris ligneux de gros diamètres (i.e. des legs biologiques; Franklin, 1993; Franklin et al., 1997; Mitchell et Beese, 2002; Gauthier et al., 2008b). À l'échelle du paysage, l'aménagement forestier basé sur la dynamique des perturbations naturelles impose de maintenir ou de recréer, par exemple, la variabilité de la taille des zones perturbées, l'abondance et la distribution des classes d'âge des peuplements ainsi que l'agencement spatial des différents types de peuplements tels qu'observés dans les paysages naturels (Angelstam, 1998; Bergeron et al., 1999; Gauthier et al., 2008b). La préservation des patrons et des structures évoqués ci-haut permettrait donc la conservation de la diversité animale et végétale ainsi que le maintien des fonctions et des processus écologiques se déroulant tant à l'échelle du peuplement qu'à l'échelle du paysage et, par conséquent, de maintenir la résilience des écosystèmes forestiers aménagés (Gunderson, 2000).

0.4. Objectifs de la thèse

Alors qu'il est maintenant établi que la paludification des peuplements d'épinette noire de la ceinture d'argile et du till de Cochrane a cours et qu'il est fortement suggéré qu'elle soit favorisée par les pratiques sylvicoles actuelles, il s'avère nécessaire d'améliorer nos connaissances sur les effets des pratiques sylvicoles sur la paludification et la productivité des peuplements *postrécolte*.

Ensuite, il importe d'identifier les pratiques sylvicoles les plus susceptibles non seulement de maintenir ou de restaurer la productivité forestière, mais également de préserver la diversité biologique, structurelle et fonctionnelle du paysage forestier régional et d'assurer sa résilience.

Dans ce contexte, l'objectif général de cette thèse est de raffiner nos connaissances des effets de diverses pratiques sylvicoles sur les propriétés des sols et sur la croissance de l'épinette noire dans des peuplements susceptibles à la paludification.

Plus spécifiquement, le premier chapitre de cette thèse a pour objectif de déterminer les effets à l'échelle du peuplement de deux méthodes de récolte (CPRS et coupe totale) et de cinq types de dépôts-drainage sur la régénération et la croissance de peuplements d'épinette noire, ainsi que sur le recouvrement de la sphaigne et de la compétition éricacée. Une meilleure compréhension des interactions possibles entre les méthodes de récolte et le dépôt-drainage pourrait permettre le réajustement des pratiques sylvicoles selon des objectifs d'aménagement à du l'échelle du paysage.

Le deuxième chapitre cherche à déterminer comment, 10 à 30 ans après la récolte, la perturbation des sols créée par diverses méthodes et saisons de récolte influence la productivité forestière. Plus spécifiquement, nos objectifs sont de (*i*) comparer les effets de la CPRS et de la coupe totale, effectuées en hiver ou en été, sur la régénération naturelle et la croissance de l'épinette noire, (*ii*) identifier les variables du sol qui favorisent la croissance de l'épinette après coupe et (*iii*) déterminer comment la croissance des peuplements issus de la récolte se compare à celle des peuplements issus de feux. Ces résultats pourraient nous permettre d'identifier le ou les traitements sylvicoles les plus aptes à reproduire les patrons de régénération et de croissance des arbres observés après feu, et les plus susceptibles de maintenir ou restaurer la productivité de peuplements d'épinette noire paludifiés.

Le troisième chapitre a pour objectif de déterminer (*i*) comment la perturbation de l'humus forestier influence la température, l'humidité, la décomposition et la disponibilité des éléments nutritifs dans des tapis de *Pleurozium schreberi* et de *Sphagnum* spp. et (*ii*) comment ces modifications influencent la nutrition et la croissance de semis plantés d'épinette noire. Ces résultats pourraient nous permettre d'identifier les conditions édaphiques les plus favorables à la croissance de semis d'épinette noire, mais aussi les caractéristiques des microsites à favoriser lors des travaux de plantation afin de maximiser les chances de réussite de ceux-ci.

Enfin, le quatrième chapitre cherche à déterminer si l'épaisseur de la couche organique peut influencer la capacité de la préparation de terrain à créer des microsites favorables à la croissance de semis d'épinette noire plantés. Plus spécifiquement, nous cherchons à déterminer (*i*) l'efficacité de diverses méthodes de préparation de terrain à produire des microsites adéquats pour la croissance des semis en fonction de l'épaisseur initiale de la couche organique, (*ii*) l'abondance relative des substrats de surface créée par diverses méthodes de préparation de terrain, (*iii*) les relations entre l'épaisseur de la couche organique et la croissance des semis d'épinette noire et (*iv*) à identifier les caractéristiques des substrats de croissance les plus favorables à la croissance des semis d'épinette noire. Ces résultats pourraient nous permettre d'identifier les conditions initiales d'épaisseur de couche organique qui sont susceptibles d'influencer l'efficacité de diverses méthodes de préparation de terrain à régénérer des peuplements paludifiés.

Globalement, cette thèse devrait d'abord nous permettre d'accroître nos connaissances des effets de la perturbation mécanique des sols sur les propriétés physico-chimiques des sols et sur la régénération et la croissance de l'épinette noire en milieu paludifié. Ensuite, elle devrait nous permettre d'identifier les conditions d'épaisseur de la couche organique qui influencent l'efficacité de la perturbation mécanique des sols à régénérer des peuplements paludifiés. Enfin, nous devrions être en mesure d'identifier la méthode et la saison de récolte les plus susceptibles de reproduire les patrons de régénération et de croissance observés après feu, et les plus susceptibles de maintenir la productivité de peuplements d'épinette noire paludifiés.

Les résultats issus de cette thèse pourraient être utilisés afin d'ajuster nos pratiques sylvicoles et permettre l'utilisation, dans certaines circonstances, de traitements perturbant les sols suffisamment sévèrement pour permettre la restauration ou le maintien de la productivité des peuplements d'épinette noire paludifiés ou susceptibles à la paludification. L'inclusion de telles pratiques parmi l'ensemble des outils sylvicoles actuellement disponibles et autorisés pourrait également permettre d'élargir la variabilité des effets des perturbations mécaniques sur les paysages forestiers et rapprocher cette variabilité de celle produite par les perturbations naturelles. La diversification des outils sylvicoles et de leurs effets sur la structure et la composition des peuplements ainsi que sur les patrons spatiaux observés à l'échelle du paysage pourrait, en conséquence, permettre le maintien des processus écologiques et de la diversité biologique et fonctionnelle des écosystèmes forestiers de la ceinture d'argile et du till de Cochrane.

CHAPITRE I

DO HARVEST METHODS AND SOIL TYPE IMPACT THE REGENERATION AND GROWTH OF BLACK SPRUCE STANDS IN NORTHWESTERN QUEBEC?

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1.1. Abstract

Machinery traffic restrictions during forest harvest have been adopted in order to minimize soil damage and protect tree regeneration. However, this practice is questioned for paludifying black spruce stands, in which severe soil disturbance by wildfire restores forest productivity. The objective of this study was to determine, eight years after harvest, how soil disturbance created by clearcutting and careful logging affected black spruce natural regeneration and growth, and how this effect varied by soil type. While regeneration density was higher following careful logging, stocking was not influenced by harvest method. Regenerating stands were taller following clearcutting despite potentially greater damages to pre-established regeneration. Compared to careful logging, clearcutting also resulted in reduced cover of Sphagnum spp. and ericaceous shrubs. Spruce stem density and stocking were both higher on organic and subhydric soils and lower on mesic soils. No significant interactions were observed between harvest method and soil type, indicating that the observation of taller black spruce stands and adequate stocking with clearcutting may be applicable to all soil types considered in this study. These results suggest that an adequate level of soil disturbance is an important part of forest regeneration, particularly in ecosystems where an autogenic reduction in productivity occurs.

1.2. Résumé

Afin de préserver les sols et la régénération durant la récolte, la circulation de la machinerie forestière est fréquemment restreinte à des sentiers déterminés. Toutefois, cette pratique est remise en question dans les peuplements d'épinette noire susceptibles à la paludification où de sévères perturbations des sols causées par le feu sont aptes à améliorer la productivité des peuplements. L'objectif de cette étude était de déterminer comment la perturbation des sols causée lors de la coupe totale et la coupe de protection affecte la régénération de l'épinette noire 8 ans après la récolte, et comment cet effet est conditionné par le type de sol. Alors que la densité de régénération de l'épinette noire était supérieure après la coupe de protection, le coefficient de distribution n'était pas influencé par la méthode de récolte. Les peuplements d'épinette régénérés après coupe totale étaient plus hauts en dépit d'un potentiel de dommage plus grand à la régénération préétablie. Comparée à la coupe de protection, la coupe totale a aussi entraîné une réduction de la couverture au sol de la sphaigne et des éricacées. La densité et le coefficient de distribution de l'épinette noire étaient supérieurs sur les sols organiques et subhydriques et inférieurs sur les sols mésiques. Aucune interaction significative n'a été observée entre la méthode de récolte et le type de sol, indiquant qu'une plus grande hauteur des peuplements et un coefficient de distribution d'épinette adéquat après coupe totale pourrait être applicable à la toute la gamme de types de sol considérée dans cette étude. Ces résultats suggèrent qu'un niveau de perturbation des sols suffisant lors des opérations forestières est nécessaire, particulièrement dans les écosystèmes où des processus autogéniques réduisant la productivité s'opèrent.

1.3. Introduction

Black spruce (*Picea mariana* [Mill] BSP) is one of the most wide-ranging and abundant conifers in North America (Burns and Honkala, 1990) and sustains an important forest industry in several regions. Historically, black spruce stands have been harvested by clearcutting (Keenan and Kimmins, 1993). The rationale for using clearcutting in black spruce stands was that clearcutting was compatible with the ecological requirements of black spruce (Keenan and Kimmins, 1993; McRae et al., 2001). However, in recent decades concerns were raised about the protection of soils and tree regeneration during forest operations, as clearcutting was thought to damage both. These concerns sparked important changes in harvest methods, and many jurisdictions in North America replaced clearcutting by careful logging, whose objectives are to protect soils and natural tree regeneration.

In certain areas however, careful logging may not be as efficient at maintaining forest productivity as previously thought. For instance in areas prone to paludification, such as parts of Alaska, northern Minnesota and the Clay Belt of eastern Canada, the productivity of black spruce stands naturally declines as a thick (>30 cm) organic layer accumulates, the water table rises, soil temperature decreases and tree root access to the mineral soil is restricted (Viereck et al., 1993; Simard et al., 2007). The understory of paludified black spruce stands are dominated by *Sphagnum* spp. and ericaceous species (e.g. *Rhododendron groenlandicum* (Oeder) Kron & Judd and *Kalmia angustifolia* L.), both of which contribute to the accumulation of the organic layer (Fenton et al., 2005) and in the case of ericaceous species, may also directly limit tree growth (Mallik, 1987; Inderjit and Mallik, 1996). Studies conducted in northeastern Canada have recently suggested that careful logging, which by definition does not disturb the accumulated organic layer, could contribute to a long-term decline in black spruce stand productivity by favouring paludification (Fenton et al., 2005; Lavoie et al., 2005). In parallel it has been suggested that harvest methods that severely disturb organic soils, and subsequently result in a reduction in organic layer thickness and/or accelerates its mineralization, could help restore stand productivity (Simard et al., 2009). Therefore while careful logging is likely to leave more residual trees than clearcutting, natural regeneration on clearcut sites may establish in more favourable microsites and have a higher growth rate than the residual stems of the carefully logged sites. In this context, the height advantage of advanced regeneration could disappear over time.

Furthermore, in a black spruce dominated landscape, stand growth and composition can respond differently following disturbance according to soil type. For instance, in the boreal mixedwoods of central Manitoba, Martin and Gower (2006) found that black spruce trees grew taller on clay soils than on sandy soils following fire, whereas in Ontario Chen et al. (2002) observed that hardwood species such as trembling aspen (*Populus tremuloides* Michx.), a species associated with reduced organic layer thickness and enhanced tree growth in black spruce stands (Légaré et al., 2004, 2005), were more frequent on well drained sites after harvest.

In this context, the objective of this study was to determine the landscape scale effects of two harvest methods (i.e. careful logging and clearcut) and five soil types (as characterized by their texture and drainage) on tree seedling density, stand height, and the cover of *Sphagnum* spp. and ericaceous shrubs, eight years after harvest. We hypothesise that (i) black spruce stem density will be higher after careful logging than after clearcutting, (ii) stand height will be greater after clearcutting than after careful logging, and (iii) the cover of the *Sphagnum* spp. carpet and of ericaceous shrubs will be lower after clearcutting than after careful logging. Regarding soil types, we hypothesise that (iv) black spruce stem density will be higher on poorly-drained soils as compared to well-drained soils, and in contrast (v) hardwood stem density will be higher on well-drained soils as compared to poorly-drained soils. A better understanding of the possible interacting effects between harvest method and soil type could allow the readjustment of silvicultural practices according to forest management objectives at the landscape scale.

1.4. Methods

1.4.1. Study area

The study area (48°50'N–50°10'N; 78°08'W–79°34'W) is located in northwestern Quebec and covers approximately 1 000 000 ha (Figure 1.1). The southern part of the study area, the Clay Belt, is covered by thick (>10 m) glaciolacustrine clay and silt deposited by the glacial Lake Ojibway, while the northern part is covered by the Cochrane till, a compact till made up of a mixture of clay and gravel, created by a southward ice flow approximately 8 000 years before present (Veillette, 1994). Thick (>30 cm) organic deposits are found in many locations in both the southern and northern parts of the study area. According to the nearest weather station (Joutel, QC), the average annual temperature was 0.1°C, and average annual precipitation was 892 mm, with 35% falling during the growing season during 1971-2000 (Environment Canada, 2009). The average number of degree-days (>5°C) is 1 249, and the frost-free season lasts about 60 days; frost can occasionally occur during the growing season. Fire frequency in the study area has diminished from a 100-year cycle to a *ca.* 400- year cycle since the little Ice Age (*ca.* 1850; Bergeron et al., 2004).

The study area is part of the western black spruce-feathermoss bioclimatic domain (Robitaille and Saucier, 1998). In some stands, balsam fir (*Abies balsamea* [L.] Mill.), tamarack (*Larix laricina* [DuRoi] K. Koch), paper birch (*Betula papyrifera* Marsh.) and trembling aspen are also found. Ericaceous shrubs such as Labrador tea (*R. groenlandicum*), sheep laurel (*K. angustifolia*), and blueberry

(*Vaccinium myrtilloides* Michx. and *V. angustifolium* Ait.) dominate the understory, while the forest floor is dominated by *Sphagnum* species (e.g. *Sphagnum recurvans sensu lato, S. capillifolium* [Ehrh.] Hedw., *S. fuscum* [Schimp.] Klinggr., *S. girgensohnii* Russ., and *S. magellanicum* Brid.) and feathermosses (e.g., *Pleurozium schreberi* [Bird.] Mitt., and *Hylocomium splendens* [Hedw.] Schimp.).

1.4.2. Forest policy context

As in most coniferous forests in North America, black spruce stands in the study region have historically been harvested by clearcutting. During clearcutting operations, machinery traffic was originally allowed across the entire cutover area, all commercial tree stems were harvested, and damage to soils and natural regeneration was usually high. During the 1990s, the ministère des Ressources naturelles et de la Faune du Québec (MRNFQ) modified the province's forest policy in order to protect natural regeneration and soil physical, chemical and biological properties, and introduced careful logging (in Quebec, cut with protection of regeneration and soils; CPRS). CPRS consists of harvesting all commercial trees (diameter at breast height > 9.1 cm) with machinery traffic restricted to parallel trails that cover ca. 25% (33% prior to March 2001) of the logged area (MRNFQ, 2003). Trails are separated by "protection strips" in which commercial stems are harvested.

The database used in this study is comprised of data from post-harvest monitoring compiled by two major forest companies in Quebec (Tembec and Norbord) between 1997 and 2007, as required by law. In the original database, 7 759 clusters were available. Clusters were excluded where planting, seeding, cleaning and/or thinning were completed following harvest to focus exclusively on natural regeneration. Moreover, in order to minimize the possible influence of pre-harvest forest composition on our results, we selected only stands that were dominated by black spruce prior to harvest (Table 1.1). Finally, it should be noted that for each response variable, the number of clusters varies from 5 to 2 258 because not all data were collected at each sampling location due to the 10-year time span covered by the database.

1.4.3. Experimental design and sampling

At each sampling location (Figure 1.1), one cluster of ten 4-m^2 circular plots was sampled. At the cluster scale, this experimental design allowed us to determine (1) stocking and stem density (i.e. number of seedlings ha^{-1}) for each tree species, (2) average stand height, and (3) percent cover of *Sphagnum* spp. and ericaceous shrubs. Stocking was determined by calculating the percentage of the ten 4-m^2 circular plots containing at least one stem taller than 0.30 m. Stem density was determined by tallying the number of stems taller than 0.30 m in three of the ten circular plots, and is reported in number of seedlings ha^{-1}. Stocking and stem density were calculated separately for black spruce and hardwood species (i.e. paper birch and trembling aspen). In these three circular plots, stand height was also determined by averaging black spruce seedling height. Finally, in each circular plot, the percent cover of *Sphagnum* spp. and ericaceous shrubs (i.e. *R. groenlandicum* and *K. angustifolia*) was noted.

1.4.4. Determination of harvest method and soil type

At each sampling location (i.e. cluster), harvest method (i.e. CPRS and clearcutting) and soil type (as determined by a combination of texture and drainage) were determined using the forest maps of the MRNFQ. Although harvest season (e.g. summer or winter) might have an important effect on tree regeneration and growth (Lafleur et al., unpublished data), the ecological classification maps of the MRNFQ do not indicate seasons. Consequently, statistical analyses were conducted without discriminating harvest season.

Surficial deposit and drainage classes were grouped to create functional groupings (hereafter referred to as soil types). Five soil types were retained, and they covered the largest surface, together accounting for approximately 85% of the study area. They are: organic (ORG), mesic lacustrine clays (MLC), subhydric lacustrine clays (SLC), mesic clay till (MCT), and subhydric clay till (SCT). Mesic soils refer to well- and moderately well-drained soils, whereas subhydric soils refer to imperfectly- and poorly-drained soils (Brais and Camiré, 1992; Saucier, 1994). MLC and SLC are predominantly found in the southern part of the study area, i.e. the Clay Belt, whereas MCT and SCT are mainly found in the northern part of the study area, i.e. the Cochrane till. Organic soils are equally distributed in the Clay Belt and on the Cochrane till.

1.4.5. Data analyses

All clusters were sampled 8 years after harvest, as required by law in Québec, therefore, we did not take cluster (stand) age into account in our analyses. In order to determine the effects of harvest method and soil type and any interactions on stocking, stem density and mean stand height, the data were analyzed using mixed effect ANOVAs. Harvest method and soil type were introduced in the model as fixed effects, while cluster was used as a random effect. The general form of the model for these analyzes was:

$$[1] \qquad Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \delta_k + \varepsilon_{ijkl}$$

where α (harvest method) and β (soil type) are fixed effects, and δ (cluster) is a random effect. When needed, data were log- or square root-transformed to meet the assumptions of normal distribution and homogeneity of variances. Analyses were conducted on the responses of black spruce, the dominant species in the study area, and hardwood species (i.e. aspen and paper birch, hereafter referred to as hardwood). Stand height was not analyzed for hardwood species because of insufficient data. As we were not able to meet the assumptions for parametric tests, even after transformation, for the data on the cover of ericaceous shrubs and *Sphagnum* spp. data were analyzed using non-parametric tests (Kruskal-Wallis and Wilcoxon). Mixed model analyses were done using the Mixed procedure in SAS (SAS Institute Inc., 2004). *Post-hoc* comparisons were made to contrast the levels of the fixed variables, and differences were deemed significant when $\alpha \leq 0.05$. Pearson correlations were then used to determine the strength of the relationships between stand height and the cover of competing vegetation.

1.5. Results

1.5.1. Regeneration and growth parameters

Stocking differed more among soil types than between harvest methods while the interaction (harvest method x soil type) was not significant for black spruce. Our results showed that overall, black spruce and hardwood stocking did not significantly differ between CC and CPRS (black spruce: CC = 61% and CPRS = 63%; hardwood: CC = 15% and CPRS = 10%; Figure 1.2). Stocking did however differ significantly among soil types. Black spruce stocking was highest on ORG (79%), intermediate on SLC (71%) and SCT (67%), and lowest on MLC (51%) and MCT (43%). Hardwood stocking was highest on MLC (33%), intermediate on SLC (11%) and MCT (10%), and lowest on SCT (6%) and ORG (4%). There were no interactions between harvest method and soil type for either black spruce or hardwood stocking.

In contrast to stocking, stem density differed both between harvest methods, and among soil types. Black spruce stem density was significantly higher after CPRS (7 743 stems ha^{-1}) than after CC (5 410 stems ha^{-1}; Figure 1.2), and was highest on

SCT, SLC and ORG (9 222, 7 766 and 7 162 stems ha^{-1}, respectively) and lowest on MCT (4 837 stems ha^{-1}) and MLC (3 894 stems ha^{-1}). In contrast to black spruce, hardwood stem density was significantly higher after CC than after CPRS (1 020 stems ha^{-1} vs. 595 stems ha^{-1}; Figure 1.2), primarily due to the very high density of stems on MCT after CC. Significant differences were also found among soil types, with higher hardwood stem density on MCT (1 594 stems ha^{-1}) and MLC (1 560 stems ha^{-1}), intermediate levels on SLC (604 stems ha^{-1}), and lower density on SCT and ORG (144 and 137 stems ha^{-1}, respectively). There were no interactions between harvest method and soil type for either black spruce or hardwood stem density.

At the stand scale, black spruce stand height was significantly higher following CC (80 cm) than following CPRS (67 cm; Figure 1.3) 8 years after harvest. Although the absolute differences were small, black spruce stand height also differed significantly among soil types, as black spruce stands were tallest on ORG (79 cm) and MCT (77 cm), intermediate on MLC and SCT (73 cm and 70 cm respectively), and shortest on SLC (68 cm). Again, no significant interactions were detected between harvest method and soil type.

1.5.2. Ericaceous shrubs and Sphagnum spp. cover

Percent cover of *K. angustifolia* and *R. groenlandicum* was significantly lower after CC than after CPRS (Figure 1.4). Soil type also influenced their percent cover, with lower cover on MCT for *K. angustifolia* and on MLC for *R. groenlandicum* (Figure 1.4). Percent cover of *Sphagnum* spp. also differed significantly between harvest methods and among soil types, with lower cover after CC than after CPRS, and significantly lower and higher cover on MCT and SLC, respectively (Figure 1.4).

1.5.3. Relationships between tree growth parameters and competing vegetation

Pearson correlations revealed that black spruce stand height was significantly negatively correlated to *R. groenlandicum* ($r = -0.256$, $p < 0.01$) and *Sphagnum* spp. ($r = -0.253$, $p < 0.01$) cover, whereas it was not significantly correlated to *K. angustifolia* ($r = -0.103$, $p > 0.05$).

1.6. Discussion

Our results are in agreement with previous studies (e.g. Tappeiner and Hennon, 2002; Kreutzweiser et al., 2008; Man et al., 2008) that indicated that careful logging (CPRS) provides a better protection to tree regeneration, ground vegetation and soil than clearcutting. Despite this our results also show that eight years after harvest clearcut stands are taller than stands carefully logged, despite the potentially greater damages to pre-established regeneration. While soil type influenced tree regeneration, stand growth and ground vegetation, there was no interaction between harvest method and soil type on spruce tree regeneration and stand height. This suggests that the impact of harvest treatment found here applies to the range of site-types considered.

1.6.1. Impact of harvest method

Our results indicate that eight years following harvest, sites harvested by CPRS and clearcutting showed similar levels of black spruce stocking. Previous studies in northern Ontario found similar results and suggested that while CPRS is specifically designed to protect regeneration, greater soil disturbance severity during clearcutting favoured seed germination and seedling establishment (Groot and Adams, 2005). Further, harvest method had a significant effect on black spruce stem density, as it was on average 45% higher following CPRS than clearcutting. As the aim of CPRS is to protect regeneration, machinery traffic is restricted to specific skid trails located 20 to 30 m apart. That spacing protects some black spruce regeneration. In contrast, during clearcutting machinery traffic is not restricted and regeneration and soil are submitted to disturbance across the entire harvested area, which explains the lower black stem density following clearcutting.

The non-significant but systematically higher stocking of hardwoods after clearcutting compared to CPRS [also found by Bujold (2005)] could be explained by the ability of trembling aspen to produce root suckers following injury to its root system (Fraser et al. 2004). Injury may be caused by harvesting operations (Corns and Maynard, 1998) and would presumably be higher after clearcutting than CPRS. Harvest method also had a significant effect on hardwood stem density, which was on average 70% higher after clearcutting than CPRS. The higher hardwood stem density following clearcutting could also be explained by the ability of trembling aspen to produce root suckers following root injury (Brumelis and Carleton, 1988).

Eight years following harvest, clearcut sites supported slightly but significantly taller black spruce stands than those harvested using CPRS. These landscape-level results are in accordance with those of a parallel study (Lafleur et al., unpublished data), which showed that at the stand scale, clearcutting tends to produce taller stands because it creates a greater abundance of microsites conducive to better tree growth.

Our results also indicate that clearcutting is more efficient than CPRS at controlling ericaceous competition, as cover of *R. groenlandicum* and *K. angustifolia* was significantly lower following clearcutting. Because soils are disturbed (both at the surface and in depth) over a larger area during clearcutting, the root systems of *R. groenlandicum* and *K. angustifolia* are more likely to be broken or disrupted, limiting or slowing down their short-term recovery. In addition, greater soil disturbance may expose mineral soil, which is known to constitute a barrier to ericaceous shrubs (Titus et al., 1995). The control of ericaceous shrubs early in stand recovery may have important consequences on stand growth as both *R. groenlandicum* and *K. angustifolia* are known to have a negative impact on black spruce growth (Mallik, 1987; Inderjit and Mallik, 1996). Furthermore, clearcutting was also more efficient than CPRS at controlling *Sphagnum* spp. cover. Whereas a *Sphagnum* spp. carpet is generally considered an appropriate seedbed (Jeglum, 1979), *Sphagnum* peat is also considered to be a poor substrate for black spruce growth (Lavoie et al., 2007). Because soils are disturbed over a larger proportion of the area during clearcutting than during CPRS, the *Sphagnum* spp. carpet is more likely to be fragmented, which slows its recovery. Therefore, in black spruce stands prone to paludification any harvest method capable of reducing ericaceous shrubs and *Sphagnum* spp. cover should also favour black spruce growth.

1.6.2. Impact of soil type

Although harvest method did not have any significant effect on black spruce stocking, our results indicate that site soil type did influence black spruce stocking. While black spruce stocking was 79% on organic sites (i.e. ORG), it dropped to 70% on subhydric sites (i.e. SLC and SCT), and to 50% on mesic sites (i.e. MLC and MCT). Similarly, black spruce stem density was significantly lower on mesic sites as compared to organic and subhydric sites. These results indicate that wetter sites (organic or subhydric) provide better microsites for black spruce establishment, while the stocking of mesic sites may be more vulnerable if harvest causes great damages to established regeneration.

Further, hardwood species had higher stocking and stem density on mesic sites (i.e. MLC and MCT) compared to the other soil types. These results are similar to those of Bujold (2005) and Laquerre et al. (2009) who both showed that mesic deposits are more liable to hardwood encroachment than subhydric or organic deposits, where excess moisture, low oxygen diffusion, and low temperatures restrict trembling aspen establishment and root suckering (Frey et al., 2003).

Although soil type had a significant effect on black spruce stand height, the absolute difference was very small. In addition, the time elapsed between stand initiation and post-harvest monitoring (i.e. eight years) is quite short, which renders hazardous any discussion on the effects on soil type on stand height. However, one can note that the soil type with the shortest stands (i.e. SLC), also has the highest *Sphagnum* spp. cover, supporting the idea that extensive *Sphagnum* carpets can restrict black spruce regeneration and growth.

Finally, the lower *Sphagnum* spp. cover on MCT could be explained both by the better drainage of mesic soil and higher hardwood density. On the Clay Belt, Légaré et al. (2005) found that the presence of aspen in black spruce stands reduced organic layer accumulation by producing litter rich in nutrients, therefore decomposing more rapidly than spruce litter.

1.6.3. Management considerations

Although it is widely acknowledged that CPRS provides a 'head-start" to stand regeneration by protecting advance growth, our results show that in a paludified landscape clearcutting yields, eight years after harvest, taller stands than CPRS, and that this conclusion applies to the full range of soil types that were studied. These results indicate that black spruce trees establishing after clearcutting have a higher growth rate than advance regeneration in CPRS. Although the results are a snapshot at age eight following harvest, it is likely that this will continue because a critical phase for black spruce growth is the early stage where a lag can persist for up to 20 years (Groot and Hökkä, 2000). As for the possible mechanisms involved, clearcutting likely disturbs the soil over a greater percentage of the area, which could stimulate soil processes, such as nutrient mineralization, and favour plant species that are functionally different in that they are prone to stimulate soil nutrient cycles (i.e. *Populus tremuloides*) either directly or by limiting the growth of the moss layer. Despite a greater destruction of the established regeneration, clearcutting would simultaneously create seedbeds that ensure site regeneration and favour microsite conditions that enhance tree growth.

Clearcutting resulted in a lower stem density than CPRS although on all soil types, stocking of black spruce was not significantly different between harvest treatments. In Québec, the provincial norms require that eight years after harvest stocking levels of free-to-grow stems >1 m tall be equal or higher than pre-harvest levels. In the study region, pre-harvest stocking level is ca. 30% and Québec's provincial norms are met ca. 10 years after harvest (L. Dumas, personal communication). Therefore, on every soil type considered in this study, both harvesting methods can produce levels of stocking that meet Québec's provincial norms. Of all soil types, mesic sites may require the most attention because of relatively low black spruce density and stocking. These results offer a paradox because it is on the wettest sites and not on the mesic ones, that stocking has been thought to be most at risk, because of soil rutting (Groot, 1998). More research may be needed to determine the optimal treatment that would restore site regeneration, and productivity as well as protect soil and water quality.

Finally, our results are in accordance with other studies and indicate that in ecosystems that are prone to an autogenic reduction in productivity (Wardle et al., 2004), a certain level of disturbance to the soil may be required to restore stand productivity. In paludified forests, a thick moss layer insulates the soil and disturbance to this layer may cause an effect similar to the assart effect (Rommell, 1935; Kimmins, 1997) in other ecosystems, i.e., a kick start for nutrient cycles and tree development in the early regeneration stage.

1.7. Conclusion

Although the restriction of machinery traffic to specific skid trails is acknowledged to help maintain forest productivity by protecting soils and regeneration (Harvey and Brais, 2002), in the black spruce stands of the Canadian Clay Belt that are prone to paludification our results have shown that clearcutting with unrestricted traffic circulation provides black spruce stands of adequate stocking and with a better growth than CPRS over the range of soil types where paludification occurs. Clearcutting, however, may have greater impact than careful harvesting on several ecosystem properties and functions that were not evaluated in this study, for instance on streamflow and water quality, biodiversity and wildlife habitats (Keenan and Kimmins, 1993). Hence, the wise use of clearcutting and careful logging, along with the creation of conservation areas, could favour, at the landscape level, the maintenance of wood production as well as that of ecosystem properties and functions. Therefore, knowing what level of disturbance is required in what types of ecological conditions to achieve optimal benefits (in terms of forest productivity as well as in terms of soil and habitat protection) may require additional work. Nonetheless, our results suggest that conventional machine traffic has historically generated conditions for adequate stocking and growth.

1.8. Acknowledgements

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Tableau 1.1. Number of clusters analysed for each response variable by edaphic class.

Response variable	MLC-CPRS[1]	MLC-CC	SLC-CPRS	SLC-CC	ORG-CPRS	ORG-CC	MCT-CPRS	MCT-CC	SCT-CPRS	SCT-CC	Total
Stocking (%)	90	23	716	178	498	26	226	32	879	22	2690
Density (nb stems ha^{-1})	172	89	1016	249	488	29	234	16	816	5	3114
Stand height (m)	419	242	2258	647	232	69	29	23	444	59	4422
Shrubs/*Sphagnum* cover (%)	82	74	381	152	121	13	15	12	109	11	970

[1] Mesic lacustrine clays (MLC), subhydric lacustrine clays (SLC), organic (ORG), mesic clay till (MCT), subhydric clay till (SCT), cut with protection of regeneration and soils (CPRS), clearcutting (CC).

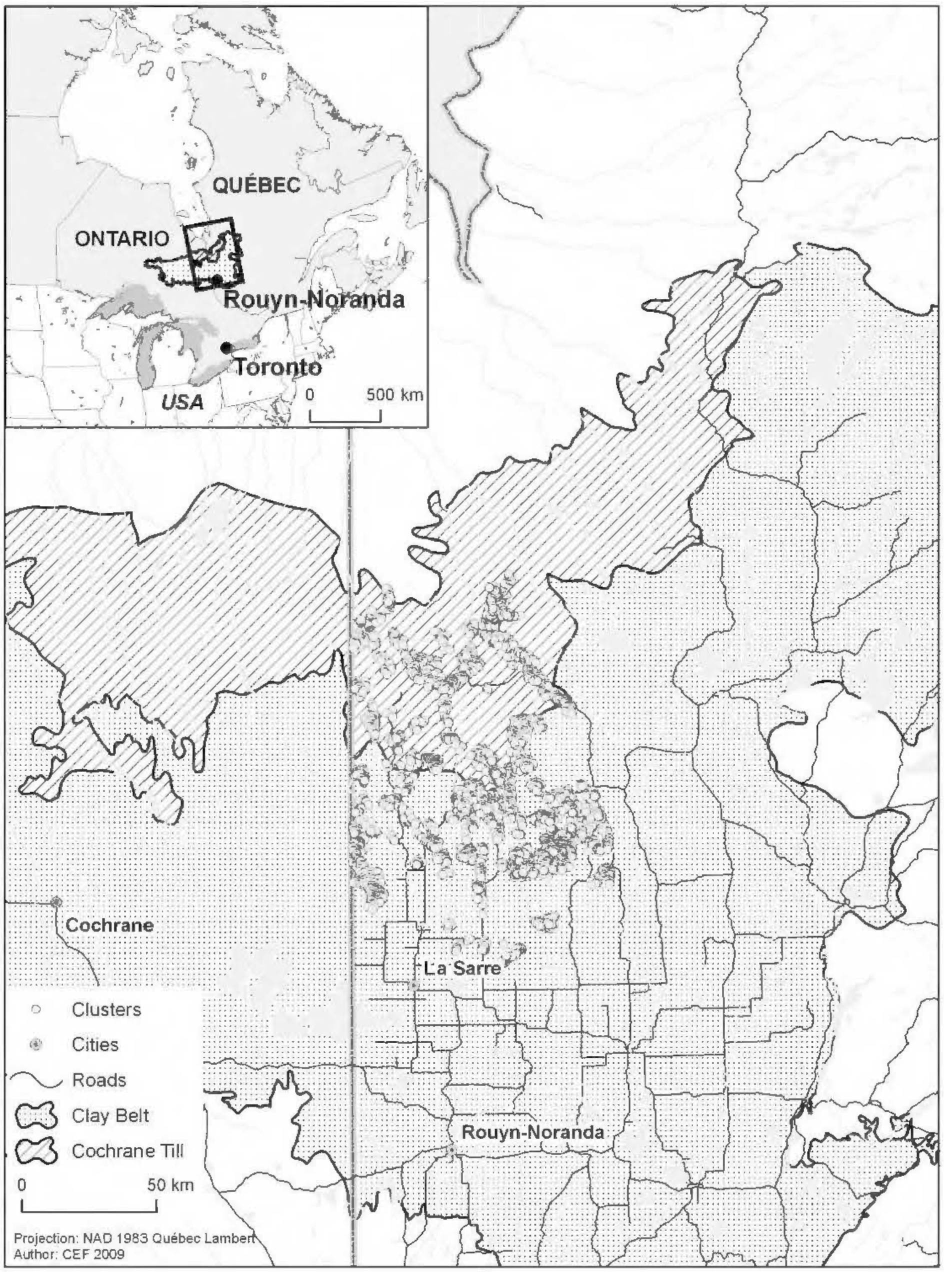

Figure 1.1. Location of the Clay Belt, the Cochrane till, the study area and the clusters in Québec (inset).

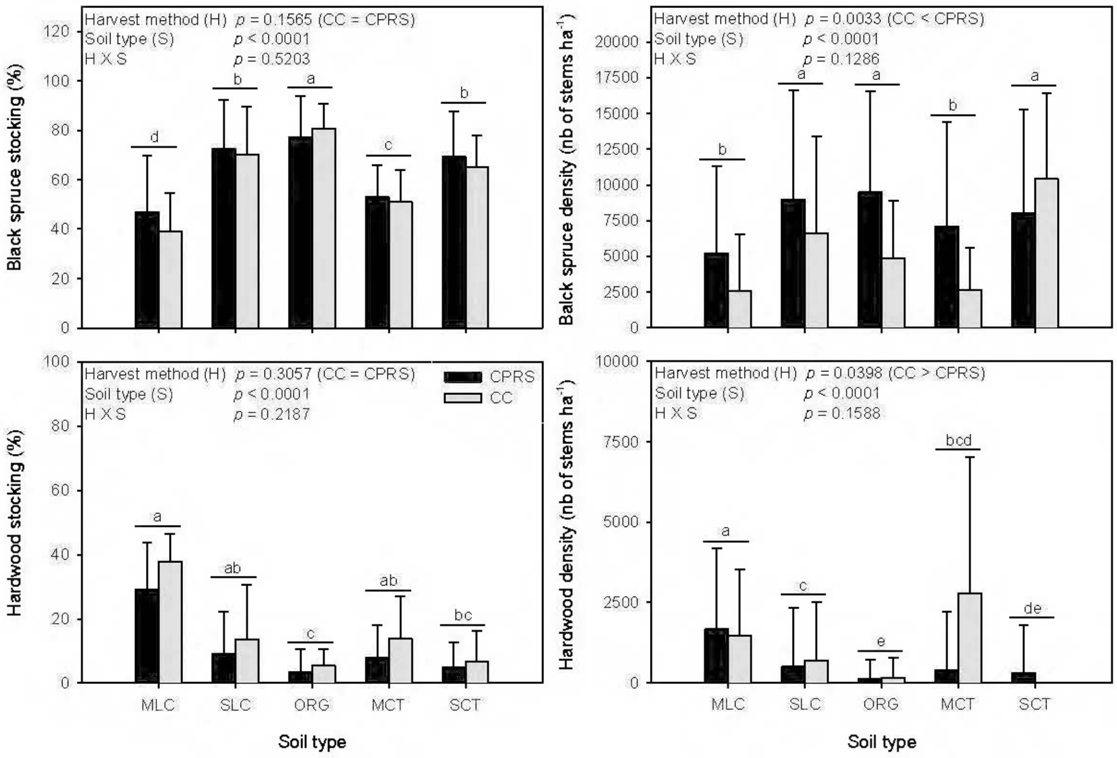

Figure 1.2. Stand regeneration parameters according to harvest method and soil type. Stocking (% ± 1 S.D.) and density (nb of stems ha^{-1} ± 1 S.D.) for black spruce and hardwoods. ORG = organic, MLC = mesic lacustrine clays, SLC = subhydric lacustrine clays, MCT = mesic clay till, SCT = subhydric clay till, CPRS = cut with protection of regeneration and soils, CC = clearcutting. Soil types identified by different letters are significantly different.

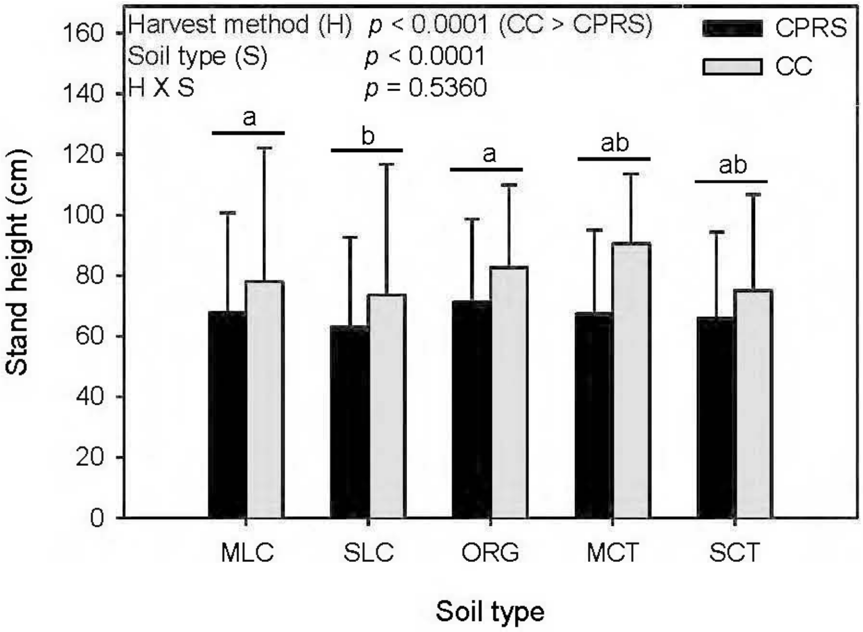

Figure 1.3. Black spruce stand height (cm ± 1 S.D.) according to harvest method and soil type. See Figure 1.2 for explanations on soil types and harvest methods. Soil types identified by different letters are significantly different.

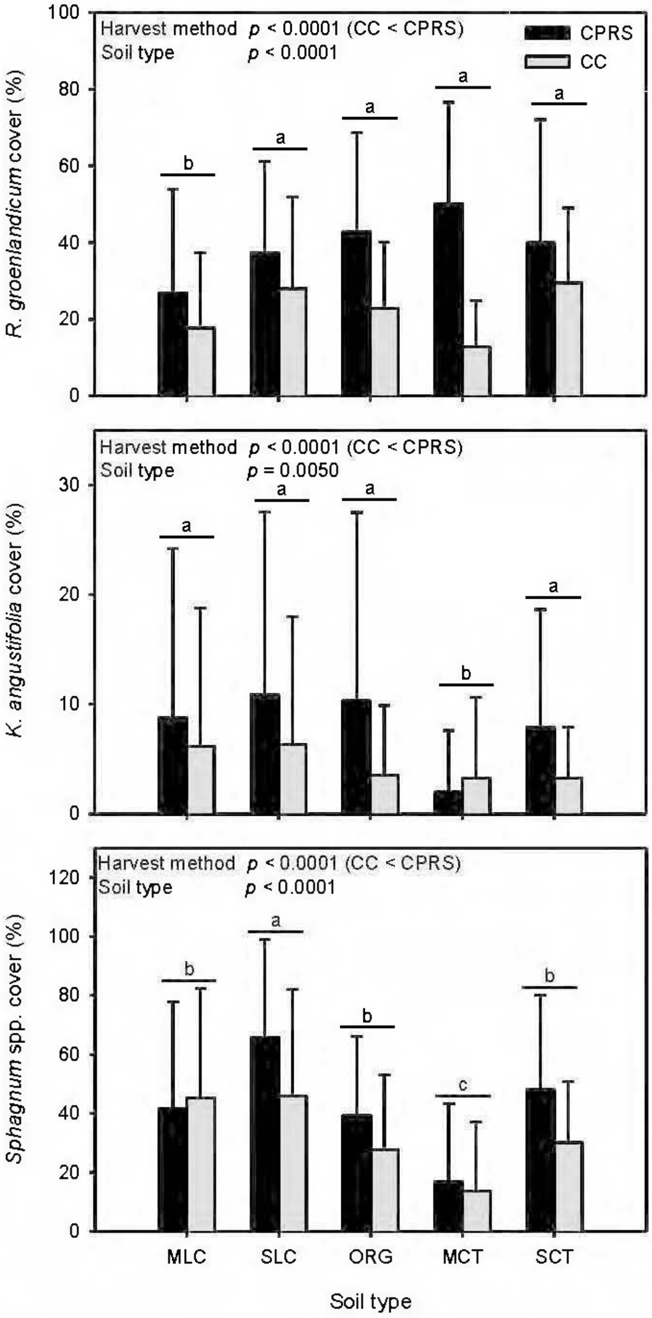

Figure 1.4. Ericaceous shrub and *Sphagnum* spp. cover (% ± 1 S.D.) according to harvest method and soil type. See Figure 1.2 for explanations on soil types and harvest methods. Soil types identified by different letters are significantly different.

CHAPITRE II

CONTRASTING EFFECTS OF SEASON AND METHOD OF HARVEST ON SOIL PROPERTIES AND THE GROWTH OF BLACK SPRUCE REGENERATION IN THE BOREAL FORESTED PEATLANDS OF EASTERN CANADA

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2.1. Abstract

It has been suggested that without sufficient soil disturbance, harvest in boreal forested peatlands may accelerate paludification and reduce forest productivity. The objectives of this study were to compare the effects of harvest methods (clearcutting vs. careful logging) and season (summer vs. winter harvest) on black spruce regeneration and growth in boreal forested peatlands of eastern Canada, and to identify the soil variables that favour tree growth following harvest. Moreover, we sought to determine how stand growth following harvest compared with that observed following fire. The average tree height of summer clearcuts was higher than that of summer carefully logged stands and that of all winter harvested sites. Summer clearcutting also resulted in a higher density of trees >3 m and >4 m tall and in a 50% reduction in *Rhododendron groenlandicum* cover, a species associated with reduced black spruce growth. Height growth of sample trees was related to foliar N and P concentrations, and to soil total N, pH and available Ca and Mg but not to harvest method or season. Our results also indicate that summer clearcutting could produce stand productivity levels comparable to those observed after high-severity soil burns. These results suggest that summer clearcutting could be used to restore forest productivity following harvest in forested peatlands, and offer further support to the idea that sufficient levels of soil disturbance may be required to restore productivity in ecosystems undergoing paludification.

Keywords: Careful logging; Clearcutting; Paludification; Peatland; *Picea mariana*; Soil disturbance; Forest productivity.

2.2. Résumé

Il est suggéré qu'en l'absence de perturbation suffisante des sols, la récolte de bois dans les tourbières forestières boréales pourrait accélérer le processus de paludification et réduire la productivité forestière. Les objectifs de cette étude étaient de comparer les effets de deux méthodes (coupe totale vs. coupe de protection) et de deux saisons (été vs. hiver) de récolte sur la régénération et la croissance de l'épinette noire dans des tourbières forestière de l'est du Canada, et d'identifier les variables du sol qui favorisent la croissance des arbres après la récolte. Nous avons également comparé la croissance des peuplements après la coupe à celle observée après des feux. La hauteur moyenne des arbres issus de coupes totales d'été était supérieure à celle des coupes de protection d'été et des coupes effectuées en hiver. La coupe totale d'été a également résulté en une plus grande densité de tiges >3m et >4 m de hauteur et en une réduction de 50% de recouvrement au sol du *Rhododendron groenlandicum,* une espèce reconnue pour ralentir la croissance de l'épinette noire. La croissance en hauteur des arbres était liée à la concentration de N et de P foliaire, ainsi qu'à la concentration de N total, au pH et à la disponibilité du Ca et Mg des sols, mais pas la à méthode ou à la saison de récolte. Nos résultats indiquent également que la coupe totale d'été peut produire des peuplements dont la productivité est comparable à celle observée à la suite des feux qui ont brûlé les sols sévèrement. Ces résultats suggèrent que la coupe totale d'été pourrait être utilisée afin de restaurer la productivité suivant la récolte dans des tourbières forestières et offrent un appui supplémentaire à l'idée qu'un niveau suffisant de perturbation des sols est nécessaire pour restaurer la productivité des écosystèmes en voie de paludification.

Mots clés: Coupe de protection; Coupe totale; Paludification; Tourbière; Épinette noire; Perturbation des sols; Productivité forestière.

2.3. Introduction

Black spruce (*Picea mariana* [Mill.] BSP) is the dominant tree species in much of the boreal forest in eastern Canada. Successional paludification (i.e. a dynamic process during which well-drained forests transform into peatlands due to successional) is a dominant process in some region of eastern Canada because of a combination of cold, humid climate, flat topography, and clay surficial deposits (Simard et al. 2007, Fenton et al. 2009). It has been shown in black spruce stands undergoing paludification that at canopy breakup (i.e. approximately 100 years post-fire), *Sphagnum* spp. mosses start expanding to the detriment of feathermosses (e.g. *Pleurozium schreberi*) (Fenton and Bergeron 2006), which induces changes in forest floor processes. Compared with feathermosses, *Sphagnum* spp. mosses have a higher carbon fixation rate (Swanson and Flanagan 2001), a higher soil temperature buffering capacity (Dioumaeva et al. 2003), and a slower decomposition rate (Turetsky 2003). As a result, thick organic layers develop over the mineral soil and change the conditions in the tree's rooting zone, which becomes colder, wetter, and oxygen-poor. In the prolonged absence of fire disturbance, these changes are accompanied by an autogenic reduction in productivity (Wardle et al. 2004) that involves reduced tree growth and stand productivity (Simard et al. 2007).

Forest fires are spatially variable, and soil burn severity varies greatly within and among fires (Miyanishi and Johnson 2002, Johnstone and Chapin 2006). In boreal ecosystems where thick organic layers are the norm, soil burn severity has significant consequences for tree regeneration (Johnstone and Chapin 2006, Greene et al. 2007) and growth (Johnstone and Chapin 2006, Simard et al. 2007), and for the structure, composition and productivity of forest (Viereck 1983, Lecomte et al. 2006a, 2006b, Simard et al. 2007). High-severity soil burns consume most of the organic forest floor (Dyrness and Norum 1983, Greene et al. 2005) and promote the establishment of productive stands on mineral soil (Dyrness and Norum 1983, Simard et al. 2007). In contrast, low-severity soil burns leave the forest floor almost intact, which provides a "head start" to the development of thick organic layers (Fenton et al. 2005, Simard et al. 2007, Shetler et al. 2008).

Over the past decades, because of an increasing demand for wood products, most of the harvest volumes allotted to forest companies in eastern Canada were located in low-productivity peatlands (Prévost et al. 2001). In the meantime, presearch and public pressure led governments and timber companies to adopt forest practices that protect the soil and advance tree regeneration. As a result, low-impact practices such as careful logging and winter harvest are now required practices in eastern Canada. However, concerns have been raised that these silvicultural practices may in some regions increase the rate of paludification because they do not sufficiently disturb the organic soil layers (Fenton et al. 2005, Lavoie et al. 2005). Ultimately, these silvicultural practices may produce growth conditions that are more similar to those associated with low-severity soil burns, leading to the establishment of low-density or patchy stands with widely variable productivity, rather than reproducing growth conditions prevailing after high-severity soil burns, which usually result in dense, productive stands (Lussier et al. 1992, Ruel et al. 2004). Consequently, the potential productivity of much of this landscape may be underestimated.

In a previous study conducted at the landscape level (Lafleur et al. 2010), we showed, 8 years after harvest, that regenerating black spruce stands were taller after clearcutting than after careful logging, regardless of soil type and drainage, and that the cover of *Sphagnum* spp. and ericaceous shrubs was also reduced by clearcutting. Together, these results suggest that soil disturbance was more severe during clearcutting than during careful logging. Since severe soil disturbance appears to be a key driver of ecosystem processes in a paludified landscape, in this study we sought to determine, 10-30 years after harvest, how soil disturbance created during different harvest operations and seasons could affect the productivity of paludified stands. The specific objectives of this study were (i) to compare the effects of different harvest methods (i.e. clearcutting *vs.* careful logging) and season (summer *vs.* winter) on black spruce regeneration and growth, (ii) to identify the soil variables that favour tree growth following harvest, and (iii) to determine how stand growth following forest harvest compares with that observed following fire. Because machinery traffic is restricted to specific skid trails during careful logging, this harvest method protects advanced regeneration and has a lower impact on soils compared with clearcutting (CC), where machinery traffic is not restricted, consequently reducing problems related to soil rutting and decreasing the need for tree planting. Likewise, in winter, snow cover and frozen ground protect soils against rutting and compaction during harvest operations, whereas in summer this protection is lacking. Consequently, soils are disturbed over a larger area during CC as compared with careful logging, and the disturbance is expected to be more severe during summer harvest than during winter harvest. Therefore, our hypotheses are: (i) clearcuts conducted during summer favour black spruce regeneration and promote tree growth compared to winter clearcuts and summer and winter careful logging; (ii) at the tree level, differences in tree growth are explained by local soil nutrient concentrations; (iii) clearcuts conducted during summer promote stand regeneration and growth at a level comparable to that of high severity soil burns. These results could help identify the harvest treatment most likely to reproduce the regeneration and growth patterns observed after high-severity soil burns and to help maintain or restore forest productivity in paludified black spruce stands.

2.4. Methods

2.4.1. *Study area*

The study area is located in the Clay Belt region of northwestern Quebec (49°48' N; 79°01' W) and is part of the western black spruce-feathermoss bioclimatic domain (Bergeron et al. 1999). According to Quebec's classification system (Robitaille and Saucier 1998), stands sampled in this study were black spruce stands with a ground cover dominated by *Sphagnum* spp. on thick organic deposits (>25 cm) with hydrous drainage (i.e. forested peatland) (Bergeron et al. 1999). In this region, the last glacial advance during the Wisconsin glaciation (ca. 8000 before present) flattened the topography and compacted the lacustrine clays that had been laid down by glacial lakes Barlow and Ojibway (Vincent and Hardy 1977).

From 1971 to 2000 the average annual temperature was 0.1°C, and average annual precipitation was 892 mm, with 35% falling during the growing season (Joutel weather station; Environment Canada 2009). The average number of degree-days (>5°C) is 1249, and the frost-free season is about 60 days, with frost occasionally occurring during the growing season.

2.4.2. *Site selection*

This study took advantage of stands that had been harvested under different forest management regimes to examine the long-term effects of different silvicultural practices on soil disturbance and black spruce growth. Forest maps produced by Tembec, the major forest company in the region, were used to identify 28 paludified stands (open multi-layer canopy with soil organic layer >25 cm thick) that had been harvested by careful logging (in Quebec, cut with protection of regeneration and soils [CPRS]) in winter (WCPRS, 5 replicates) or in summer (SCPRS, 5 replicates), and stands that had been clearcut in winter (WCC, 8 replicates) or in summer (SCC, 10 replicates). Because forest regulations and practices changed over time, and sites were harvested over a period of *ca.* 20 years, there was some overlap between management practices (Table 2.1). Only sites with a slight slope (<4%) and a clay mineral soil covered with a thick (>25 cm) organic layer were selected.

Prior to and after harvest, the tree layer of the sampling sites was dominated by black spruce, while Labrador tea (*Rhododendron groenlandicum*) and sheep laurel (*Kalmia angustifolia*) dominated the shrub cover. *Sphagnum fallax sensu lato, S. capillifolium, S. rubellum, S. russowii, S. fuscum, S. magellanicum* and feathermosses (mainly *Pleurozium schreberi*) dominated the forest floor.

2.4.3. Plot layout and survey

At each site, the direct results of harvest at the stand and tree levels were assessed through a series of nested plots. Specifically, three 400 m^2 circular plots were randomly installed at each site, each placed 50 m apart to ensure independence of the sampling points. The effects of harvest method and season at the stand level were assessed in two ways. First, black spruce stand height was estimated by measuring and averaging the total height of all black spruce stems taller than 1.3 m located in each circular plot. Second, stem density was assessed by determining the number of stems (> 1.3 m tall) ha^{-1} in each circular plot (total area sampled = 1200 m^2). Then, three sample trees were randomly selected in each circular plot. On these trees, we determined the total increment of the last 3 years (i.e. 3-year annual increment; 3YAI) and sampled foliage for nutrition analyses. Furthermore, these same trees were sampled for stem analysis, which enabled us to compare tree growth during the first 10 years following harvest (hereafter referred to as "height at age 10"). Cross-sections were taken at ground level, 0.3 m, 1 m, 1.3 m, 2 m, and every meter thereafter, and were then polished (400 grit) and cross-dated using standard dendrochronological techniques (Stockes and Smiley 1968). For trees established before harvest, we used the inflection in the age-height growth curve (indicating growth release following harvest) as age 0 (Curtis 1964). Because the degree of decomposition of the soil organic layers is known to influence the growth of black spruce seedlings (Lavoie et al. 2007), we characterized the microsite of each sample tree by determining the proportion of their root system present in the fibric (von Post scale = 0-4; Damman and French 1987) and mesic (von Post scale = 5-8; Damman and French 1987) organic layers. Then, the organic layer (at a depth of 10-20 cm, i.e. where the bulk of the roots were located) was sampled for nutrient analysis. Finally, in order to assess the effect of harvest on *Sphagnum* and ericaceous shrub cover (i.e. *K. angustifolia* and *R. groenlandicum*), visual estimates were made in four 4-m^2 sub-plots established in each 400-m^2 circular plot; species were evaluated individually so that total cover can exceed 100%. Surveys were conducted during the summer of 2006, 2007, and 2008.

2.4.4. Soil and foliar analyses

Chemical properties of all microsites were evaluated using substrate analysis (C:N, N_{tot}, P, Ca, Mg and pH) of the organic layer samples, and foliar nutrition was determined using foliar N and P concentrations.

Following sampling, organic soil samples were air-dried for 48 h, returned to the laboratory and frozen. Immediately prior to analysis, all 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 (Carter 1993). Total C and N were determined by wet digestion and analyzed with a LECO CNS-2000 analyzer (LECO Corporation, St. Joseph, MI). Extractable inorganic P was determined by the Bray II method (Bray and Kurtz 1945), and exchangeable Ca and Mg were extracted using unbuffered 0.1 M $BaCl_2$ and determined by atomic absorption (Hendershot and Duquette 1986).

Needle samples were collected in mid-September 2007 and 2008 when the growing season had ended. Needle samples were collected on the three sample trees selected for stem analysis, thus yielding a total of 252 samples. 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 all needles from an individual tree were mixed. These samples were oven-dried at 70°C for 48 h. After drying, needles were separated from twigs and ground. Total N was determined as it was for the soil samples on a CNS analyzer, while phosphorus was determined following calcination at 500°C and dilution with hydrochloric acid (Miller 1998). Phosphorus was analyzed by colorimetry (Lachat Instruments, Milwaukee, WI).

2.4.5. Statistical analyses

The effects of harvest method and season on stand-level parameters (i.e. black spruce stand height, density of stems taller than 2, 3, and 4 m, and cover of *Sphagnum* spp. and ericaceous shrub) were determined using two-way mixed-effect ANOVAs. Harvest method and season were introduced into these models as fixed effects, plot and site as random effects, and time since harvest as a covariate. Then, two-way mixed-effect ANOVAs were used to analyze the effects of harvest method and season on the growth parameters (i.e. 3YAI and height at age 10) of sample trees, using harvest method and season as fixed effects, plot and site as random effects, and sample tree total height as a covariate. Next, two-way mixed-effect ANOVAs were used to analyze the effects of harvest method and season on soil physico-chemistry and foliar nutrition. In these models, harvest method and season were introduced as fixed effects, and plot, site and tree as random effects. Finally, we used Pearson correlations to determine the strength of the relationships between 3YAI and height at age 10, and soil physico-chemical variables, foliar nutrition, and tree rooting location (i.e. % of the root system in the fibric and mesic layers).

Prior to analysis, residuals were tested for normality and homogeneity of variances, and were log- or square root-transformed when necessary. For the covariance analyses, we also tested for interactions between fixed effects and covariates. Mixed-effects analyses were done using the MIXED procedure in SAS (SAS Institute Inc. 2004). Post-hoc comparisons (Tukey HSD) were made to contrast the levels of the fixed variables, and differences were deemed significant when $p \leq 0.05$, except for interactions that were considered significant when $p \leq 0.10$.

2.4.6. Comparing harvest methods with wildfires

Because one of the general objectives of this study was to compare the effects of wildfires with those of harvest practices, we compared our results on stand height with a dataset from a previous study held in the same study area that compared the effects of low- and high-severity soil burns on forest productivity (Simard et al. 2007). In this study, all black spruce stems in 10 m ×10 m plots were sampled for stem analyses. Cross-sections were taken at ground level, 0.4 m, 1 m, 4 m, and every 4 m thereafter, and were then polished (400 grit) and cross-dated using standard dendrochronological techniques (Stockes and Smiley 1968). All stands were dominated by black spruce and located on clay soils. We used a subset of Simard et al.'s (2007) data, i.e., three paired low- and high-severity fires that occurred around 1907, 1916 and 1948 (Simard et al. 2007). To compare the results of the two studies, we compared the effects of the type of disturbance (i.e. harvest treatments [SCC, WCC, SCPRS and WCPRS] and soil burn severity [low- and high-severity soil burns]) on stand height and density of stems taller than 2, 3, and 4 m using one-way mixed-effect ANOVAs. The type of disturbance was introduced into these models as a fixed effect, plot as random effects, and time since disturbance as a covariate. Due to the large difference in stand age between stands originating from harvest (mean = 19.9 yrs, S.D. = 5.2) and those originating from fire (mean = 77.3 yrs, S.D. = 21.5), we used the stem analysis data from Simard et al. (2007) to estimate tree height at age 20. Therefore, time since disturbance was set at 20 for the sites originating from fire.

Although we recognize that climate was likely different during the first 10 years of growth between the forest stands originating from wildfires (which occurred in the early and mid-20th century) and those originating from forest harvest (which occurred in the late 20th century), we nonetheless believe that these comparisons could reveal important similarities in terms of growth between stands originating from wildfires or from forest harvest of varying soil disturbance severities. These preliminary results could help identify the harvest method most likely to reproduce the effects of high-severity soil burns in terms of stand growth rate and productivity, and therefore adjust forest harvest practices to maintain or restore forest productivity in paludified black spruce stands.

2.5. Results

2.5.1. Effects of harvest method and season on stand-scale parameters

2.5.1.1. Stand growth

Both harvest method and season had a significant effect on stand growth parameters. Season of harvest had a significant effect on mean stand height, with taller stands after summer than after winter harvest (Figure 2.1a), while the effect of harvest method was marginally significant (CC > CPRS; $p = 0.0730$). More importantly, however, the significant interaction between harvest method and season reveals that stands were approximately 35% taller after SCC than after WCC ($p = 0.0007$), SCPRS ($p = 0.0148$) and WCPRS ($p = 0.0046$; Figure 2.1a).

Furthermore, summer harvest produced a significantly greater number of stems >3 m and >4 m ha^{-1} (respectively 2.5 times and 4 times more stems per hectare), and a marginally significantly greater number of stems >2 m ha^{-1} than winter harvest (Figure 2.1b). The significant interaction between harvest method and season reveals that SCC produced 6 times more stems >4 m per hectare than the three other harvest method/season combinations (Figure 2.1b). These last results, together with those for stand height, suggest that SCC disturbed the forest floor more intensively and over a larger area than any of the three other harvest method/season combinations.

2.5.1.2. Sphagnum and ericaceous shrub cover

Neither harvest method nor season or their interaction had a significant effect on *Sphagnum* spp. or *K. angustifolia* (Figure 2.2) percent cover. Harvest method, however, had a significant effect on *R. groenlandicum* cover (Figure 2.2), which was approximately 2 times higher after CPRS than after CC. The significant interaction between harvest method and season indicates that *R. groenlandicum* cover was lower after SCC than after both WCPRS ($p = 0.0899$) and SCPRS ($p = 0.0016$), and that it was also lower after WCC as compared with after SCPRS ($p = 0.0087$; Figure 2.2).

2.5.2. Effects of harvest method and season on study trees and soil variables

Harvest method ($p = 0.5772$), season ($p = 0.2901$) or their interaction ($p = 0.8437$) had no effect on sample tree height at age 10 (across all harvest method/season combinations, $\overline{\chi} = 100$ cm, S.E. = 3.6 cm). Likewise, harvest method ($p = 0.8267$), season ($p = 0.3992$) or their interaction ($p = 0.5010$) did not have an effect on sample tree 3YAI (across all harvest method/season combinations, $\overline{\chi} = 48$ cm, S.E. 1.4 cm).

Similarly, harvest method and season had no significant effect on soil C/N, N_{tot}, P_{avail}, Ca, Mg or pH, nor was the interaction between them significant, except for a significant interaction for C/N (Table 2.2). Post-hoc contrasts indicated that SCPRS had a significantly ($p = 0.0459$) higher C/N than WCPRS.

Foliar N concentration was significantly higher after clearcutting (CC) than after CPRS (Figure 2.3). However, neither season nor the interaction between harvest method and season had an effect on foliar N concentration. Foliar P concentration did not significantly differ between harvest methods and seasons, nor was their interaction significant (Figure 2.3).

2.5.2.1. Linking organic layer physico-chemical properties and foliar nutrition to tree growth parameters

Table 3 shows the correlations between soil physico-chemical properties with sample tree height at age 10 and 3YAI. While tree height at age 10 was significantly negatively correlated to C/N, it showed significant positive correlations with organic layer N_{tot}, Ca and Mg and pH. P_{avail} showed no correlation with tree height at age 10. Contrary to height at age 10, 3YAI was not significantly correlated to any soil variables.

Although N and P foliar nutrition was positively correlated to 3YAI, these correlations were not significant. However, both N and P foliar nutrition showed significant positive correlations with tree height at age 10 (Table 2.3).

Finally, both 3YAI and height at age 10 were correlated to the proportion of the tree's root system growing in the fibric (negative correlation) and mesic (positive correlation) layers (Table 2.3). Appendix 2.1 shows the average proportion of the tree's root system growing in fibric, mesic and humic organic matter, and in mineral soil according to harvest method and season of harvest.

2.5.3. Comparisons between wildfires and harvested stands

Disturbance type had a significant effect on stand height. Stands originating from SCC and high-severity soil burns were significantly taller than those originating from the other types of disturbance (Figure 2.4).

Disturbance type also had a significant effect on stem density. High-severity soil burns produced a significantly greater number of stems >2 m and >3 m than any other types of disturbance (Figure 2.5). In addition, SCC produced a significantly greater number of stems >3 m than both WCC and WCPRS, and both for stems >2 m and >3 m, SCC produced an average number of stems equivalent to low-severity soil burns (Figure 2.5). Finally, both SCC and high-severity soil burns produced a significantly greater number of stems >4 m than any other types of disturbance (Figure 2.5).

2.6. Discussion

This study supports our first hypothesis that clearcuts conducted during summer favour the growth of black spruce stands over winter clearcuts and summer and winter CPRS. In addition, in agreement with our second hypothesis, our results show that following harvest individual tree growth is related to microsite chemical properties, in particular soil N_{tot} and C/N as well as pH and exchangeable Ca and Mg. Finally, the growth of black spruce stands that have beenn clearcut during summer was similar to that of post-fire stands, which supports our third hypothesis that in forested peatlands, summer clearcuts promote the growth of black spruce stand at a level comparable to high-severity fire.

2.6.1. Effects of harvest method and season on stand- and tree-scale parameters

Both mean stand height and the abundance of trees > 4 m were greater in SCC sites as compared to the other harvest method/season combinations, suggesting that SCC generates a greater proportion of the area that is conducive to rapid growth. The observation of more rapid stand growth with CC as compared to CPRS was confirmed by a parallel study conducted on a combination of soil types and soil drainage conditions on the Clay Belt (Lafleur et al. 2010).

At the stand level, levels of soil disturbance were also reflected in differences in percent cover of *R. groenlandicum*. Harvest methods had an effect on *R. groenlandicum* cover, which was 50% lower following CC than after CPRS, while the significant interaction between harvest method and season indicated that *R. groenlandicum* cover was higher in SCPRS sites as compared to SCC and WCC sites. Reduced *R. groenlandicum* cover after CC may have had important consequences for tree growth as this species is known to interfere with black spruce growth (Inderjit and Mallik 1996, 1997). These authors suggested that the production of water-soluble phenolic compounds by *R. groenlandicum* and changes in nutrient availability were possible sources of the interference of *R. groenlandicum* with black spruce growth.

At the individual tree level, differences in the level of soil disturbance could be reflected in the soil physico-chemical properties of microsites. Our results showed that height at age 10 was both positively correlated to soil N_{tot} and negatively correlated to soil C/N. In black spruce stands, soil disturbance, such as may occur during logging activities, is known to accelerate organic matter mineralization and to increase nutrient availability (Keenan and Kimmins 1993, Simard et al. 2001, Locky and Bayley 2007). In forested peatlands, where black spruce seedling growth is N-limited (Munson and Timmer 1989, Timmer and Munson 1991), any soil disturbance that increases N availability is likely to favour their growth.

Furthermore, both foliar N and P concentrations showed positive correlations with individual tree height at age 10. These results could indicate that although nutrient availability was not different among harvest method/season combinations, nutrient uptake may have been facilitated in microsites supporting larger trees. Because high foliar N and P concentrations have been linked to faster growth and higher photosynthetic activity of conifers (Macdonald and Lieffers 1990), and because N and P uptake is influenced by soil temperature (Van Cleve et al. 1981, BassiriRad 2000, Domisch et al. 2002), any soil disturbance likely to increase soil temperature is also liable to facilitate or to increase nutrient uptake and favour tree growth.

The proportion of the root system in the fibric and mesic organic layers was correlated to tree growth and height (i.e. 3YAI and height at age 10). Because the fibric layer is considered a poor growth medium for black spruce (Greene et al. 1999, Lavoie et al. 2007), and the mesic layer a good growth medium (Lavoie et al. 2007), trees with a high proportion of their root system in the mesic layer may have had access to a larger pool of nutrients. The thickness of the fibric layer, known to be a poor growth substrate, is related to site type but may also be influenced by soil disturbance during harvest operations as it is located on the top portion of the soil.

Thus, the nutritional quality of microsites and the position of the root system (i.e. whether the roots are mainly in the fibric or mesic organic layers) are important factors explaining tree growth following harvest operations in forested peatlands. In this study, we found no significant differences in the sample tree 3YAI or height at age 10 between harvest methods or seasons, nor did we find any interactions between these variables. Therefore our results suggest that at the tree level each harvest method and season was able to create a variety of microsites in terms of nutritional conditions, including nutrient-rich microsites that favoured tree growth.

2.6.2. Harvest method vs. wildfire

Only SCC was able to produce black spruce stands with an average height that was comparable to that of stands originating from high-severity soil burns, whereas all other harvesting treatments produced stands that had a mean height similar to that of low-severity soil burns (Figures 2.4 and 2.5). Furthermore, both SCC and high-severity soil burns resulted in a greater abundance of trees >4 m as compared with the other types of disturbance. Comparing the effects of soil burn severity on stand development in the boreal forest of northwestern Quebec, Lecomte et al. (2006a) showed that high-severity soil burns resulted in higher initial tree density as compared with low-severity soil burns, whereas Ilisson and Chen (2009) showed that black spruce recruitment after clearcutting was comparable to that of wildfire. Therefore, at the stand level, SCC could create growth responses more similar to those of high-severity soil burns than any other harvest method/season treatment combinations. This study suggests that SCC could be used in paludified black spruce stands if management objectives include restoring stand productivity and slowing paludification.

2.7. Conclusions

Our results showed that in paludified black spruce stands of the Clay Belt, SCC was better suited than any other harvest method/season combinations we tested to favour stand regeneration and growth. Summer clearcuts likely disturbed the soil over a greater proportion of the cutover area, which may have resulted in a greater abundance of microsites conducive to better tree growth, as shown by the greater abundance of trees >4 m in SCC sites compared with other harvest treatments. More importantly, SCC produced soil conditions favourable to tree growth in greater abundance, producing overall stand growing conditions that were comparable to high-severity soil burns. The concern that greater soil damage by rutting during summer operations (Morris et al. 2009) could decrease site productivity in organic soils was not verified one or two decades following harvest. These results therefore suggest that SCC reproduces to some extent the effects of high-severity soil burns (i.e. in terms of growth rate at the tree level, and in terms of mean stand height and density of trees taller than 4 m at the stand level). In turn, this suggests that SCC could be used in forest management strategies to help restore forest productivity when harvesting has inadvertently decreased potential stand productivity by favouring paludification. However, clearcutting may have greater impact than careful logging on several ecosystem properties and functions not evaluated in this study such as streamflow, water quality, and biodiversity and wildlife habitats (Keenan and Kimmins 1993). Hence, the simultaneous use of clearcutting and careful logging, along with the creation of conservation areas, could favour, at the landscape level, the maintenance of wood production as well as that of ecosystem properties and functions.

Finally, in agreement with other studies, we showed that soil disturbance may be required to restore productivity in ecosystems undergoing autogenic reduction in productivity (Wardle et al. 2004). In paludified forests, a thick organic layer insulates the soil, and mechanical disturbance to this layer may cause an effect similar to the assart effect (Kimmins 1997), i.e. a kick start for nutrient cycles and tree development in the early regeneration stage. However, to achieve optimal productivity following forest harvest, the appropriate level of soil disturbance to specific site and drainage conditions needs to be better defined.

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Tableau 2.1. Characteristics of the 28 paludified black spruce stands of the Clay Belt used in this study.

Harvest method	Site No.	Harvest year	Sampling year	TSH[1] (yr)	OL[2] thickness (cm ± 1 SD)
Summer clearcut (SCC)	CN-23	1975	2007	32	74.1 (26.3)
	CN-71	1975	2008	33	77.5 (38.2)
	CN-69	1980	2007	27	106.3 (19.0)
	MI-54	1982	2008	26	39.6 (27.9)
	MI-55	1982	2008	26	58.3 (35.3)
	CN-68	1984	2006	22	47.2 (17.2)
	MI-66	1986	2006	20	80.0 (22.8)
	MS-63	1986	2007	21	78.8 (26.7)
	VP-32	1990	2006	16	63.6 (37.8)
	WA-45	1993	2007	14	25.3 (11.7)
Winter clearcut (WCC)	WA-43	1982	2006	24	73.5 (29.8)
	MI-64	1982	2006	24	37.8 (31.3)
	MI-53	1986	2007	21	36.9 (22.4)
	MI-52	1987	2006	19	41.1 (21.3)
	VP-39	1989	2006	17	51.1 (10.2)
	VP-40	1989	2006	17	51.7 (17.3)
	MI-62	1991	2006	15	77.2 (26.4)
	VP-33	1993	2006	13	40.6 (11.8)
Summer CPRS[3] (SCPRS)	VP-35	1989	2007	18	121.1 (2.3)
	VP-36	1989	2007	18	41.3 (13.1)
	VP-37	1989	2007	18	58.2 (20.7)
	CS-11	1990	2006	16	37.2 (16.4)
	WA-44	1994	2006	17	57.8 (23.5)
Winter CPRS (WCPRS)	WA-42	1989	2007	18	32.7 (16.1)
	MI-56	1989	2007	18	121.2 (1.7)
	MI-58	1991	2007	16	105.3 (19.7)
	CN-24	1994	2007	13	46.1 (12.9)
	CN-70	1996	2007	11	77.0 (11.3)

[1] TSH = time since harvest

[2] OL = organic layer

[3] CPRS = cut with protection of regeneration and soils

Tableau 2.2. Means (± SE) of soil properties under black spruce trees after summer and winter clearcut and summer and winter cut with protection of regeneration and soils (CPRS) in paludified black spruce stands.

Treatment	C/N	N_{tot} (%)	P_{avail} (mg g^{-1})	Ca (cmol(+) kg^{-1})	Mg (cmol(+) kg^{-1})	pH
Clearcut						
Summer	42.1 (2.3)	1.27 (0.05)	0.029 (0.001)	27.7 (3.1)	5.1 (0.3)	4.11 (0.05)
Winter	44.1 (1.9)	1.20 (0.05)	0.032 (0.002)	35.9 (4.5)	6.5 (0.4)	4.25 (0.09)
CPRS						
Summer	55.1 (2.2)	0.92 (0.04)	0.029 (0.001)	21.2 (1.9)	4.7 (0.4)	3.92 (0.07)
Winter	41.6 (3.1)	1.22 (0.06)	0.030 (0.003)	26.0 (2.7)	6.0 (0.7)	4.28 (0.09)
p-value						
Harvest (H)	0.2190	0.1566	0.9405	0.3272	0.7008	0.6256
Season (S)	0.2003	0.2801	0.8587	0.3476	0.2443	0.1666
H X S	0.0547	0.1002	0.2065	0.9816	0.5875	0.3589

Tableau 2.3. Correlations between 3-year annual height increment and height at age 10, and soil variables, foliar nutrition and proportion (%) of the root system located in fibric and mesic organic layers.

Variable	3-year annual increment		Height at age 10	
	r	*p*-value	r	*p*-value
Soil variable				
C/N	-0.102	0.133	-0.243	**<0.001**
N_{tot}	0.106	0.120	0.270	**<0.001**
P	0.001	0.994	0.083	0.222
Ca	0.020	0.780	0.229	**<0.001**
Mg	0.120	0.086	0.262	**<0.001**
pH	0.023	0.738	0.270	**<0.001**
Foliar nutrition				
N	0.100	0.127	0.215	**<0.001**
P	0.116	0.077	0.148	**0.022**
Root system				
Fibric	-0.208	**0.002**	-0.241	**<0.001**
Mesic	0.145	**0.029**	0.183	**0.004**

Appendix 2.1. Proportion (% ± S.E.) of tree's root system growing in fibric, mesic and humic organic matter, and in mineral soil according to harvest method and season of harvest.

Treatment	Fibric	Mesic	Humic	Mineral
Clearcut				
Summer	68.1 (3.1)	26.2 (2.9)	3.7 (0.9)	2.0 (0.4)
Winter	64.7 (3.1)	24.0 (2.4)	8.5 (1.4)	2.8 (0.5)
CPRS[1]				
Summer	73.9 (3.5)	24.3 (3.5)	1.5 (0.5)	0.3 (0.1)
Winter	73.6 (4.0)	23.9 (3.6)	2.5 (1.7)	0.0 (0.0)
p-value				
Harvest (H)	0.1871	0.7352	0.1250	ND[2]
Season (S)	0.8964	0.6618	0.3895	ND
H × S	0.6360	0.8660	0.4922	ND

[1] CPRS = Cut with protection of regeneration and soils

[2] ND = Not determined

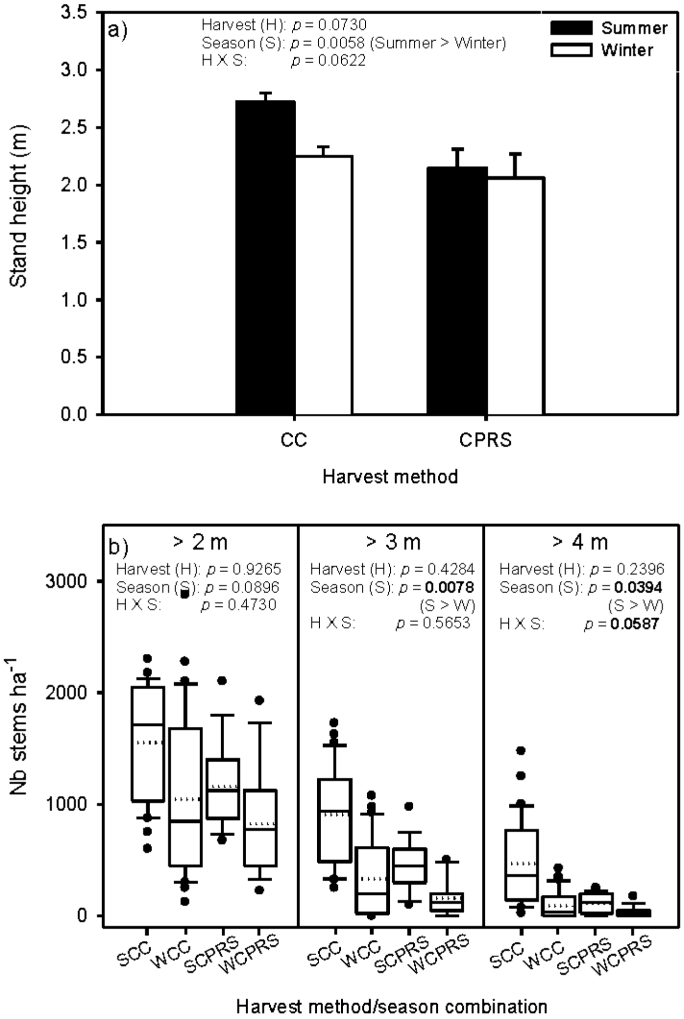

Figure 2.1. Black spruce mean stand height (m ± 1 S.E) according to harvest method and season. Values are adjusted means after controlling for time since harvest. CC = clearcut, CPRS = cut with protection of regeneration and soils. b) Box plots showing stem density of black spruce taller than 2 m, 3 m and 4 m according to harvest method and season. Values are adjusted means after controlling for time since harvest. The solid black lines represent the median; the dotted line, the mean; the vertical boxes, the 25th and 75th percentiles; the upper and lower bars, the 10th and 90th percentiles; black dots show outliers outside the 10th and 90th percentiles. SCC = summer clearcut, WCC = winter

clearcut, SCPRS = summer cut with protection of regeneration and soils, WCPRS = winter cut with protection of regeneration and soils.

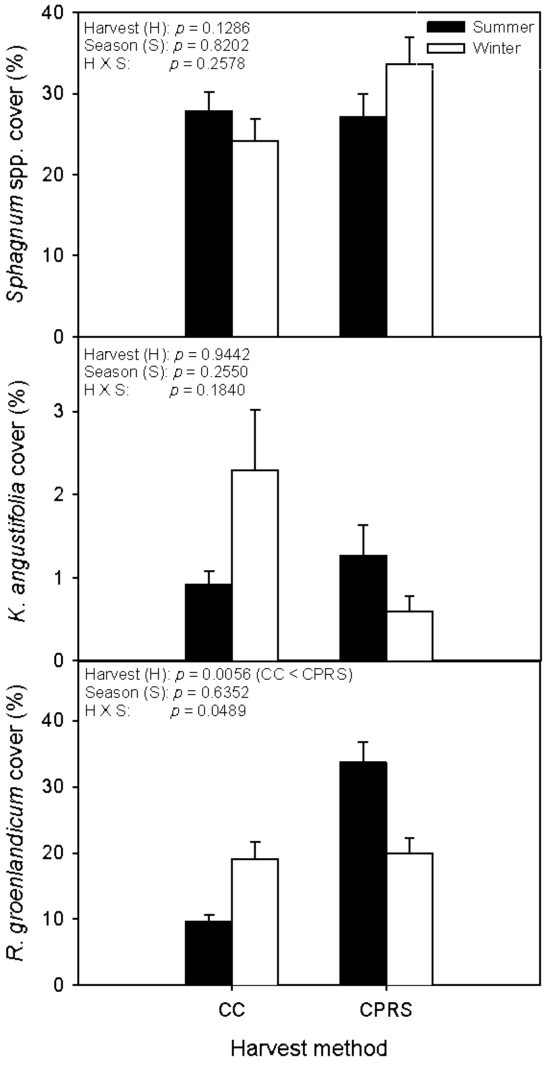

Figure 2.2. *Sphagnum* spp. and ericaceous shrubs cover (% ± 1 S.E.) according to harvest method and season. Values are adjusted means after controlling for time since harvest. CC = clearcut, CPRS = cut with protection of regeneration and soils.

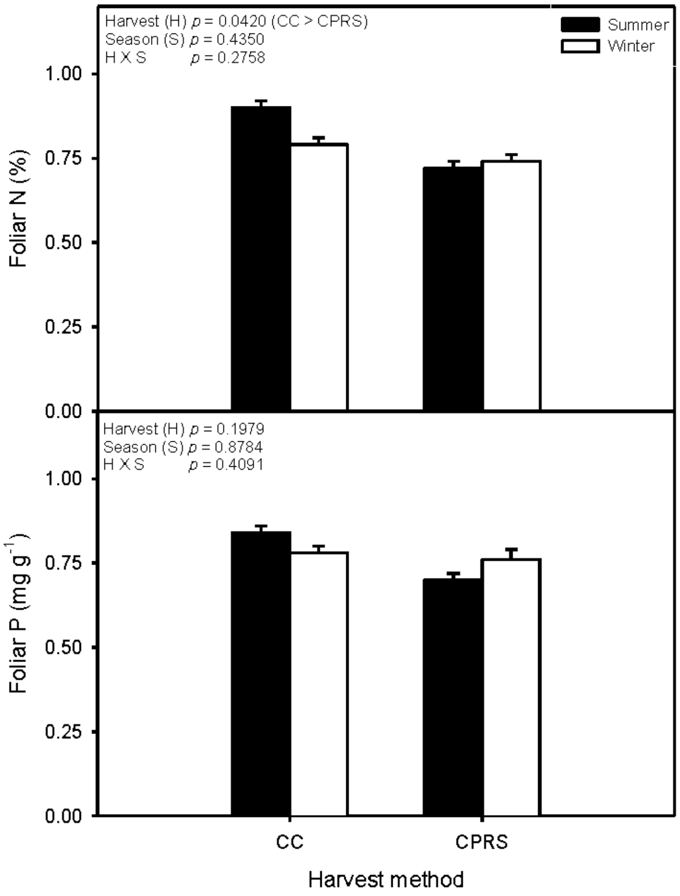

Figure 2.3. Black spruce foliar N (% ± 1 S.E.) and P (mg g^{-1} ± 1 S.E.) according to harvest method and season. CC = clearcut, CPRS = cut with protection of regeneration and soils.

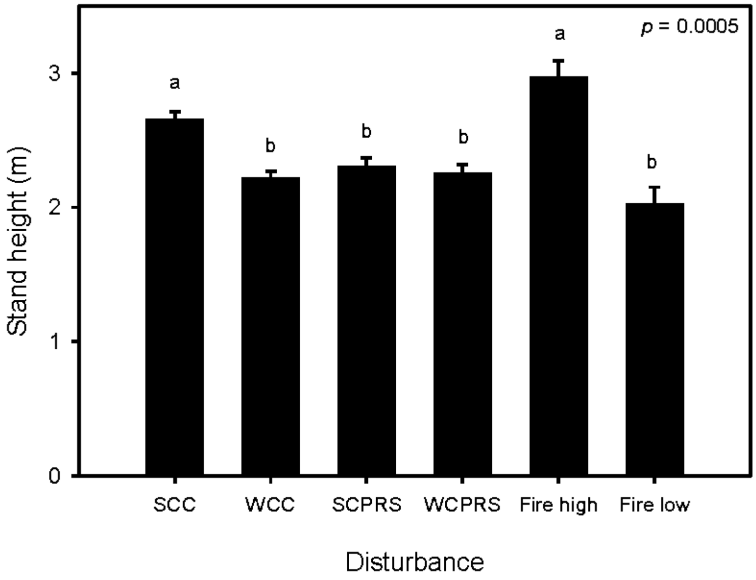

Figure 2.4. Black spruce mean stand height (m ± 1 S.E) according to harvest treatment and soil burn severity. Values are adjusted means after controlling for time since disturbance. SCC = summer clearcut, WCC = winter clearcut, SCPRS = summer cut with protection of regeneration and soils, WCPRS = winter cut with protection of regeneration and soils; Fire high = high-severity soil burn; Fire low = low-severity soil burn. Disturbances identified by different letters are significantly different.

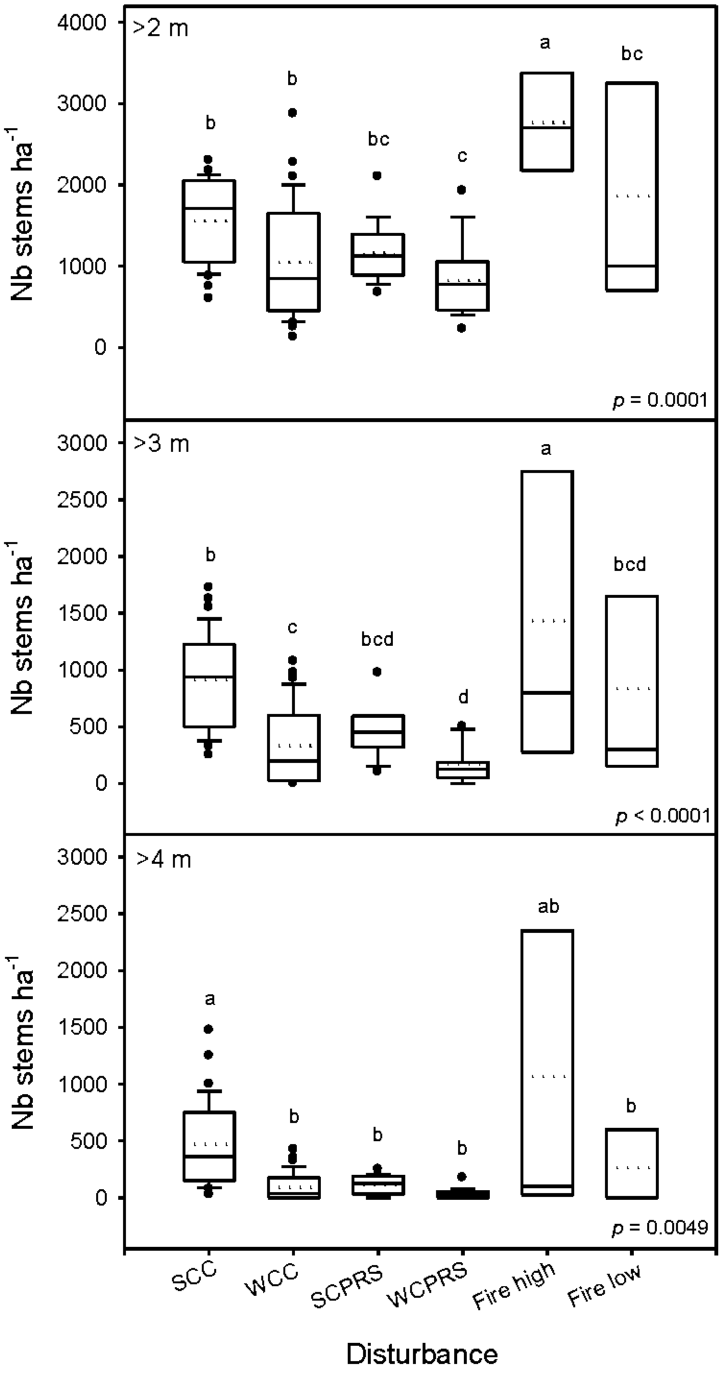

Figure 2.5. Box plots showing stem density of black spruce taller than 2 m, 3 m and 4 m according to harvest treatment and soil burn severity. Values are adjusted means after controlling for time since harvest. The solid black lines represent

the median; the dotted line, the mean; the vertical boxes, the 25th and 75th percentiles; the upper and lower bars, the 10th and 90th percentiles; black dots show outliers outside the 10th and 90th percentiles. SCC = summer clearcut, WCC = winter clearcut, SCPRS = summer cut with protection of regeneration and soils, WCPRS = winter cut with protection of regeneration and soils; Fire high = high-severity soil burn; Fire low = low-severity soil burn. Disturbances identified by different letters are significantly different.

CHAPITRE III

GROWTH AND NUTRITION OF BLACK SPRUCE SEEDLINGS IN RESPONSE TO DISRUPTION OF *PLEUROZIUM* AND *SPHAGNUM* MOSS CARPETS

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Manuscrit soumis à *Plant and Soil*

3.1. Abstract

Aims Mechanical soil disturbance usually promotes tree growth, this effect often being ascribed to the exposure of mineral soil. In lowland boreal forests, however, the thick organic layer covering the ground may preclude the exposure of mineral soil.

Methods We disturbed *Sphagnum* spp. and *Pleurozium schreberi* carpets to see how disturbance influenced substrate physico-chemistry and the growth of planted *Picea mariana* seedlings.

Results Disturbed carpets, whether *P. schreberi* or *Sphagnum* spp., were warmer than undisturbed carpets. *Pleurozium schreberi* carpets had lower volumetric water content and higher decomposition index than *Sphagnum* spp. carpets, whereas disturbance had no effect on these variables. *Pleurozium schreberi* had higher N_{tot} and lower C/N than *Sphagnum* spp., whereas disturbance had no effect on these variables. Moss disruption increased seedling growth rates as well as their foliar N and P concentrations in both substrates while these variables remained higher in *P. schreberi* than in *Sphagnum* spp. within a given treatment. Seedling growth was positively correlated to microsite N_{tot} and to foliar N and P concentrations.

Conclusions The growth of planted seedlings was influenced both by the type of substrates and substrate disturbance. Disturbance of the organic layer is sufficient to promote seedling growth. The implications of these results for forest management are discussed.

Keywords: black spruce, foliar nutrition, lowland boreal forest, *Pleurozium*, seedling growth, growth substrate disturbance, *Sphagnum*

3.2. Résumé

Objectifs La perturbation mécanique des sols favorise généralement la croissance des arbres, cet effet étant souvent attribué à l'exposition du sol minéral. Dans des forêts boréales de basses terres, toutefois, l'épaisse couche organique qui couvre le sol minéral peut empêcher l'exposition du sol minéral.

Méthodes Nous avons perturbé des tapis de *Sphagnum* spp. et de *Pleurozium schreberi* pour voir comment la perturbation influence leur physico-chimie ainsi que la croissance de semis de *Picea mariana* plantés.

Résultats Les tapis perturbés, que ce soit *P. schreberi* ou *Sphagnum* spp., étaient plus chaud que les tapis non perturbés. Les tapis de *P. schreberi* avaient un plus faible contenu volumétrique en eau et un indice de décomposition supérieure que les tapis de *Sphagnum* spp., alors que la perturbation n'a pas eu d'effet sur ces variables. Le *P. schreberi* avait une concentration de N_{tot} plus élevée et un C/N plus bas que les *Sphagnum* spp., alors que la perturbation n'a pas eu d'effet sur ces variables. La perturbation des mousses a augmenté le taux de croissance des semis ainsi que leur concentration foliaire en N et P dans les deux types de substrats, alors que ces variables étaient plus élevées dans le *P. schreberi* que dans les *Sphagnum* spp. La croissance des semis était positivement corrélée au N_{tot} des microsites ainsi qu'à la concentration foliaire en N et P.

Conclusions La croissance de semis plantés était influencée autant par le type de substrat que par la perturbation. La perturbation des couches organiques est suffisante pour promouvoir la croissance des semis. Nous discutons des implications de ces résultats pour l'aménagement forestier.

Mots clés : croissance des semis, épinette noire, forêt boréale de basses terres, nutrition foliaire, perturbation des substrats de croissance, *Pleurozium*, *Sphagnum*

3.3. Introduction

Throughout the boreal forests of North America and Eurasia, a moss layer, composed mainly of feathermosses (e.g. *Pleurozium schreberi* [Bird.] Mitt.) and *Sphagnum* spp., dominates the understory. This layer contributes to the creation and maintenance of low soil temperature and nutrient availability conditions (Bonan and Shugart, 1989) found in these forests. Through its effects on edaphic conditions, the moss layer influences several ecosystem processes such as net primary production (Bisbee et al., 2001; Gower et al., 1997) and soil respiration (O'Connell et al., 2003). At the stand scale, edaphic conditions tend to be heterogeneously distributed and vary according to moss species. For instance, *Sphagnum* spp. usually have a higher C/N than *P. schreberi* (Lavoie et al., 2007a), and water content is usually higher in *Sphagnum* spp. carpets than in *P. schreberi* carpets (Williams and Flanagan, 1996). These factors contribute to the low decomposition rate of *Sphagnum* spp. (Lang et al., 2009; Turetsky, 2003) and nutrient availability is usually lower in *Sphagnum* spp. carpets (Jeglum, 1981; Lavoie et al., 2007a) as compared to *P. schreberi* carpets. Consequently, microsites (i.e. the local features of the soil surface that characterize a seedling's growing environment such as physico-chemistry or microclimate; Whittaker and Levin, 1977) of *P. schreberi* are considered a better growth substrate for black spruce than *Sphagnum* spp. In the boreal forests of North America, these varying substrate conditions have been shown to account for most of the variability observed in individual tree height in even-aged coniferous stands (Macdonald and Yin, 1999).

Mechanical site preparation (MSP) is commonly used to improve the survival and growth of planted tree seedlings, and to ensure the successful regeneration of harvested sites (Sutherland and Foreman, 1995). In upland boreal forests, soil disturbances such as those that occur during MSP have been shown to increase the growth of planted tree seedlings by (i) reducing competing vegetation cover and consequently reducing competition for available nutrients (Örlander et al., 1990; Staples et al., 1999), (ii) enhancing root growth due to reduced soil bulk density and higher soil temperatures (Burdett et al., 1983; Örlander et al., 1990), and (iii) increasing N mineralization due to increased soil temperatures and improved soil moisture (Fleming et al., 1994; Hallsby, 1994; Johansson, 1994; Örlander et al., 1990). The beneficial effects of MSP are usually linked to the exposure of mineral soil or to the mixture of organic and mineral soils (Sutherland and Foreman, 1995). Although MSP treatments such as plowing have been shown to be effective methods for improving tree growth in lowland boreal forests growing on deep (>30 cm) organic deposits (Örlander et al., 1990), the exposure of mineral soil or the mixture of organic and mineral soils during MSP may be difficult due to the thickness of the organic layer. Consequently, in lowland boreal forests the effects of MSP on soil disturbance are more likely to be limited to the organic layer.

In upland boreal forests, soil disturbance occurring during MSP unequivocally affects soil properties and influences tree growth and stand productivity; however, the effects of soil disturbance in lowland boreal forests are poorly known, as are the relationships between tree seedling growth and substrate disturbance. In this study, we sought to identify (i) how physical disruption of the forest floor influences temperature, moisture, decomposition and nutrient availability in *P. schreberi* and *Sphagnum* spp. microsites, and (ii) how these modifications, in turn, influence the growth and nutrition of black spruce (*Picea mariana* [Mill] BSP) seedlings, one the most abundant and important commercial tree species in the North American boreal forest (Burns and Honkala, 1990). In the lowland boreal forests of northeastern North America undergoing paludification, Simard et al. (2007) observed that a strong decline in black spruce growth with time since fire was accompanied by a restricted rooting in mineral soils as the organic layer thickens. We first hypothesized that substrate physico-chemical conditions as well as the decomposition rates of a standard substrate would vary with moss species, with higher volumetric water content (VWC) in *Sphagnum* spp. and higher temperature, nutrient concentration and decomposition rate in *P. schreberi*. Second, we hypothesized that substrate disturbance would reduce VWC and increase substrate temperature, decomposition rate and nutrient concentration. Finally, we hypothesized that both substrate type and disturbance would influence black spruce seedling growth and nutrition, with higher growth rates and foliar N and P concentrations in disturbed *P. schreberi* microsites.

3.4. Material and methods

3.4.1. Study area

This study was conducted in a black spruce stand that was initiated following careful logging (in Quebec, cutting with protection of regeneration and soils) in 2003. The study area is located in the Clay Belt region of northwestern Quebec (49°48' N; 79°01' W) and is part of the western black spruce-feathermoss bioclimatic domain (Bergeron et al., 1999). The stand sampled in this study was, prior to harvest, a black spruce stand with *Sphagnum* spp. on thick organic deposits (>30 cm) with hydrous drainage (Bergeron et al., 1999). In this region, the last glacial advance during the Wisconsin glaciation (ca. 8000 BP) flattened the topography and compacted the lacustrine clays that had been laid down by glacial lakes Barlow and Ojibway (Vincent and Hardy, 1977).

Prior to harvest, the tree layer of the sampling site was dominated by black spruce. Labrador tea (*Rhododendron groenlandicum* Oeder) and sheep laurel (*Kalmia angustifolia* L.) dominated the shrub cover, whereas *Sphagnum subfulvum, S. magellanicum, S. fallax sensu lato, S. capillifolium, S. russowii, S. fuscum, S. rubellum,* and feathermosses (mainly *P. schreberi*) dominated the forest floor.

From 1971 to 2000, average annual temperature was 0.1°C and average annual precipitation was 892 mm, with 35% falling during the growing season (Joutel weather station; Environment Canada, 2009). The average number of degree-days (>5°C) was 1249, and the frost-free season was about 60 days, with frost occasionally occurring during the growing season.

3.4.2. Experimental design and treatment

At the chosen site, we established an experimental plantation. Twenty-five randomly distributed >4 m^2 patches of each of *P. schreberi* (hereafter referred to as *Pleurozium*) or *Sphagnum* spp. (hereafter referred to as *Sphagnum*) located between skid trails were identified. Then, each patch was divided into two sections of equal surface (>2 m^2): one section was assigned a soil disturbance treatment and the other was left intact to serve as a control. The section assigned with the disturbance treatment was hand-disturbed using pruning shears, forks and claw cultivators to a depth of approximately 25 cm. Our disturbance treatment did not expose the mineral soil and did not result in the mixture of organic and mineral soils. The objectives of the soil disturbance were to (i) disrupt the structure of the organic layers, (ii) eliminate competing vegetation (especially ericaceous shrubs) at the soil surface, (iii) shear tree and shrub root systems, and (iv) mix disturbed soil and vegetation as would be the case during harvest operations and site preparation. Then, each section of the patch was planted with two containerized black spruce seedlings (200 seedlings total). In order to avoid undesired effects from surrounding soils and intraspecific competition, seedlings were planted near the center of their respective section and approximately 50 cm apart. Initially, 250 2-year-old containerized seedlings were obtained from the provincial nursery of Trécesson, Québec, Canada. At the time of planting, 200 seedlings (mean height = 55.5 cm [S.D. = 0.3]; mean root collar diameter [RCD] = 0.76 cm [S.D. = 0.01]) were randomly selected (Table 3.1; initial height and RCD were not significantly different between substrates or disturbance treatments, and among substrate and disturbance combinations). We used the remaining 50 seedlings (initial height = 55.5 [S.E. = 0.5] and RCD = 0.76 cm [S.E. = 0.02], t-test not significantly different from the 200 planted seedlings at p = 0.9846 for initial height and p = 0.8471 for initial RCD) to determine seedling stem and foliage biomass at the time of planting. The seedlings were oven-dried at 70°C for 48 h. Dry mass was measured on an analytical balance (precision 0.01 g) separately for the stem and foliage. Initial stem and foliage biomass were 8.31 g (S.E. = 0.21) and 3.89 g (S.E. = 0.10), respectively. Because total height and RCD did not significantly differ between planted and sub-sampled seedlings, we assumed that initial stem and foliage biomass of the 200 planted seedlings did not differ significantly from that of the sub-sampled seedlings. Planted seedlings remained on the site for two growing seasons, i.e. from September 2007 to September 2009.

At the end of the second growing season, organic layers (0-10 cm) were sampled for nutrient analyses. Seedlings were also surveyed for total height increment and were harvested for biomass measurements. In the laboratory, seedlings were oven-dried at 70°C for 48 h. Dry mass was measured on an analytical balance (precision 0.01 g) separately for the stem and foliage. Height increment and stem and foliage biomass increments were then expressed as percentages.

3.4.3. Substrate and foliar analyses

Following sampling, soil samples were air-dried for 48 h, returned to the laboratory and frozen. Immediately prior to analysis, all 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 (Carter, 1993). Total C and N concentrations were determined by wet digestion and analyzed with a LECO CNS-2000 analyzer (LECO Corporation, St.

Joseph, MI). Extractable inorganic P was determined by the Bray II method (Bray and Kurtz, 1945).

Needle samples were collected in mid-September 2009 when the growing season had ended. Needle samples were selected from the current year's growth and were sampled from various positions on the seedling and mixed. These samples were oven-dried at 70°C for 48 h. After drying, needles were separated from twigs and ground. Total N was determined as for the soil samples on a CNS analyzer, while P was determined following calcination at 500°C and dilution with hydrochloric acid (Miller, 1998). Phosphorus was analyzed by colorimetry (Lachat Instruments, Milwaukee, WI).

Following the approach of Koerselman and Meuleman (1996), we also examined the relative concentration of N and P in foliage to assess the potential for N and P limitation of seedling growth. According to this approach, plants are more likely to be limited by N when $N/P \leq 14$, by P when $N/P \geq 16$, and co-limited by N and some other elements when $14 < N/P > 16$.

3.4.4. Decomposition index

We used buried wooden sticks as an index of decomposition rate. Rates of decomposition were estimated for a 2-year period by loss of mass of five wooden sticks buried in 16-mm nylon mesh bags. Prior to burial, wooden sticks were oven-dried (at 105°C for 48 h) and weighed on an analytical balance (precision 0.01 g). A total of 150 bags were buried. The bags were evenly distributed among the four treatment combinations (Table 3.1) and were buried horizontally at a depth of 10 cm (i.e. where the bulk of the planted seedlings' root systems were located), and at a minimum distance of 10 cm from the seedlings. At the end of the experiment, the bags were recovered and the wooden sticks were cleaned from coarse and fine debris before drying at 105°C for 48 h. Then, the wooden sticks were weighed on an analytical balance (precision 0.01 g) to determine the remaining mass. Percent mass loss (%ML) after 2 years of field incubation was calculated using the following equation:

$$[1] \qquad \%\mathrm{ML} = \left[\left(X_0 - X_1 \right) / X_0 \right] \times 100$$

where X_0 represents the initial wooden stick dry mass (g) and X_1 represents the final wooden stick dry mass (g) after 2 years of incubation.

3.4.5. Substrate temperature and water content

Substrate temperature was monitored from September 2007 to September 2009 using temperature data loggers (Thermochron® iButtons, model DS1921G, Maxim Integrated Products, Inc., Sunnyvale, CA). Temperature data loggers were evenly distributed among the four treatment combinations (total of 54; Table 3.1) and were buried at a depth of 10 cm and at an approximate distance of 10 cm from the seedlings. Each temperature data logger was paired with a buried bag. At the end of each growing season (i.e. during the last weeks of September), loggers were retrieved to extract the data. Substrate average temperature for the growing season (i.e. from May 1 to September 15) and substrate cumulative degree-days (>0°C; up to September 15) were calculated for each logger.

Finally, at the end of the experiment, substrate moisture was measured in each section as volumetric soil water content (VWC) by Time Domain Reflectometry (TDR; Field Scout Soil Moisture Meter Model TDR 300, Spectrum Technologies, Inc., Plainfield, IL). The probes were inserted into the soil in the top 10 cm of the organic layer. VWC was expressed as a percentage.

3.4.6. Statistical analyses

The effects of substrate type and disturbance treatment on substrate VWC and temperature, decomposition index, substrate chemistry (i.e. C/N, N_{tot} and P), growth parameters (i.e. height increment and stem and foliage biomass increment), and foliar nutrients (i.e. N and P concentrations, and N/P) were first contrasted using two-way mixed-effects ANOVAs. Substrate and disturbance were introduced in the model as fixed effects, whereas patch was used as a random effect. Variable residuals were tested for normality and homogeneity of variances, and the data were log or square root transformed when necessary. Mixed-effects analyses were done using the *Mixed* procedure in SAS (SAS Institute Inc., 2004). Differences were deemed significant when $\alpha \leq 0.05$, except for interactions that were considered significant when $p \leq 0.10$.

Then, we used principal components analysis (PCA) to identify relationships among substrate variables. Next, redundancy analysis (RDA) was used to identify the potential links between tree growth parameters and soil variables. RDA is a multivariate direct gradient analysis method in which species response curves (in this study, tree growth parameters) are presumed to have linear relationships with environmental gradients (in this study, soil variables). The results of the RDA were expressed in a biplot. As a 1-unit difference in nutrient concentration is probably much more important at low concentrations than it is at high concentrations, soil N_{tot} and P concentrations were log transformed as suggested by Palmer (1993). To support the PCA and RDA, Pearson correlations were used to determine the strength of the relationships between tree growth parameters and soil variables. PCA and RDA were performed using Canoco v4.5 (ter Braak and Smilauer, 2002).

3.5. Results

3.5.1. Substrate physico-chemical properties

3.5.1.1. Temperature, water content and decomposition index

During the growing season, disturbed substrates, i.e. *Pleurozium* or *Sphagnum*, were on average 0.85°C warmer (ANOVA, p = 0.0120) than undisturbed substrates (Figure 3.1a). Although during the growing season temperatures did not differ between *Pleurozium* and *Sphagnum* (ANOVA, p = 0.1792; Figure 3.1b), in early May temperatures in *Pleurozium* increased more rapidly than in *Sphagnum*, and reached the critical threshold of 3°C for root growth (Tryon and Chapin 1983) approximately 6 days earlier than in *Sphagnum* (data not shown). In addition, during the first 2 weeks of May, temperatures in *Pleurozium* were on average 0.5°C warmer than in *Sphagnum* (Figure 3.1b).

Volumetric water content (VWC) differed significantly between substrates, with *Pleurozium* having lower VWC than *Sphagnum*, whereas substrate disturbance had no effect on VWC (Table 3.2). The decomposition index also differed significantly between substrates, as wooden sticks located in *Pleurozium* decomposed more rapidly than those located in *Sphagnum* (Table 3.2). Substrate disturbance, however, had no effect on the decomposition index. No significant interactions were detected between substrate and disturbance treatment for VWC or decomposition index, indicating that the effects of substrate and disturbance treatment were independent.

3.5.1.2. Chemistry

Substrate analyses made at the end of the second growing season showed that *Pleurozium* had significantly higher N_{tot} and lower C/N than *Sphagnum* (Table 3.2), while the concentrations of P did not differ significantly between substrates. Disturbance had no effect on substrate nutrient concentration and C/N, and no significant interactions were detected between substrate and disturbance treatment (Table 3.2), indicating that the effects of substrate and disturbance treatment were independent.

3.5.1.3. Correlations among soil properties

As illustrated by the PCA (Figure 3.2) and confirmed by Pearson correlations, at the end of the experiment the decomposition index was negatively correlated to substrate VWC (r = -0.390, $p < 0.0001$), but not to C/N (r = -0.113, p = 0.17), while substrate N_{tot} (r = 0.196, $p < 0.05$) and P (r = 0.251, $p < 0.01$) were positively correlated to VWC. Neither N_{tot} nor P were significantly correlated to the decomposition index, the substrate average temperature for the growing season or substrate cumulative degree-days, nor was the decomposition index significantly correlated to the substrate average temperature for the growing season or substrate cumulative degree-days (data not shown).

3.5.2. Seedling growth and nutrition

3.5.2.1. Growth increment

Two years after planting, seedlings planted in *Pleurozium* had significantly greater % height increment, as well as greater % foliar and stem biomass increments than those planted in *Sphagnum* (Figure 3.3). Likewise, seedlings planted in disturbed substrates, whether *Pleurozium* or *Sphagnum*, had significantly greater % height increment and % foliar and stem biomass increments than those planted in undisturbed substrates (Figure 3.3). No significant interactions were detected between substrates and disturbance treatments for any of these parameters, indicating that the effects of substrate and disturbance treatment on black spruce growth were independent.

3.5.2.2. Foliar nutrition

The contrasting effects of substrate and disturbance treatment were also reflected in foliar N and P concentrations and in foliar N/P. Seedlings planted in *Pleurozium* had significantly higher foliar N and P concentrations and foliar N/P than those planted in *Sphagnum* (Figure 3.4). Likewise, seedlings planted in disturbed substrates had significantly higher foliar N and P concentrations and foliar N/P than those planted in undisturbed substrates (Figure 3.4). No significant interactions were detected between substrates and disturbance treatments for foliar N and P concentrations, indicating that the effects of substrate and disturbance treatment were independent. However, the significant interaction (p = 0.0513) between substrates and disturbance treatments for N/P indicated that seedlings planted in undisturbed *Sphagnum* had significantly ($p < 0.05$) lower N/P than the other three substrate/disturbance combinations.

3.5.3. Correlations between soil properties and seedling nutrition and growth

As illustrated by the RDA biplot (Figure 3.5) and confirmed by Pearson correlations, foliar P concentration was negatively correlated to VWC (r = -0.250, $p <$ 0.01), whereas both foliar N (r = 0.181, $p < 0.05$) and P (r = 0.283, $p < 0.001$) concentrations were positively correlated to the decomposition index. Furthermore, Pearson correlations revealed that foliar N concentration was positively correlated to substrate N_{tot} (r = 0.407, p < 0.0001), whereas foliar P concentration was not correlated to substrate P (r = 0.043, p = 0.556).

RDA and Pearson correlations also revealed that every growth parameter was negatively correlated to VWC and C/N, and positively correlated to substrate N_{tot} (Figure 3.5 and Table 3.3). In addition, Pearson correlations showed that every growth parameter was positively correlated to foliar N and P concentrations and foliar N/P (Table 3.3). Finally, the substrate average temperature for the growing season and substrate cumulative degree-days were not correlated to any of the growth parameters considered in the study (data not shown).

3.6. Discussion

In agreement with our first hypothesis, substrate type had a significant effect on substrate physico-chemistry, with higher VWC in *Sphagnum*, and higher decomposition index and N_{tot} in *Pleurozium*, although temperature did not differ between the substrates. However, in contrast with our second hypothesis, disturbance did not influence substrate VWC, decomposition index or nutrient concentrations, although temperatures were significantly higher in disturbed substrates. Finally, in concordance with our last hypothesis, both substrate type and disturbance had significant, non-interacting effects on black spruce growth and foliar nutrition: disturbed microsites favored black spruce nutrient uptake and growth while *Pleurozium* microsites offered a better growing substrate than *Sphagnum* microsites.

The observed differences in physico-chemical properties between *Sphagnum* and *Pleurozium* have already been shown by a number of authors (e.g. Jeglum, 1981; Lang et al., 2009; Lavoie et al., 2007a; Turetsky, 2003; Williams and Flanagan, 1996). Similarly, there exists an extensive literature on the effects of both natural and anthropogenic disturbances on soil properties in the boreal forest (e.g. McRae et al., 2001; Örlander et al., 1990; Sutherland and Foreman, 1995). Therefore, our discussion will focus on the effects of both the type of substrate and substrate disturbance on the growth of planted black spruce seedlings and on the possible mechanisms involved.

3.6.1. Substrate type and seedling growth

Although *Pleurozium* and *Sphagnum* spp. average temperatures did not differ significantly during the growing season, temperature in *Pleurozium* was ca. 0.5°C warmer than in *Sphagnum* spp. for nearly 2 weeks and reached 3°C (the soil temperature at which root initiation starts in black spruce; Tryon and Chapin, 1983) approximately 6 days earlier than in *Sphagnum* spp. Although slight, this difference could have been important in terms of growth increment as low soil temperature during the early part of the growing season may limit spruce seedling nutrient acquisition through three possible mechanisms. First, Tryon and Chapin (1983) showed that as soil temperature (at 10 cm) increased from 2°C to 12°C, black spruce seedling root elongation increased from 0.5 mm day^{-1} to 2.0 mm day^{-1}. Second, low soil temperatures limit nutrient uptake by restraining the mass flow of ions to the roots due to increased water viscosity (Marschner, 1995). Finally, low soil temperatures reduce the metabolic activity within spruce seedlings, limiting the uptake of both N (Orem and Sheriff, 1995) and P (Dighton and Harrison, 1983). Furthermore, it has been shown for some tree species that the permeability of the cell membrane decreases as soil temperature drops, which increases resistance to water movement within the root (Wan et al., 2001) and may therefore limit nutrient uptake. Consequently, because *Pleurozium* warmed up more rapidly than *Sphagnum* spp. in early May, root initiation may have started earlier in seedlings planted in *Pleurozium*, which likely lengthened their growing season and favored their growth. We therefore expected to observe positive correlations between substrate temperature and growth parameters; this, however, proved not to be the case. Two possible explanations for this absence of correlation are (1) the slight difference in seasonal average temperature and cumulative degree-days (data not shown) between substrates and (2) the relatively small number of temperature data loggers installed. Indeed, temperature variability between substrates (i.e. *Pleurozium* or *Sphagnum*) was quite large; this may have prevented us from detecting any relationship between substrate temperature and growth parameters.

Furthermore, differences in substrate VWC may also have accounted for growth differences observed between seedlings planted in *Pleurozium* and *Sphagnum*. As reviewed by Grossnickle (2000) for several North American spruce species, excess soil water may limit seedling growth through reduced substrate aeration and lowered net photosynthesis and nutrient uptake. Our results are in accordance with those of Grossnickle (2000) as foliar N and P concentrations were negatively correlated with VWC, indicating lower nutrient uptake with increasing substrate VWC. Lower VWC may thus in part explain higher growth rates in seedlings planted in *Pleurozium* rather than in *Sphagnum*.

In addition, in boreal ecosystems, one of the main N inputs is from N_2 fixation by cyanobacteria hosted by feathermosses, such as *Pleurozium schreberi* (DeLuca et al., 2002; Limpens et al., 2006). In this study, black spruce seedlings planted in *Pleurozium*, whether disturbed or not, likely benefited from this readily available source of N to increase their height and stem and foliar biomass more than seedlings planted in *Sphagnum*. These results are similar to those of Lavoie et al. (2007a, b) who showed that black spruce seedlings established in *Pleurozium* had better growth than those established in *Sphagnum*.

Finally, our results regarding N/P suggest that in lowland boreal forests N is more limiting to plant growth than P. This is in contradiction with some studies that suggest that in lowland ecosystems P is more limiting than N (see review by Walbridge and Navaratnam, 2006). In terrestrial ecosystems, the weathering of primary and secondary minerals is the ultimate source of P (Walker and Syers, 1976). As organic matter accumulates over the mineral soil, lowland forests become isolated from the underlying influence of the mineral soil, and P gradually becomes less available for plant growth. Because substantial additional inputs of P are unlikely to occur in lowland forest ecosystems, both biological and pedological P stores should be tightly conserved. The strong P resorption efficiencies in black spruce observed by Chapin and Kedrowski (1983) may explain why, in contradiction with other studies, we did not observe P limitations. Furthermore, in lowland ecosystems, subsurface lateral water flow is possible (Gafni and Brooks, 1990). That water flow and its nutrient loading (including P) could have alleviated P limitations by providing sufficient amounts of P for seedling growth.

3.6.2. Substrate disturbance and seedling growth

In boreal forests, MSP usually results in lowered soil moisture (Spittlehouse and Stathers, 1990), increased soil temperature (Örlander et al., 1990), and increased nutrient mineralization and availability (Sutherland and Foreman 1995). Contrary to our expectations, however, substrate disturbance (whether in *Pleurozium* or *Sphagnum*) did not result in increased decomposition rate of the standard substrate, increased nutrient concentrations and lowered VWC. Substrate structure (e.g, *Sphagnum* carpets are usually dense and have a high water-holding capacity) may first have prevented the lowering of substrate VWC. Second, the particular substrate conditions (i.e. high VWC) and chemistry (i.e. C/N > 45 and presence of secondary metabolites such as phenols and sphagnum acid) prevailing in lowland boreal forests may have constrained substrate decomposition and limited increases in nutrient concentrations.

Nonetheless, disturbance increased substrate temperature, both in *Pleurozium* and *Sphagnum*. Substrate disturbance is known to increase substrate temperature through reduced bulk density (Spittlehouse and Stathers, 1990; Sutherland and Foreman, 1995). Because the growth of spruce seedlings has been found to be influenced by soil temperature, we were expecting to observe positive correlations between soil temperature and growth parameters. Yet, we did not find any relationship between substrate temperature and black spruce seedling growth increment, perhaps due to the small differences observed in substrate seasonal average temperature and substrate cumulative degree-days, and the relatively small number of temperature data loggers used in this study.

Although we found little effect of disturbance on substrate properties (except for temperature), disturbance nonetheless resulted in significantly higher growth rates in black spruce seedlings planted both in *Pleurozium* and *Sphagnum* spp. Our results also show that the exposure of mineral soil or its mixing with organic substrate is not necessary to improve seedling growth conditions.

3.7. Conclusion and management considerations

Our study showed that in lowland black spruce stands the growth of planted black spruce seedlings was influenced both by the type of substrate and substrate disturbance. On the one hand, *Pleurozium* favored seedling growth over *Sphagnum*, likely because of higher N availability and lower VWC, and possibly because it reached critical the temperature for root growth initiation earlier in May than *Sphagnum*. On the other hand, disturbed substrates could have favored seedling growth over undisturbed substrates because of higher average temperature during the growing season, although we lack clear support for this. Two years after planting, disturbed *Pleurozium* microsites supported taller and heavier black spruce seedlings than other microsites. These results show that in forests growing on deep organic deposits, disturbance of the organic layer is sufficient to improve black spruce seedling growth conditions, and that the mixing of mineral and organic soil is not mandatory. Although our results only illustrate what happens during the first 2 years after planting, it is likely that these results apply to a longer period of time because a critical phase for black spruce growth is the early stage where a lag can persist for up to 20 years (Groot and Hökkä, 2000).

In the eastern Canadian boreal forest, tree planting is commonly used to avoid regeneration failure and rapidly increase stand density following harvest. Similarly, postharvest site preparation is widely used to improve growth conditions of planted seedlings. Since both the type of substrate and substrate disturbance influence seedling growth through various mechanisms, the rapid and appropriate selection of suitable planting microsites is a crucial step in the restoration of stand productivity following harvest in the boreal forest.

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3.9. References

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Tableau 3.1. Number of containerized black spruce seedlings, buried bags and temperature data loggers installed in each substrate and treatment combinations, and initial total height and root collar diameter (RCD) of seedlings planted in disturbed and undisturbed *Pleurozium* and *Sphagnum* patches.

					Seedling metrics[2]	
Treatment	Seedlings	Buried bags	Thermometer[1]		Total height (cm ± 1 SE)	RCD (cm ± 1 SE)
Sphagnum						
Disturbed	50	38	14		55.2 (0.8)	0.75 (0.02)
Undisturbed	50	37	13		54.8 (0.6)	0.74 (0.02)
Pleurozium						
Disturbed	50	38	14		55.7 (0.7)	0.76 (0.02)
Undisturbed	50	37	13		56.3 (0.6)	0.77 (0.01)
Total	*200*	*150*	*54*	*Mean*	*55.5 (0.3)*	*0.76 (0.01)*

[1] Each temperature data logger was paired with a buried bag.

[2] Both for total height and RCD, initial measurements were not significantly different ($p > 0.05$) between substrates or disturbance treatments, nor was the interaction term.

Tableau 3.2. Means (± 1 SE) of substrate volumetric water content (VWC), decomposition index (DI) and chemical properties for disturbed and undisturbed *Pleurozium* and *Sphagnum* microsites.

Treatment	VWC (%)	DI[1] (%)	C/N	N_{tot} (%)	P (mg g^{-1})
Sphagnum					
Disturbed	27.4 (1.7)	24.5 (3.3)	55.1 (2.1)	0.86 (0.02)	0.14 (0.01)
Undisturbed	25.9 (1.6)	22.9 (2.9)	59.4 (2.8)	0.81 (0.02)	0.13 (0.01)
Pleurozium					
Disturbed	20.0 (1.7)	32.2 (2.6)	48.2 (1.1)	0.98 (0.03)	0.14 (0.01)
Undisturbed	20.8 (1.4)	32.8 (2.9)	45.1 (1.0)	1.03 (0.03)	0.13 (0.01)
p-value					
Substrate (S)	**0.0030**	**0.0003**	**0.0005**	**<0.0001**	0.7396
Disturbance (D)	0.8468	0.8893	0.7867	0.8894	0.1817
S X D	0.4683	0.9165	0.1729	0.1374	0.7856

[1] Percent mass loss of buried wooden sticks

Tableau 3.3. Pearson correlation coefficient between substrate physico-chemical properties and foliar nutrition, and black spruce seedling growth parameters.

Growth parameters	Soil physico-chemical properties				Foliar nutrition		
	VWC	C/N	N_{tot}	P	N	P	N/P
% height increment	-0.182^{*}	-0.264^{***}	0.308^{****}	0.080^{ns}	0.593^{****}	0.486^{****}	0.358^{****}
% stem biomass increment	-0.191^{*}	-0.222^{**}	0.278^{***}	0.048^{ns}	0.624^{****}	0.483^{****}	0.387^{****}
% foliage biomass increment	-0.131^{*}	-0.270^{***}	0.314^{****}	0.084^{ns}	0.606^{****}	0.483^{****}	0.378^{****}

[1] RDC = Root collar diameter

$^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; $^{****}p < 0.0001$; ns = not significant

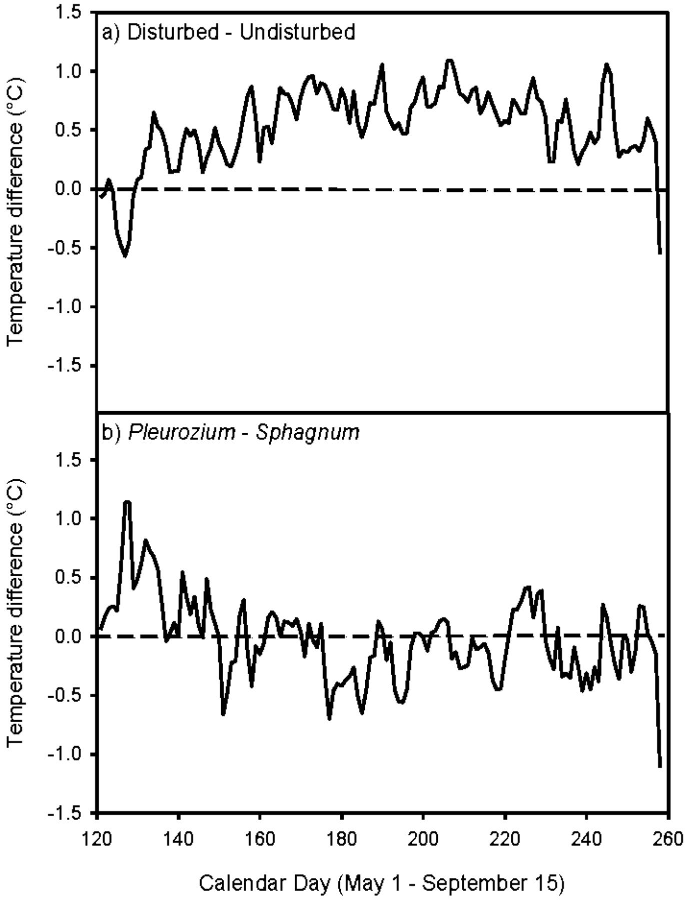

Figure 3.1. Differences in substrate temperature at a 10 cm depth during the growing season (May 1 to September 15) according to a) disturbance treatment and b) substrate type. In panel (a) values above 0°C indicate that temperatures were warmer in disturbed substrates, while values under 0°C indicate that temperatures were warmer in undisturbed substrates. In panel (b) values above 0°C indicate that temperatures were warmer in *Pleurozium*, while values under 0°C indicate that temperatures were warmer in *Sphagnum*.

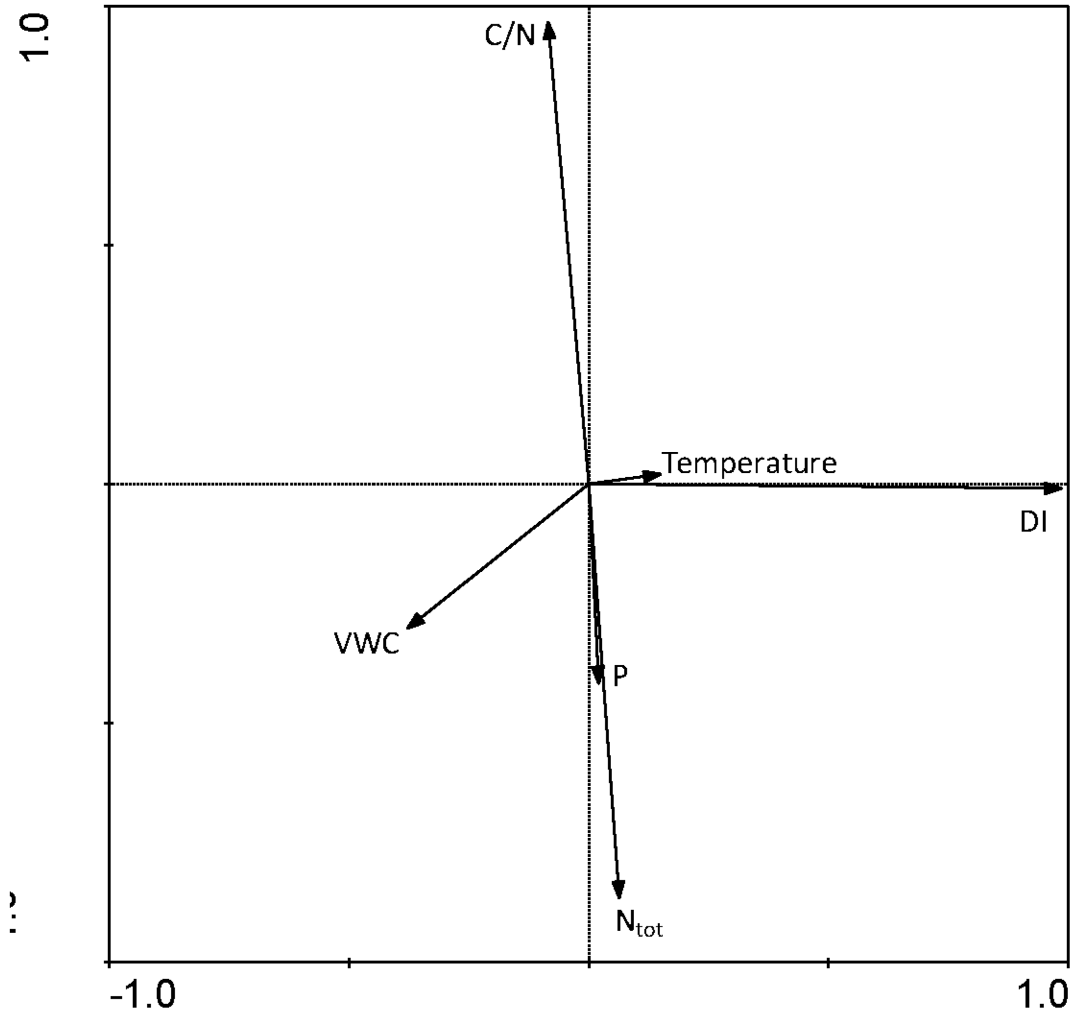

Figure 3.2. Principal components analysis (PCA) showing the relationships among substrate variables. Variables are as follows: N_{tot}, total N concentration (%); P, P concentration (mg g^{-1}); C/N, C/N ratio; VWC, volumetric water content (%); DI, decomposition index (%); Temperature, average temperature for the growing season (°C).

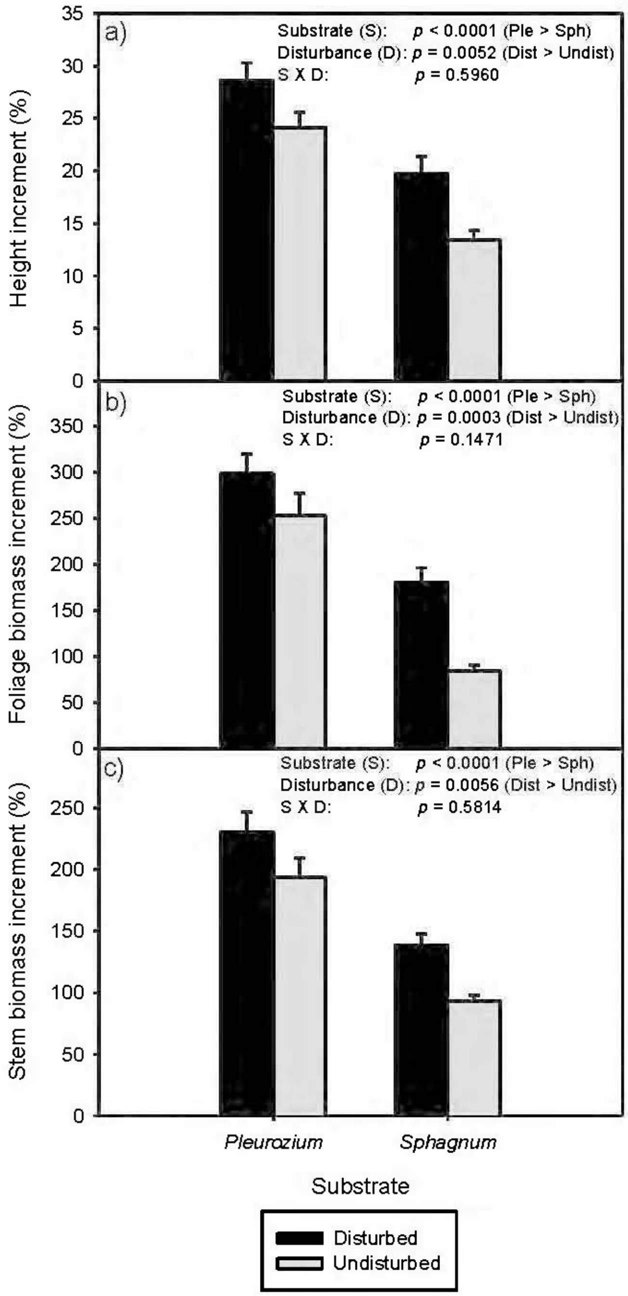

Figure 3.3. Black spruce seedling height increment and stem and foliar biomass increment according to substrate type and disturbance treatment.

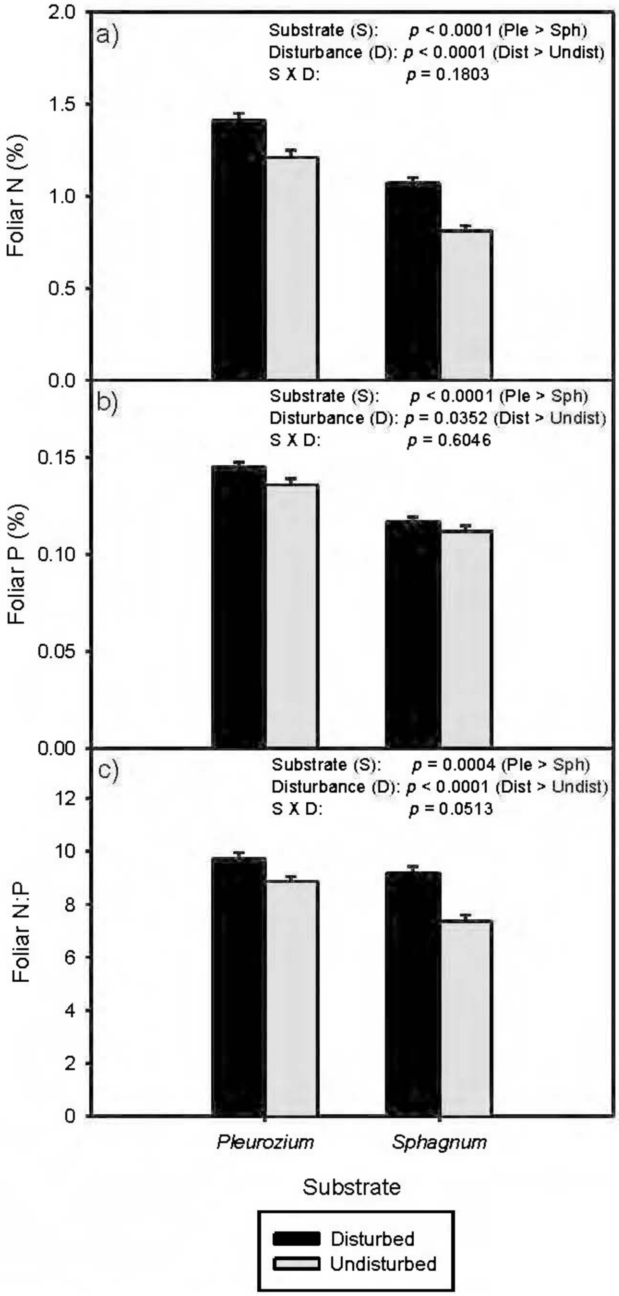

Figure 3.4. Black spruce seedling foliar N and P concentrations and N/P according to substrate type and disturbance treatment.

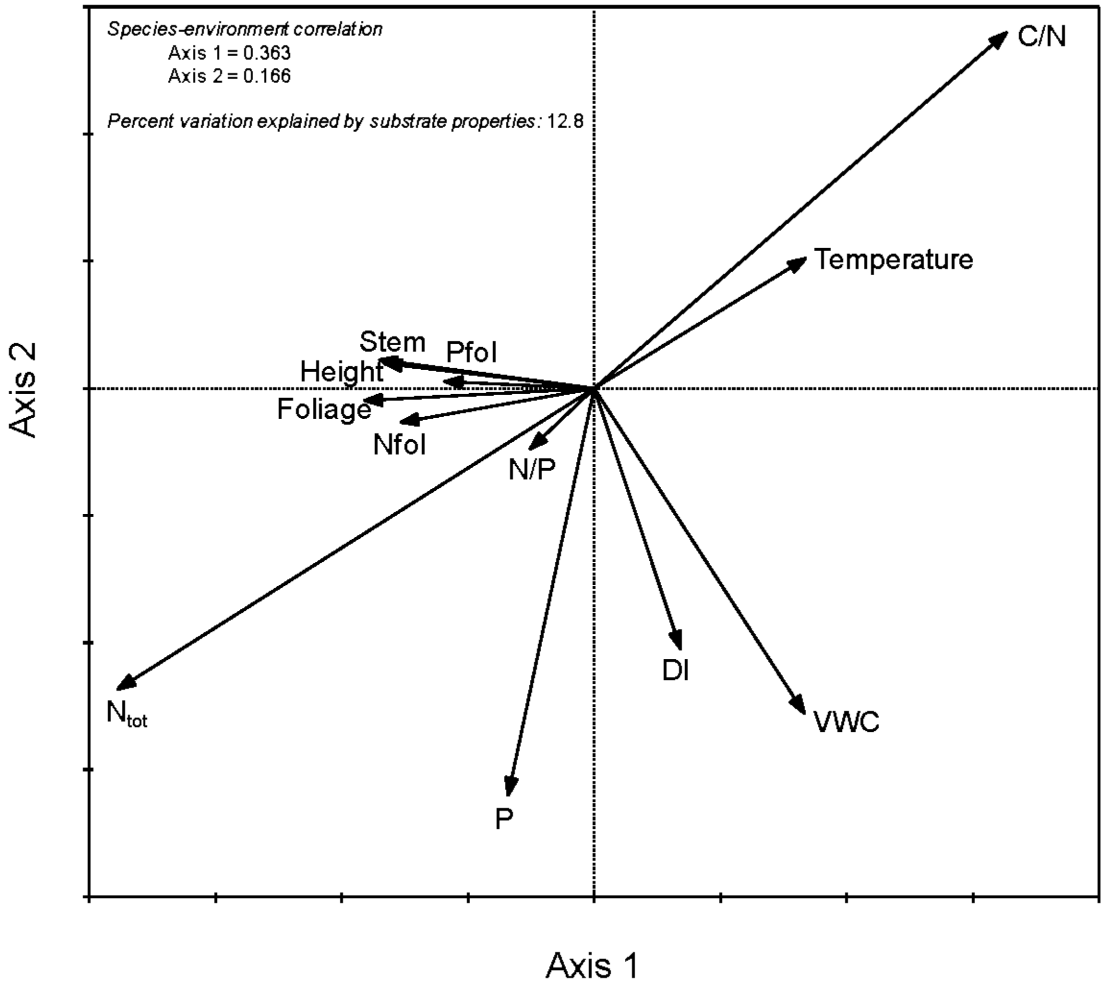

Figure 3.5. Redundancy analysis (RDA) showing the relationships between black spruce seedling nutrition and growth, and substrate variables. Nutrition and growth parameters are as follow: Height, height increment (%); Foliage, foliage biomass increment (%); Stem, stem biomass increment (%), Nfol, foliage N concentration (%); Pfol, foliage P concentration (%); N/P, foliage N/P ratio. Substrate variables are as follows: N_{tot}, total N concentration (%); P, P concentration (mg g^{-1}); C/N, substrate C/N ratio; VWC, volumetric water content (%); DI, decomposition index (%); Temperature, average temperature for the growing season (°C).

CHAPITRE IV

EFFICIENCY OF DIFFERENT MECHANICAL SITE PREPARATION TECHNIQUES IN STIMULATING TREE GROWTH IN BLACK SPRUCE PEATLANDS WITH VARIABLE ORGANIC LAYER THICKNESS.

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4.1. Abstract

In forest ecosystems, regeneration success and growth of post-disturbed stands have been related to variations in forest floor thickness. Here, we sought to determine the ability of different mechanical site preparation (MSP) techniques to improve the growth conditions of planted black spruce seedlings on organic sites (mean = 70.1 cm; min = 31.0 cm; max = 129.0 cm) and to determine how the success of MSP is conditioned by the thickness of the organic layer. Overall, seedlings of site prepared blocks were taller than those that were not treated, irrespectively of MSP techniques, likely owing the greater abundance of exposed mineral soil and mesic substrates created during MSP. Mounding (MD) and patch scarification (PS) were able to expose mineral soil over a greater surface relative to disc scarification (SC) and the control, whereas the combined surface of exposed mineral soil and mesic substrates was higher in MSP treatments relative to the control. Individual seedling growth was influenced by substrate type and drainage. Seedlings planted in moderately- and well-drained mesic substrates and mineral soil were taller than those planted in poorly drained fibric substrates. Once these effects are taken into consideration, MSP treatment had not additional influence on seedling performance. Overall, the lightest treatment (i.e. SC) was efficient because it succeeded in creating appropriate microsite despite thick organic layers.

Keywords: black spruce, forest floor disturbance, mechanical site preparation, organic layer thickness, seedling growth

4.2. Résumé

Le succès de régénération et la croissance des écosystèmes forestiers ont été reliés à la variation de l'épaisseur de la couche organique. Dans cette étude, nous avons cherché à déterminer la capacité de différentes méthodes de préparation mécanique de terrain à améliorer les conditions de croissances de semis d'épinette noire plantés dans des stations organiques (moyenne = 70. 1 cm; min = 31.0 cm; max = 129.0 cm) et à déterminer comment l'épaisseur de la couche organique conditionne le succès de la préparation de terrain. Dans l'ensemble, les semis des parcelles soumis à la préparation de terrain étaient plus grands que ceux des parcelles non traitées, peu importe la méthode de préparation de terrain, vraisemblablement en raison de la plus grande abondance de substrat de croissance constitué de sol minéral et de matière organique mésique créée lors de la préparation de terrain. La mise en butte et le scarifiage par placeau ont été en mesure d'exposer le sol minéral sur une plus grande surface de l'aire en régénération par rapport au scarifiage par disque et au témoin, alors que la surface combinée de sol minéral et de matière organique mésique était plus grande après préparation de terrain comparativement aux témoins. La croissance individuelle des semis a été grandement influencée par le type de substrat de croissance et son drainage. Les semis plantés dans des substrats mésiques et minéraux dont le drainage était bon ou moyen ont eu une meilleure croissance que ceux plantés dans des substrats fibriques et mal drainés. Une fois ces effets pris en considération, la préparation de terrain n'a pas eu d'effets additionnels sur la croissance des semis. Dans l'ensemble, le traitement le moins sévère (i.e. le scarifiage par placeau) a été efficace parce qu'a l'instar des traitements plus sévères (i.e. la mise en butte et le scarifiage par placeau) celui-ci a été en mesure de créer des microsites appropriés malgré une couche organique épaisse.

Mots clés: couche organique, croissance de semis, épinette noire, perturbation des sols, préparation de terrain.

4.3. Introduction

The variation in forest floor thickness commonly observed in forest ecosystems (Qian & Klinka, 1995; Schöning et al., 2006; Šamonil et al., 2008) influences tree growth (Geyer et al. 1980; Meredieu et al. 1996) and the vertical distribution of soil physico-chemical properties (Bringmark, 1989; Jobbágy & Jackson, 2001; Legout et al., 2008). In the North American boreal forest, forest floor thickness has been related to post disturbance regeneration success (Greene et al., 2005; Jayen et al., 2006; Meunier et al., 2007), stand spatial structure (Lavoie et al., 2007*a*) and stand growth (Johnstone & Chapin, 2006).

In boreal forest ecosystems, paludification (i.e. a dynamic process during which a terrestrial habitat transforms into a peatland) is a major process (Lavoie et al., 2005; Kuhry & Turunen, 2006). Paludification results in the development of a thick organic layer over the mineral soil that induces changes in the rooting zone of trees, causing them to become progressively colder, wetter, and oxygen-poor. In the prolonged absence of forest floor disturbance these changes are accompanied by an autogenic reduction in tree growth and stand productivity (Simard et al., 2007). High-severity soil burns, which consume most of the organic layer (Dyrness & Norum, 1983; Greene et al., 2005), have been shown to promote the establishment of productive post-disturbance stands on mineral soil (Dyrness & Norum, 1983; Simard et al., 2007), whereas low-severity soil burns leave the forest floor almost intact, and consequently promote the establishment of less productive stands on thick organic layers (Fenton et al., 2005; Simard et al., 2007; Shetler et al., 2008). Likewise, in two parallel studies we have shown that harvest systems that disturb the organic forest floor over a large area (e.g. clearcutting conducted during summer) regenerate stands that are more productive than stands regenerated by harvest systems that minimize soil disturbance (e.g. careful logging and winter harvest) (Lafleur et al., 2010, submitted *a*).

Following harvest, mechanical site preparation (MSP) is commonly used to improve the survival and growth of planted tree seedlings, and to ensure the successful regeneration of harvested sites (Sutherland & Foreman, 1995). Common MSP treatments aim at removing the overlying organic layer and expose the mineral soil. In the boreal forests of Fennoscandia and North America, soil disturbances such as those created during MSP have been shown to increase the growth of planted spruce seedlings by (i) reducing competition for available nutrients by reducing the cover of competing vegetation (Staples et al., 1999; Sutherland & Foreman, 2000), (ii) enhancing root growth via reduced soil bulk density and increased soil temperatures (Burdett et al., 1983; Örlander et al., 1990), and (iii) increasing N mineralization and uptake due to increased soil temperatures and improved soil moisture (Johansson, 1994; Nordborg et al., 2003).

In a case study conducted in black spruce stands prone to paludification, Lavoie et al. (2007*a*) showed that the surface topography of disturbed sites (both wildfire and harvest) appeared relatively flat although the thickness of the organic layer was highly variable due to the undulating nature of the underlying mineral deposit. They reported that the interaction between microtopography and accumulation of organic matter led to poor black spruce (*Picea mariana* [Mill.] BSP) growth following harvest (Lavoie et al. 2007*a*). They concluded that organic matter accumulation would restrict the ability of standard mechanical site preparation techniques, such as disc scarification, to expose the mineral soil and to create planting microsites favourable for seedling growth. Consequently, the accumulation of organic matter could at some point lead to a situation where the probability of restoring pre-harvest productivity with mechanical site preparation would be low and consequently harvested forest stands would be converted to peatlands. Nonetheless, in a parallel study conducted in a recently harvested black spruce stand growing on thick organic deposits (> 30 cm), we found that disruption of the surficial organic layers was sufficient to promote the growth of planted black spruce seedlings (Lafleur et al., submitted *b*). Consequently, the exposure of mineral soil by harvest or MSP may not be necessary to promote seedling growth in stands growing on organic deposits. Therefore, MSP could in some situations be an effective way to promote tree growth and help regenerate stands prone to paludification despite deep or variable organic layer thickness

In this context, we sought to determine if the thickness of the organic layer could influence the ability of different MSP techniques to create favourable planting microsites (i.e. the local features of the soil surface that characterize a seedling's growing environment such as physico-chemistry or microclimate; Whittaker & Levin, 1977) for the growth of planted black spruce seedlings. In order to create adequate planting microsites, different MSP techniques use different soil disturbance strategies. For instance, some techniques aim at breaking up and mixing the forest floor (with or without the underlying mineral soil), whereas other techniques specifically aim at exposing the mineral soil. Here, we contrasted three MSP techniques: disk scarification + crushing (SC) which aimed at breaking up and mixing the forest floor, and patch scarification (PS) and mounding (MD) both of which consisted in exposing the mineral soil. These MSP treatments were chosen not only because of the different strategies used to disturbed the forest floor, but also because of their likely different capacities to expose mineral soil over a large area (SC < MD < PS). Specifically, we wanted to determine the effects of MSP treatments on (i) stand-level parameters, i.e. stocking and stand height, and (ii) the relative abundance of potential planting microsites, as influenced by the thickness of the organic layer, and (iii) identify the growth substrates, both in terms of substrate type and drainage, that are conducive to better growth of individual black spruce seedlings. First, we hypothesized that MSP, regardless of soil disturbance strategy, would produce denser and taller stands relative to the control. Then, we hypothesized that MSP treatments would be able to increase the frequency of mesic organic matter and mineral substrates at the soil surface and at rooting depth (i.e. 5-15 cm) relative to the control, and that this frequency would be modulated by the thickness of the organic layer. Furthermore, in a study conducted in the same region, Lavoie et al. (2007*b*) showed that mesic organic matter and mineral soil were more favourable to black spruce growth than fibric organic matter. Consequently, we hypothesized that mesic organic matter and mineral soil would favour black spruce seedling growth compared to fibric organic matter. Finally, we postulated that stand height would be related to the ability of MSP techniques to increase the frequency of expose mineral soil and mesic organic matter at the soil surface and at rooting depth relative to the control.

4.4. Material and methods

4.4.1. Study area

The study area is located in the Clay Belt region of northwestern Quebec (49^{o}52' N; 78^{o}46' W) and is part of the western black spruce-feathermoss bioclimatic domain (Bergeron et al., 1999). Prior to harvest, the stands sampled were classified as black spruce stands with *Sphagnum* on thick organic deposits (> 30 cm) with hydrous drainage (i.e., forested peatlands) (Bergeron et al., 1999). In this region, the last glacial advance during the Wisconsin glaciation (ca. 8000 before present) flattened the topography and compacted the lacustrine clays that had been laid down by glacial lakes Barlow and Ojibway (Vincent & Hardy, 1977). Because of this combination of a cold, humid climate, flat topography and clay surficial deposits, stands in this region are prone to paludification.

Prior to harvest, the tree layer of the sampled stands was dominated by black spruce. Labrador tea (*Rhododendron groenlandicum* Oeder) and sheep laurel (*Kalmia angustifolia* L.) dominated the shrub cover, whereas *Sphagnum angustifolium, S. capillifolium, S. rubellum, S. russowii, S. fuscum, S. magellanicum* and feathermosses (mainly *Pleurozium schreberi*) dominated the forest floor.

According to the nearest weather station (Joutel, Quebec), the average annual temperature for the 1971-2000 period was 0.1°C, and average annual precipitation was 892 mm, with 35% falling during the growing season (Environment Canada, 2010). The average number of degree-days (>5°C) is 1249, and the frost-free season is approximately 60 days; frost can occasionally occur during the growing season.

4.4.2. Site selection and site preparation

The selected area was harvested by careful logging (in Quebec cut with protection of regeneration and soils, CPRS) during the winter of 2002; mechanical site preparation was applied in June 2003 and the site was planted in September 2004. Prior to the mechanical site preparation treatment, the selected area was divided into 15 blocks (0.5 to 2.1 ha), each of which was randomly assigned one of four site preparation treatments, i.e. (i) disk scarification + crushing (4 blocks), (ii) patch scarification (4 blocks), (iii) mounding (4 blocks), and (iv) control (3 blocks).

Disk scarification + crushing (SC) aimed first at loosening and breaking up the forest floor, and second at knocking down residual standing stems and breaking slash by machinery. The treatment was completed using a Komatsu D65PX tractor dozer equipped with a crushing roll and a disk scarifier. According to Cormier (2004), SC was able to expose mineral soil in areas where the organic layer was relatively thin (i.e. < 30 cm) and woody debris scarce.

Patch scarification (PS) consisted in removing the organic layer and exposing mineral soil over a surface of approximately 15 m^2. Patches were created by pushing the slash and the organic layer during the extension movement of the articulated arm. The treatment was done using a Komatsu PC250LC excavator. The machinery operator had instruction to work from the skid trails and to install patches approximately 3 m apart. Patch scarification created on average 230 patches ha^{-1} (Cormier, 2004). This treatment exposed mineral soil in all site conditions (Cormier, 2004).

Mounding (MD) was done using the same excavator used for patch scarification. In that case, however, the machinery operator had instructions to create patches of exposed mineral soil approximately 4 m^2 in size. The slash and organic layers were first removed from the surface by the extension movement of the articulated arm. Then the exposed mineral soil was dug to a depth of approximately 20 cm and a mound ca. 2 m^2 and 20 cm high was created next to the hole. Compared to patch scarification, this technique created smaller but more abundant patches of exposed mineral soil. On average mounding created ca. 370 mounds ha^{-1} (Cormier, 2004). As was the case for PS, this treatment exposed mineral soil in all site conditions (Cormier, 2004).

Finally, controls (CT) consisted of blocks harvested by careful logging but not submitted to any of the above-mentioned site preparation techniques.

Following site preparation, blocks were planted with 2-year old containerized black spruce seedlings following Quebec's provincial norms for planting. These norms state that in the boreal forest a minimum of 1500 seedlings ha^{-1} should be planted and that these should be planted at 2 m intervals (MRNF, 2010). At the time of planting, seedlings were on average 24.8 cm tall (S.E. = 0.46).

4.4.3. Plot layout and survey

We first determine the effect of the MSP treatments on stand regeneration and growth. Specifically, in each block, stocking was determined using three grids of 30 quadrats (2 m × 2 m). Stocking was determined by calculating the percentage of the thirty 4-m^2 quadrats containing at least one seedling taller than 0.30 m. The mean of the three grids was then calculated. Stocking of planted seedlings refers to the proportion of the 2 × 2 m quadrats with at least one planted seedling over 30cm in height, while total stocking refers to the proportion of quadrats with at least one black spruce stem, regardless of its origin [i.e. planted or natural seedlings, or layers (a common form of sexual reproduction in black spruce where branches become rooted)]. In addition, we determined total height and current year increment (CYI) of each planted seedling located within the quadrats.

Then, in each block we identified the type of substrate found at the soil surface and at a depth of 5-15 cm (i.e. where the bulk of planted black spruce root systems are located in boreal peatlands; Lavoie et al., 2007*b*) , every 5 m along two 50-m linear transects. At each sampling spot, we also estimated the thickness of the organic layer (OL) prior to MSP by measuring the thickness of the OL at the nearest adjacent location positioned between skid trails, i.e. where the forest floor had not been disturbed by harvest or MSP operations. Because it is likely that OL thickness changed between the moment MSP was completed and the time we did the sampling, these transects allowed us to determine how OL thickness prior to MSP influenced the frequency of potential planting microsites created by the different site preparation treatments.

Finally, the effects of substrate type and drainage on individual seedling growth were assessed through a series of nested plots. Specifically, three 300 m^2 (i.e. 10 m × 30 m) plots were installed in each block. In these plots, we searched for black spruce seedlings planted in microsites consisting of the combination of the three most frequent substrates found at 5-15 cm depth (i.e. fibric and mesic organic material [von Post scale = 0-4 and 5-8 respectively; Damman & French, 1987], and mineral soil; Table 4.2) and three drainage classes (i.e. well-, moderately- and poorly-drained). Drainage classes were determined following Saucier (1994). For each substrate/drainage combination, we intended to sample 2 seedlings, for a total of 810 seedlings. However, due to the uneven distribution of the substrates and drainage classes across the study area, it was not possible to achieve this goal. We sampled 494 seedlings. Table 4.1 shows the distribution of the sampled seedlings according to MSP treatment, substrate type and drainage. Seedling total height and CYI were measured. Then, seedlings were harvested for biomass measurements. In the laboratory, seedlings were oven-dried at 70°C for 48 hours. The foliage and root system dry mass were measured separately on an analytical balance (precision 0.01 g) This survey allowed us to identify the type of growth substrates (in terms of substrate type and drainage) most conducive to individual seedling growth.

4.4.4. Statistical analyses

First, one-way mixed-effect ANOVAs were used to contrast the effects of MSP treatments on stand-level parameters, i.e. stocking and stand height. MSP treatment was introduced in the model as a fixed effect, whereas grid and quadrat were used as random effects.

Then, the effect of MSP treatments on the frequency of potential growth microsites was determined using one-way mixed-effect ANOVA. MSP treatment was introduced in the model as a fixed effect, plot and block as random effects, and OL thickness as a covariate.

Finally, the effects of MSP treatment, substrate type and drainage on individual black spruce seedling growth (i.e. total height, CYI, and foliage and root system dry mass) were contrasted using three-way mixed-effects ANOVAs. MSP treatment, substrate type and drainage were introduced in the models as fixed effects, whereas plots and blocks were used as random effects. Owing to the absence of samples for certain levels of some fixed effects (e.g. moderately-well and poorly drained mineral soil in the control treatment; Table 4.1), we constructed a priori contrasts to answer the following questions: (*i*) regardless of drainage, as compared with CT, does MSP increase total height, CYI and root and foliage biomass of seedlings planted in fibric and mesic organic matter (SC + MD + PS vs. CT)? (*ii*) regardless of drainage, and for CS, MD and PS treatments only, do seedlings planted in mesic organic matter (Mes) and mineral soil (Min) have higher growth rates than those planted in fibric organic matter (Fib) (Mes + Min vs. Fib)? (*iii*) regardless of MSP treatment, and for fibric and mesic organic matter only, do seedlings planted in well (W) and moderately well (MW) drained substrate have higher growth rates than those planted in poorly drained (P) substrates (W + MW vs. P)?

Variable residuals were tested for normality and homogeneity of variances, and the data were log or square root transformed when necessary. In the case of the covariance analyses, we also tested for interactions between fixed effects and the covariate. Mixed-effects analyses were done using the *Mixed* procedure in SAS, and a priori contrasts were constructed using the CONTRAST statement (SAS Institute Inc., 2004). Differences were deemed significant when $\alpha \leq 0.05$.

4.5. Results

4.5.1. Stand scale parameters: stocking and stand height

Regardless of the origin of the stems (i.e. whether from planted, seed or layer origin), MSP had no effect on total stocking of black spruce seedlings (Figure 4.1A). Likewise, MSP had no statistically significant effect on the stocking of planted black spruce seedlings, although it was approximately 40% higher in the disc scarification + crushing (SC) and mounding (MD) sites than in the patch scarification (PS) and control (CT) sites (Figure 4.1B).

However, MSP had an effect on stand growth parameters. Stands were significantly taller in SC, MD and PS sites as compared with CT sites (Figure 4.2A), whereas CYI was significantly higher in MD and PS sites as compared with CT sites (Figure 4.2B).

4.5.2. Frequency of potential growth microsites

Mechanical site preparation treatments considered in this study were able to produce a wide variety of potential planting microsites at the soil surface (Table 4.2). After adjusting for OL thickness prior to MSP (see Table 4.3 for information regarding average OL thickness according to treatment and block), the relative abundance of fibric and mesic organic matter and *Sphagnum* spp. did not differ significantly among treatments, whereas the relative abundance of mineral soil was significantly higher in MD and PS sites as compared with SC and CT sites (Table 4.2). Likewise, at rooting depth (i.e. 5-15 cm), the relative abundance of fibric and mesic organic matter did not differ significantly among treatments, whereas the relative abundance of mineral soil was significantly higher in MD and PS sites as compared with SC and CT sites (Table 4.2). Hence, OL thickness influenced the capacity of the different MSP treatments to expose mineral soil but not mesic organic matter.

4.5.3. Individual seedling growth

According to our three-way mixed-effect model, MSP had no effect on individual seedling growth parameters, while both substrate type and drainage significantly influenced individual seedling growth (Table 4.4, Figures 4.3 and 4.4). First, seedlings planted in mesic organic matter and mineral soil grew taller and were heavier than those planted in fibric organic matter. Second, seedlings planted in well and moderately well drained substrates grew taller and were heavier than those planted in poorly drained substrates. In addition, both for total height and CYI, the significant interaction between substrate type and drainage (Table 4.4, Figures 4.3 and 4.4) indicated that globally total height and CYI were higher in moderately-well and well drained mesic and mineral substrates as compared to a poorly drained fibric substrate. Otherwise, the absence of two-way and three way interactions between substrate type and drainage, and MSP treatment indicated that the effects of these fixed variables on growth parameters were independent of each other. Hence, the efficiency of MSP treatments was not dependant substrate type or drainage.

Furthermore, despite the incompleteness of our database, pre-planned contrasts allowed us to identify significant differences among MSP treatments and to detail the significant differences found by our general model for substrate type and drainage. First, regardless of drainage, black spruce seedlings planted in either fibric or mesic organic matter had greater total height, CYI and root and foliar dry mass in SC, MD and PS sites as compared with CT sites (Table 4.5, Figures 4.3 and 4.4). Second, black spruce seedlings planted in mesic organic matter and mineral soil had significantly greater total height, CYI as well as root and foliar dry mass than those planted in fibric organic matter (Table 4.5, Figures 4.3 and 4.4). Third, for both fibric and mesic organic matter, seedlings planted in well drained or moderately-well drained microsites had greater total height, CYI as well as root and foliar dry mass than those planted in poorly drained microsites (Table 4.5, Figures 4.3 and 4.4). Finally, while seedling growth did not differ between well drained and moderately well drained substrates, seedlings planted in mineral soil had higher root and foliar dry mass than those planted in mesic organic matter (Table 4.5, Figures 4.3 and 4.4).

4.6. Discussion

In agreement with our first hypothesis, at the stand scale planted black spruce seedling growth was greater in the three MSP treatments compared to the control. Our second hypothesis was also upheld as despite variations in OL thickness, some MSP treatments (more precisely mounding [MD] and patch scarification [PS]) were able to create a higher frequency of mineral microsites compared to the control. Finally, mesic organic matter and mineral soil constituted the most favourable growth microsites for planted black spruce seedlings, and this effect was modulated by substrate drainage, which is in agreement with our third hypothesis.

4.6.1. Individual seedling growth

As observed by Lavoie et al. (2007*b*), we detected better growth in seedlings planted in mesic organic matter and mineral soil as compared to those planted in fibric organic matter. According to Lavoie et al. (2007*b*), these substrates constitute better growth microsites than fibric organic matter owing to both higher nutrient availability and uptake. As shown by Figure 4.4A, better root growth could also account for better height growth in mesic organic matter and mineral soil.

In addition, substrate drainage also explained differences in growth among substrate types; seedlings in well-drained and moderately well-drained substrates were taller and heavier than seedlings in poorly drained substrates. As reviewed by Grossnickle (2000), excess soil water may limit seedling growth through reduced substrate aeration, lowered net photosynthesis and nutrient uptake. In a parallel study, we also observed reduced growth of black spruce seedlings planted in poorly drained organic substrate (Lafleur et al., submitted *b*).

These results therefore suggest that soil disturbances that promote tree establishment in mesic organic matter or mineral soil and that improve moisture conditions of growth substrates are likely to favour the growth of individual black spruce seedlings.

4.6.2. Frequency of potential growth microsites

The higher frequency of mineral soil observed both at the surface and at rooting depth (after adjusting for OL thickness) is likely due to the different soil disturbance strategy used by the MSP treatments we contrasted. Indeed, while disc scarification + crushing (SC) disturbed primarily the forest floor surface (i.e. the top 30 cm; Cormier, 2004; personal observation), both MD and PS were successful at exposing the mineral soil.

However, the similar frequency of mesic organic matter (both at the surface and at rooting depth) among MSP treatments and the control indicated that forest harvest alone was as efficient as MSP treatments at disturbing the forest floor surface and at creating mesic microsites.

Therefore, while OL thickness had no influence on the ability of MSP treatments to create a higher frequency of mesic microsites relative to the control, it did reduce the ability of SC to expose mineral soil relative to MD and PS.

4.6.3. Stand scale parameters: stocking and stand height

Total stocking was similar among MSP treatments or between MSP treatments and CT. This result is likely due to the relatively large number of residual stems left by careful logging (Nguyen-Xuan et al., 2000).

Although CS and MD had ca. 40% higher planted stocking than both PS and CT, this difference was not significant. This is likely due to (i) large within-block variations in total stocking and (ii) Quebec's provincial norms that require a minimum of 1500 planted seedlings ha^{-1} in the boreal forests (MRNF, 2010).

Despite this absence of significant difference in the stocking of planted seedlings, planted stands were taller in SC, MD and PS as compared to the control, and current year increment was higher in MD and PS as compared to the control. These observations are likely the result of the higher frequency of mineral soil (both at the surface and at rooting depth) in MD and PS as compared with SC and CT. In addition, when combined together the frequency of mineral soil and mesic organic matter found at the surface amounts to 63,8%, 62.5%, 57.5% and 46.7%, respectively in MD, PS, SC and CT. Likewise, at rooting depth the combined frequency of mineral soil and mesic organic matter amounts to 73,7%, 72.5%, 84.3% and 67.2%, respectively in MD, PS, SC and CT. Together, these results confirm that in black spruce stands growing on thick (>30 cm) organic deposits, MSP is likely to increase the frequency of growth substrates conducive to better seedling growth following harvest and, consequently, to promote stand growth.

Considering that (i) SC favoured seedling regeneration and growth at levels similar to MD and PS, and (ii) SC is more cost efficient than both MD and PS (PS and MD are respectively two and three times more expensive than SC to treat an equivalent surface; Cormier, 2004), both from economical and forest regeneration stand points, and as long as it can expose mesic organic matter or mineral soil, SC seems to be a relevant MSP technique to use in order to increase the frequency of microsites conducive to better growth and to regenerate post-logged black spruce stands growing on organic deposits.

4.7. Conclusions and management considerations

This study shows that at the individual tree scale, substrate type and drainage are more important than MSP to explain black spruce seedling growth in forested peatlands. Our results also confirm that substrate drainage should be considered during planting operations and that seedling growth is higher on mesic organic matter and mineral soil compared to fibric organic matter. Furthermore, regardless of MSP treatment, stand growth was similar among SC, MD and PS treatments. Although black spruce is not considered very responsive to soil disturbance (Thiffault et al., 2006), these results suggest that disturbance of the organic layer should be sufficient to improve growth substrate conditions and to promote the growth of planted black spruce seedlings following MSP in forested peatlands (Lafleur et al., submitted *b*). Although this study reports the results of the effects of MSP on seedling growth only for the first few years following treatment, it is likely that this effect may be sustained over time. Indeed, Thiffault et al. (2004) reported that scarification in a post-harvest black spruce stand had a sustainable impact on microsite characteristics and planted seedling growth for at least 10 years. Therefore, MSP could help restore forest productivity following harvest or, at least, could delay the conversion from closed-crown, productive forests to forested peatlands.

In the paludified black spruce forests of northwestern Quebec, is has been shown that high-severity soil burns (which consume most of the organic layer) promote the establishment of productive post-disturbance stands on mineral soil, whereas low-severity soil burns leave the forest floor almost intact, and promote the establishment of less productive stands on thick organic layers. In this study, despite thick organic layers, some MSP techniques (i.e. MD and PS) were able to expose soil mineral over approximately 30% of the site prepared area, suggesting that MSP could to some extent reproduce the effects of high-severity fires on mineral soil exposition. However, this hypothesis remains to be tested.

Combined with other silvicultural treatments known to severely disturb soils, such as summer clearcutting and prescribed burning, MSP techniques (properly implemented in an ecosystem management approach) could therefore contribute to maintain ecosystem productivity and resilience in landscapes where forests are prone to paludification, such as the Clay Belt of eastern Canada.

4.8. Acknowledgements

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Tableau 4.1. Number of seedlings sampled by mechanical site preparation treatment, rooting substrate and substrate drainage.

	Mechanical site preparation treatment											
	Crushing			Mounding			Patch scar.			Control		
Drainage	Fib	Mes	Min	Fib	Mes	Min	Fib	Mes	Min	Fib	Mes	Min
Well	24	24	24	21	21	24	19	17	24	15	12	0
Moderate	19	22	0	16	23	0	20	16	0	13	15	0
Poor	17	11	0	19	19	0	19	16	0	11	13	0

Note: Fib, fibric organic matter, Mes, mesic organic matter, Min, mineral soil.

Tableau 4.2. Frequency (%) of potential growth substrates found at the soil surface and at a depth of 5-15 cm according to MSP treatment, after adjusting for organic layer thickness. Within a line, treatments identified with different letters are significantly different.

	Mechanical site preparation treatment[1]					
Substrate	SC	MD	PS	CT	*F*-value	Prob. > *F*
Surface						
CWD[2]	8.7	3.7	1.3	8.3	ND[3]	ND
Lichen	0.0	0.0	3.7	5.0	ND	ND
Fibric	6.3	11.1	2.5	1.7	1.196	0.400
Mesic	47.5	32.5	37.5	41.7	0.404	0.753
Humic	3.7	6.3	5.0	0.0	ND	ND
Mineral	10.0*b*	31.3*a*	25.0*a*	5.0*b*	5.448	**0.021**
P. schreberi	3.8	0.0	7.5	13.3	ND	ND
Polytrichum spp.	10.0	5.0	13.7	0.0	ND	ND
Sphagnum spp.	10.0	10.0	3.8	25.0	0.414	0.749
5-15 cm depth						
Fibric	23.0	20.9	9.5	32.8	0.544	0.664
Mesic	60.8	40.0	55.1	61.1	0.736	0.552
Humic	3.3	6.6	6.2	0.0	ND	ND
Mineral	12.9*b*	32.5*a*	29.2*a*	6.1*b*	3.927	**0.048**

[1] SC, disc scarification + crushing; MD, mounding; PS, patch scarification; CT, control.

[2] Coarse woody debris.

[3] ND, not determined because sample size too small.

Tableau 4.3. Mean organic layer thickness (cm ± S.E.) prior to MSP by treatment and block. Treatments did not significantly differ; $p = 0.242$ ($F = 1.43$).

	Treatment			
Block	Crushing	Mounding	Patch scar.	Control
1	31.1 (12.4)	44.9 (12.4)	46.3 (14.1)	51.9 (28.8)
2	45.7 (17.6)	56.2 (26.2)	48.2 (28.5)	59.7 (38.5)
3	55.2 (25.2)	94.1 (25.2)	94.5 (29.3)	97.2 (39.2)
4	85.7 (18.6)	129.4 (27.8)	114.3 (19.7)	—
Mean	*54.4 (13.6)*	*80.7 (20.3)*	*77.3 (19.8)*	*74.6 (24.0)*

Tableau 4.4. Results of three-way ANOVAs describing the statistical significance of the effect of MSP treatment, substrate type and drainage on black spruce seedling growth parameters using organic layer (OL) thickness as a covariate.

Variable	Source	*F*-value	Prob. > *F*
Height	MSP (M)	0.53	0.6610
	Substrate (S)	37.12	**<0.0001**
	Drainage (D)	31.65	**<0.0001**
	S X D	5.04	**0.0072**
	M X S	1.62	0.1554
	M X D	1.05	0.3822
	M X S X D	0.78	0.5852
	OL X M	1.88	0.1141
CYI[1]	MSP (M)	1.56	0.1997
	Substrate (S)	15.07	**<0.0001**
	Drainage (D)	11.57	**<0.0001**
	S X D	5.52	**0.0045**
	M X S	1.39	0.2305
	M X D	0.74	0.6159
	M X S X D	0.60	0.7337
	OL X M	1.30	0.2681
Root dry mass	MSP (M)	0.34	0.7974
	Substrate (S)	25.11	**<0.0001**
	Drainage (D)	9.09	**0.0002**
	S X D	1.36	0.2599
	M X S	2.16	0.0627
	M X D	0.45	0.8408
	M X S X D	0.19	0.9786
	OL X M	1.05	0.3824
Foliage dry mass	MSP (M)	0.61	0.6079
	Substrate (S)	14.32	**<0.0001**
	Drainage (D)	12.92	**<0.0001**
	S X D	2.43	0.0920
	M X S	1.71	0.1372
	M X D	0.73	0.6243
	M X S X D	0.51	0.7985
	OL X M	1.98	0.1015

[1] Current year increment.

Tableau 4.5. Results of pre-planned contrasts for seedling growth parameters.

	Total height		CYI		Root dry mass		Foliage dry mass	
Contrasts	*F*-value	Prob. > *F*	*F*-value	Prob. > *F*	*F*-value	Prob. > *F*	*F*-value	Prob. > *F*
SC + MD + PS vs. CT (Fib + Mes only)	5.26	**0.0225**	5.96	**0.0153**	3.69	**0.0570**	4.28	**0.0407**
Mes + Min vs. Fib (SC, MD + PS only)	59.47	**<0.0001**	24.82	**<0.0001**	35.99	**<0.0001**	22.99	**<0.0001**
Mes vs. Min (SC, MD + PS only)	0.01	0.9262	0.24	0.6274	18.86	**<0.0001**	5.18	**0.0246**
W + MW vs. P (Fib + Mes only)	63.19	**<0.0001**	22.86	**<0.0001**	18.17	**<0.0001**	25.80	**<0.0001**
W vs. MW (Fib + Mes only)	0.15	0.6997	0.33	0.5639	0.00	0.9925	0.02	0.8888

Note: SC, crushing; MD, mounding; PS, patch scarification; CT, control; Fib, fibric organic matter; Mes, mesic organic matter; Min, mineral soil; W, well drained substrate; MW, moderately well drained substrate; P, poorly drained substrate.

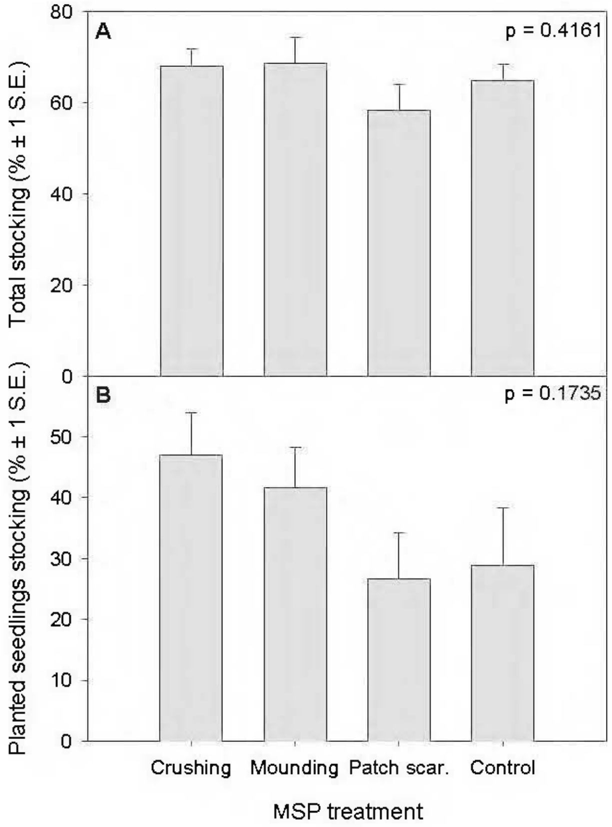

Figure 4.1. Total (A) and planted (B) black spruce seedling stocking by MSP treatment.

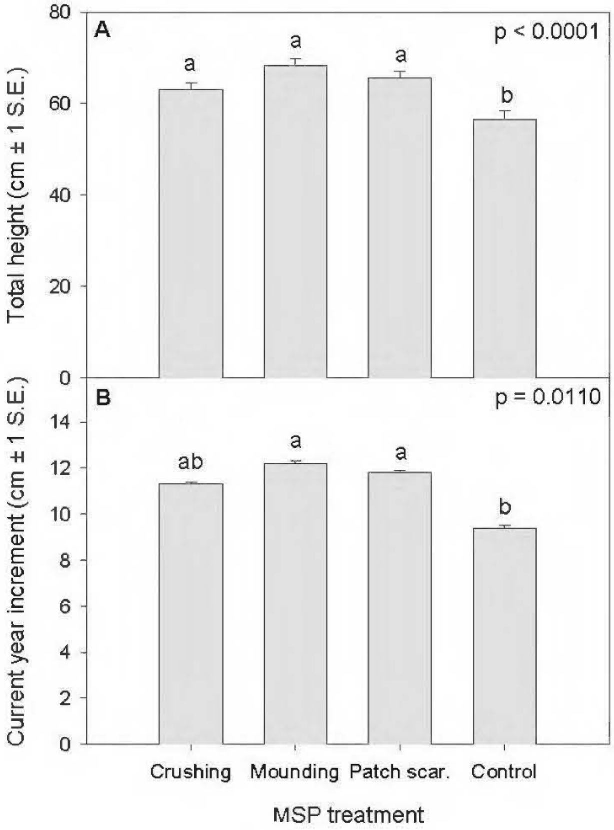

Figure 4.2. Total height (A) and current year increment (B) of black spruce stands (planted seedlings only) by MSP treatment.

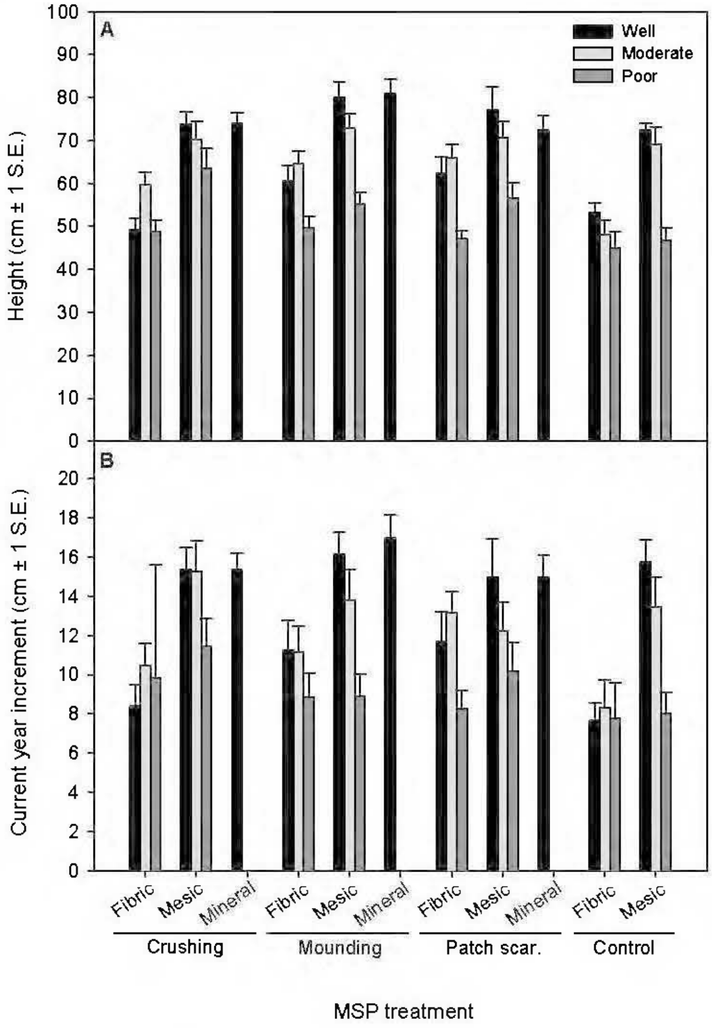

Figure 4.3. Total height (A) and current year increment (B) of planted black spruce seedlings by MSP treatment, substrate type and drainage.

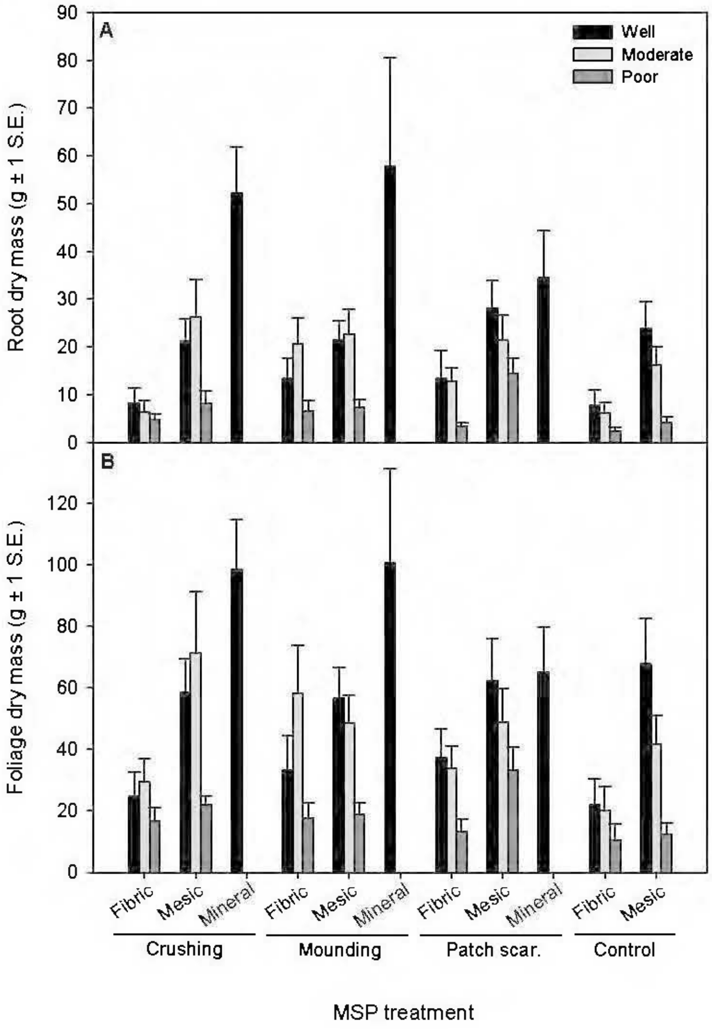

Figure 4.4. Root (A) and foliage (B) dry mass of planted black spruce seedlings by MSP treatment, substrate type and drainage.

CONCLUSION GÉNÉRALE

C.1. L’importance de la perturbation des sols

Les feux de forêts constituent sans contredit la perturbation dominante en forêt boréale. Ces perturbations provoquent d’importants changements dans les conditions de croissance des végétaux et amorcent un processus de succession végétale au cours duquel la composition et la structure des peuplements forestiers subiront des modifications importantes. En l’absence prolongée de perturbation, on observe toutefois une importante diminution de la productivité des peuplements forestiers boréaux (Vitousek et Farrington, 2001; Wardle et al., 2003, 2004). La perturbation du sol par le feu permettra d’augmenter la productivité et la biomasse forestière, entre autres, par la remise en disponibilité des éléments nutritifs séquestrés dans la matière organique.

Dans les pessières noires de la ceinture d’argile et du till de Cochrane, il a été démontré que la sévérité des feux influence fortement l’épaisseur de la matière organique ainsi que ses propriétés physico-chimiques et, ultimement, la productivité des peuplements forestiers. D’une part, les feux sévères consument presque entièrement la couche organique et permettent l’établissement de peuplements productifs dont les arbres auront facilement accès aux ressources nutritives du sol minéral (Fenton et al., 2005; Simard et al., 2007). D’autre part, les feux peu sévères laissent en place une épaisse couche de matière organique qui empêche les semis nouvellement établis d’accéder au sol minéral (Simard et al., 2007). Les feux peu sévères sont par conséquent susceptibles d’accélérer le processus de paludification. À l‘échelle du paysage forestier de la ceinture d’argile et du till de Cochrane, une diminution de la fréquence des feux ou de leur sévérité est donc susceptible de faire basculer l'écosystème forestier de la région d'un état productif (i.e. pessière fermée) vers un état improductif (i.e. tourbière forestière ouverte).

Par ailleurs, d'autres études menées dans les forêts tourbeuses de la ceinture d'argile ont suggéré que les méthodes de récolte actuelles visant à protéger la régénération et à minimiser la perturbation des sols (p. ex., la CPRS) étaient susceptibles de favoriser la paludification en raison d'une perturbation des sols dont la sévérité serait insuffisante (Fenton et al., 2005, 2009; Lavoie et al., 2005).

Ces études portant sur la sévérité des feux et sur les pratiques sylvicoles actuelles suggèrent donc que la perturbation des sols est nécessaire au maintien et à la restauration de la productivité des peuplements susceptibles à la paludification, et que la sévérité de la perturbation pourrait influencer leur productivité.

C'est donc dans ce contexte qu'ont été entrepris les travaux ayant mené à la rédaction de cette thèse. Globalement, les résultats issus de nos travaux viennent d'abord appuyer la thèse de Wardle et al. (2003, 2004) qui veut qu'en forêt boréale la perturbation des sols permette d'augmenter la croissance et la productivité forestière, du moins à court terme, et que cet accroissement soit fortement influencé par les propriétés physico-chimiques des sols. Ensuite, nos résultats soutiennent l'hypothèse qu'en forêt boréale tourbeuse la régénération et la croissance des arbres suivant la récolte sont influencées par la sévérité de la perturbation de la couche organique à l'échelle du peuplement. Enfin, nos résultats montrent qu'une perturbation mécanique suffisamment sévère (p. ex., une coupe totale effectuée l'été) de la couche organique est capable de régénérer des peuplements dont la croissance et la productivité est similaire à celle produite par des feux qui brûlent sévèrement la couche organique.

La section qui suit résume et synthétise les résultats et les conclusions des chapitres constituant cette thèse.

C.2. La perturbation mécanique en tourbière forestière

C.2.1. Effets de la perturbation à l'échelle du peuplement

Bien que par rapport à la coupe totale la CPRS procure un certain avantage à la régénération et à la croissance des peuplements en protégeant la régénération préétablie, nos travaux montrent que dans le paysage entourbé de la ceinture d'argile et du till de Cochrane la coupe totale a été en mesure de produire, au cours des premières décennies suivant la récolte, des peuplements d'épinette noire plus hauts que la CPRS (Chapitres 1 et 2). Ces résultats indiquent donc qu'en forêt tourbeuse les peuplements d'épinette noire initiés par une coupe totale auraient un taux de croissance plus élevé que les peuplements initiés par une CPRS. De plus, la saison de récolte s'est avérée interagir avec la méthode de récolte pour influencer positivement la régénération et la croissance des peuplements. En effet, la coupe totale effectuée l'été fut en mesure de produire des peuplements plus hauts que la coupe totale d'hiver et que la CPRS effectuée l'été ou l'hiver (Chapitre 2).

Par ailleurs, malgré l'absence de protection à la régénération préétablie, la coupe totale a permis la régénération de peuplements dont le coefficient de distribution est adéquat par rapport aux normes provinciales (Chapitre 1; L. Dumas, communication personnelle).

Parmi les mécanismes permettant d'expliquer ces résultats, la coupe totale, particulièrement celle effectuée l'été, aurait vraisemblablement permis de perturber la couche organique sur une plus grande proportion des aires de récolte que la CPRS et les coupes d'hiver. Ceci aurait résulté en une plus grande abondance de microsites favorables à la croissance des arbres, tel qu'illustré dans le Chapitre 2 par la plus grande abondance d'arbres de plus de 4 m dans les coupes totales d'été que dans les autres traitements.

Par ailleurs, ces résultats s'appliquent à une vaste gamme de types de dépôt-drainage, allant des tills argileux mésiques aux dépôts tourbeux, en passant par des dépôts glaciolacustres subhydriques (Chapitre 1), ce qui indiquerait qu'une grande proportion des peuplements de la région pourrait réagir favorablement, en termes de croissance et de productivité forestière, à la coupe totale, particulièrement si elle est effectuée durant l'été. Ainsi, en dépit d'une plus grande destruction de la régénération préétablie, la coupe totale permettrait de créer simultanément (*i*) des lits de germination qui assurent la régénération du peuplement et (*ii*) des microsites favorables à la croissance des arbres.

Bien que dans certaines conditions d'habitats la restriction de la circulation de la machinerie forestière à des sentiers biens définis permette de maintenir la productivité forestière en protégeant les sols et la régénération (Harvey et Brais 2002), dans les peuplements d'épinette noire paludifiés de la ceinture d'argile la libre circulation de la machinerie permettrait la régénération de peuplements dont le coefficient de distribution est adéquat par rapport aux normes provinciales et dont la croissance est supérieure aux peuplements issus de CPRS, ces résultats s'appliquant aux principaux types de dépôts retrouvés dans la ceinture d'argile. Toutefois, la coupe totale pourrait avoir des impacts plus importants que la CPRS sur certaines propriétés et fonctions des tourbières forestières, par exemple sur la biodiversité et les habitats fauniques ainsi que sur l'écoulement et la qualité des eaux (Keenan et Kimmins, 1993). Ainsi, l'usage simultané de la coupe totale et de la CPRS, ainsi que la création d'aires de conservation, pourrait permettre de maintenir à l'échelle du paysage les activités forestières de même que les propriétés et les fonctions des écosystèmes forestiers. Il appert donc primordial d'acquérir davantage de connaissances sur les effets de perturbations d'intensités variables sur la régénération et la croissance de peuplements possédant des caractéristiques d'habitats variées afin d'être en mesure d'ajuster adéquatement l'intensité des récoltes et de maintenir ou restaurer la productivité des peuplements.

C.2.2. Effets de la perturbation à l'échelle de l'arbre

En forêt boréale, la croissance des arbres, en plus d'être influencée par les variables climatiques, est fortement influencée par la disponibilité des éléments nutritifs et de l'eau (Van Cleve et Zasada, 1976; Chapin et al., 1986; Bonan et Shugart, 1989; Näsholm et al., 1998). En raison de températures relativement froides qui limitent le potentiel d'évapotranspiration et des dépôts de surface relativement mal drainés, le bilan hydrique des peuplements d'épinette noire de la ceinture d'argile et du till de Cochrane est positif (Brown, 2010). Ces conditions favorisent l'accumulation de la matière organique, le rehaussement de la nappe phréatique et la diminution de la température des sols, et ultimement défavorisent la décomposition de la matière organique et la minéralisation des éléments nutritifs (particulièrement celle de l'azote (N) et du phosphore (P)) (Taylor et al., 1987; Payette, 2001; Charman, 2002; Moore and Basiliko, 2006). La croissance des arbres et la productivité des peuplements s'en trouvent par conséquent limitées (Larsen, 1982; Payette, 2001; Simard et al., 2007).

Par ailleurs, la surabondance de l'eau ainsi que la diminution de la température des sols peuvent aussi influencer la croissance des arbres en agissant directement sur les processus physiologiques. Tout d'abord, une surabondance d'eau dans les sols peut limiter la croissance des arbres en réduisant l'aération du substrat de croissance et par conséquent la respiration racinaire (Bergman, 1959; Kozlowski et al., 1991), le taux de photosynthèse (Zaerr, 1983; Levan et Riha, 1986; Dang, 1991; Lamhamedi et Bernier, 1994) et l'assimilation des éléments nutritifs (Lieffers et Macdonald, 1990; Macdonald et Lieffers, 1990). Ensuite, les basses températures des sols ont pour effet (*i*) de ralentir la croissance racinaire des arbres (Tryon et Chapin, 1983), (*ii*) de limiter l'assimilation des éléments nutritifs en restreignant leur diffusion vers les racines en raison de l'augmentation de la viscosité de l'eau (Marschner, 1995), (*iii*) de réduire l'activité métabolique du système racinaire des arbres, limitant ainsi l'assimilation de N (Orem et Sheriff, 1995) et du P (Dighton et Harrison, 1983), et (*iv*) de réduire la perméabilité des membranes cellulaires. L'ensemble de ces changements a pour effet d'augmenter la résistance du mouvement de l'eau à l'intérieur des racines (Wan et al., 2001) et, ultimement, de limiter l'assimilation des éléments nutritifs et la croissance des arbres.

Les résultats issus de nos travaux suggèrent qu'à l'instar des autres écosystèmes boréaux, la croissance des épinettes noires des forêts tourbeuses de la ceinture d'argile est fortement influencée par les propriétés physico-chimiques de la couche organique (Chapitres 2 et 3). En effet, des variables comme l'humidité et la teneur en éléments nutritifs de la couche organique étaient corrélées à la croissance des arbres et des semis (Chapitres 2 et 3).

Ces résultats suggèrent que dans le contexte d'un paysage forestier susceptible à la paludification comme celui de la ceinture d'argile et du till de Cochrane, i.e. là où l'absence prolongée ou l'insuffisance de perturbation des sols est susceptible de diminuer la productivité forestière, toute perturbation apte à diminuer le contenu en eau des sols et à augmenter la disponibilité des éléments nutritifs est susceptible d'améliorer les conditions de croissance des arbres et d'augmenter la productivité des peuplements.

Dans ce contexte, le Chapitre 3 montre que la croissance de semis plantés d'épinette noire est effectivement influencée par la perturbation du substrat. Cet effet ne viendrait toutefois pas de l'augmentation de la disponibilité des éléments nutritifs ou de la diminution de l'humidité des substrats perturbés, mais plutôt d'autres facteurs que nous n'avons pu considérer au cours de cette étude, par exemple de l'élimination de la végétation concurrente ce qui aurait induit une diminution de la compétition pour l'accès aux éléments nutritifs.

Par ailleurs, nos résultats confirment les résultats des travaux de Jeglum (1979, 1981) et Lavoie et al. (2007a, b) et montrent que la nature du substrat influence également la croissance des semis d'épinette noire (Chapitres 3 et 4). D'une part, les substrats constitués de *Pleurozium* ont permis une meilleure croissance des semis que les substrats constitués de sphaignes, vraisemblablement en raison d'une plus grande disponibilité de N et d'un contenu volumétrique en eau plus bas, et possiblement parce que le *Pleurozium* a atteint la température critique d'amorce de la croissance des racines d'épinette noire plus tôt au printemps que la sphaigne (Chapitre 3). D'autre part, les substrats mésiques (échelle de von Post 5-8; Damman et French, 1987) et les sols minéraux constituent également de meilleurs microsites de croissance que les substrats fibriques (échelle de von Post 1-4; Damman et French, 1987) (Chapitre 4).

Le Chapitre 3 révèle de plus que les semis plantés dans des microsites perturbés constitués de *Pleurozium* avaient une meilleure croissance que ceux plantés dans les microsites non perturbés ou constitués de sphaignes. Ce dernier résultat montre que la perturbation des sols favorise la croissance de l'épinette et souligne l'importance du choix du microsite lors du reboisement des sites récoltés.

Suivant la récolte de la matière ligneuse, la préparation de terrain est fréquemment utilisée afin de régénérer les sites récoltés. Spécifiquement, la préparation de terrain a pour objectifs de créer des microsites favorables à la croissance des semis en quantité suffisante et de favoriser la survie et la croissance des semis (Sutherland et Foreman, 1995). Outre le drainage, d'autres méthodes de préparation de terrain ont été relativement peu utilisées en tourbière forestière, principalement en raison de l'épaisse couche organique qui serait susceptible de limiter l'efficacité de certaines techniques (p. ex., le scarifiage) à exposer le sol minéral ou à le mélanger avec la matière organique (Örlander et al., 1990). Nos résultats montrent toutefois que la perturbation du substrat organique, même superficielle (i.e. sans mélange avec le sol minéral), influence positivement la croissance des semis d'épinette noire par rapport aux substrats non perturbés (Chapitres 3 et 4) et que l'épaisseur de la couche organique influencerait peu ce résultat (Chapitre 4). De fait, peu importe la méthode utilisée, la préparation de terrain a été capable de réduire l'épaisseur de la couche organique d'environ 30 cm. Plus important encore, peu importe le traitement et l'importance de la réduction de l'épaisseur de la couche organique, la croissance des peuplements était comparable entre les sites soumis à la préparation de terrain (Chapitre 4).

Nos résultats suggèrent donc que la perturbation du sol forestier est suffisante pour améliorer les conditions de croissance de semis plantés d'épinette noire et, par conséquent, qu'il n'est pas nécessaire de mélanger le sol minéral au sol organique (Chapitres 3 et 4). Bien que nous ne rapportions des résultats de croissance de semis que pour les 2 à 4 premières années suivant la mise en terre, il est vraisemblable que cet effet puisse perdurer plus longtemps. En effet, Thiffault et al. (2004) rapportent que la scarification *post* récolte d'un peuplement d'épinette noire a eu des effets durables sur les caractéristiques des microsites et la croissance de semis pendant au moins 10 ans.

Enfin, notons que la plantation d'arbres suivant la récolte est communément utilisée en forêt boréale afin d'éviter des échecs de régénération et de rapidement augmenter la densité des peuplements. De même, la préparation de terrain est largement utilisée afin d'améliorer les conditions de croissances des semis. Ainsi, puisque tant le type de substrat que la perturbation de la couche organique (Chapitres 3 et 4) influencent la croissance des semis, la préparation de terrain ainsi que la sélection adéquate des microsites de plantation semblent être des éléments essentiels à la restauration de la productivité des peuplements suivant la récolte en forêt boréale.

C.2.3. Coupe vs. Feu

Dans le contexte de l'aménagement forestier basé sur les perturbations naturelles, il s'avère essentiel non seulement de comprendre les effets des perturbations naturelles ou de la récolte sur la régénération et la croissance des peuplements forestiers, mais également de reconnaître les différences entre elles afin d'être en mesure d'ajuster nos pratiques sylvicoles et de rapprocher leurs effets de celles des perturbations naturelles.

Ces dernières années, des études menées dans les pessières à mousses de la ceinture d'argile ont permis de mettre en lumière l'importance de la sévérité de la perturbation des sols sur la régénération et la croissance des peuplements (Fenton et al., 2005; Simard et al., 2007). La comparaison de nos résultats portant sur l'interaction méthode de récolte/saison (Chapitre 2) avec les résultats de Simard et al. (2007), montre que la coupe totale d'été est susceptible de créer, à l'échelle du peuplement, des conditions de croissance comparable à celles créées par les feux sévères (Chapitre 4). Ces résultats suggèrent donc que la coupe totale d'été reproduit, du moins à cours terme, les effets (en termes de taux de croissance à l'échelle de l'arbre et de densité d'arbres >4 m) des feux sévères et qu'elle pourrait être intégrée dans les plans d'aménagement afin d'aider à maintenir ou à restaurer la productivité des peuplements d'épinette noire sur sol tourbeux. Toutefois, il reste à déterminer si la coupe totale d'été est en mesure de reproduire les effets des feux sévères sur d'autres aspects de l'écosystème, par exemple, sur les propriétés physico-chimiques de la couche organique et la succession végétale.

C.3. Conclusion

Depuis peu, le concept d'aménagement durable des forêts se trouve au cœur de la politique forestière québécoise (Gouvernement du Québec, 2010). Le maintien de la biodiversité et des processus écologiques fait donc désormais partie des éléments qui doivent être pris en compte lors de la préparation des plans d'aménagement forestier.

Parallèlement, il s'est développé au cours des dernières années un intérêt grandissant pour le développement d'approches d'aménagement forestier basées sur la dynamique des perturbations naturelles (Attiwill, 1994; Bergeron et Harvey, 1997). Le raisonnement s'articulant autour de cette approche veut qu'un aménagement des forêts qui favorise le développement de peuplements et de paysages ayant une composition et une structure semblables à celles des écosystèmes naturels devrait favoriser le maintien de leur diversité biologique et de leurs fonctions (Franklin, 1993; Hunter, 1999; Gauthier et al., 2008b). C'est dans ce contexte que l'aménagement écosystémique a été proposé comme un moyen permettant de répondre à divers enjeux en milieu forestier.

Afin de parvenir à créer des paysages aménagés ayant les mêmes caractéristiques que les paysages naturels, les aménagistes forestiers devront non seulement raffiner leurs connaissances de la dynamique des perturbations naturelles et de leurs effets sur les écosystèmes forestiers, mais également diversifier et adapter les traitements sylvicoles en fonctions des caractéristiques, parfois particulières, des territoires aménagés. Parmi ces traitements, la coupe totale et la CPRS se situent de part et d'autre du gradient de sévérité de perturbation des sols. Les résultats de cette thèse suggèrent donc que leur utilisation adéquate et simultanée, ainsi que celle d'autres méthodes de récolte et de traitements sylvicoles (par ex. la coupe partielle, coupe à rétention variable et la préparation de terrain), pourrait permettre d'élargir le gradient des effets des opérations forestières à l'échelle du paysage et ainsi aider à maintenir la diversité biologique, structurelle et fonctionnelle des paysages forestiers. En retour, le maintien de ces attributs permettrait d'assurer la résilience des paysages forestiers de la région couverte par la ceinture d'argile.

Malgré les pas importants faits au cours des dernières décennies pour comprendre la dynamique et le fonctionnement des paysages forestiers et pour adapter nos pratiques forestières afin d'assurer leur résilience, plusieurs questions restent en suspens. De même, les résultats issus des travaux entrepris au cours de cette thèse soulèvent d'autres questions qui nécessiteront d'être abordées afin de raffiner nos connaissances des effets de la perturbation des sols et de la couche organique sur la dynamique de régénération de peuplements et, par conséquent, pour nous permettre d'ajuster nos pratiques sylvicoles tant à l'échelle du peuplement qu'à l'échelle du paysage:

- Dans quelles conditions de terrain (p. ex., en termes de pente, microtopographie, épaisseur de la couche organique, profondeur de la nappe phréatique) est-il souhaitable de perturber sévèrement la couche organique?
- Pour des raisons de conservation, quelle proportion du territoire devrait demeurer paludifiée?
- Afin de maintenir la variabilité de la structure forestière à l'échelle du paysage, quelle proportion du territoire aménagé devrait être allouée à d'autres méthodes de récolte (p. ex., coupe partielle, coupe sélective)?
- Quels sont les impacts (aux échelles du peuplement et du paysage) de la coupe totale vs. CPRS sur les stocks de C de la couche organique?

C.4. Références citées dans l'introduction et la conclusion générale

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ANNEXE I

RESPONSE OF NORTHEASTERN NORTH AMERICAN FORESTS TO CLIMATE CHANGE: WILL SOIL CONDITIONS CONSTRAIN TREE SPECIES MIGRATION?

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A1.1. Abstract

Plant species distribution and plant community composition vary along environmental gradients. At the continental scale, climate plays a major role in determining plant distribution, while at the local and regional scales vegetation patterns are more strongly related to edaphic and topographic factors. The projected global warming and alteration of the precipitation regime will influence tree physiology and phenology, and is likely to promote northward migration of tree species. However the influence of soil characteristics on tree species migration is much less well understood. Considering the broad tolerance of most tree species to variations in soil factors, soils should not represent a major constraint for the northward shift of tree species. However, locally or regionally, soil properties may constrain species migration. Thus, while climate change has the potential to induce a northward migration of tree species, local or regional soil properties may hinder their migratory response. These antagonistic forces are likely to slow down potential tree migration in response to climate change. Because tree species respond individualistically to climate variables and soil properties, new tree communities are likely to emerge from climate change.

Key words: climate change, tree migration, soil properties, temperate forest, boreal forest

A1.2. Résumé

La distribution des espèces et la composition des communautés végétales varient le long de gradients environnementaux. À l'échelle continentale, le climat joue un rôle primordial dans la distribution des espèces végétales, alors qu'aux échelles locale et régionale la distribution des espèces est surtout influencée par les variables édaphiques et la topographie. Le réchauffement climatique projeté et l'altération du régime des précipitations sont susceptibles d'influencer la physiologie et la phénologie des arbres, et d'entraîner leur migration vers le nord. Toutefois, l'influence des caractéristiques des sols sur le potentiel migratoire des arbres est peu connue. Puisque la plupart des espèces d'arbres possèdent une grande tolérance aux variations édaphiques, les sols ne devraient pas constituer un obstacle majeur à leur migration vers le nord. Toutefois, localement ou régionalement, les sols pourraient posséder des propriétés qui pourraient restreindre la migration des espèces. Alors que les changements climatiques ont le potentiel de provoquer la migration des espèces vers le nord, localement ou régionalement les propriétés des sols pourraient limiter leur capacité migratoire. Ces forces en opposition pourraient restreindre le potentiel migratoire des arbres en réponse aux changements climatiques. Parce que les espèces d'arbres répondent de manière individuelle aux variables climatiques et aux propriétés des sols, de nouvelles communautés d'arbres pourraient résulter des changements climatiques.

Mots clés: changements climatiques, forêt boréale, forêt tempérée, migration des arbres, propriétés des sols

A1.3. Introduction

Plant species distribution and plant community composition vary along environmental gradients (Allen and Hoekstra, 1990; Levin, 1992), and several community and landscape studies have linked species responses to environmental gradients at different spatial scales (Raisa, 1999; Hollingsworth et al., 2006). For instance, at the continental scale climate plays the most important role in determining plant distribution and community composition (Woodward, 1987; Neilson, 1995), while at the local and regional scales vegetation patterns are more strongly related to edaphic and topographic factors (Ertsen et al., 1995; Iverson et al., 1997). Across all scales, temperature and the balance between precipitation and evapotranspiration are particularly important, as they largely control the rates of biological reactions, for instance microbial activity (Hobbie, 1996; Moore et al., 1999) and net primary productivity (Nemani et al., 2003).

According to the most recent report of the Intergovernmental Panel on Climate Change, warming of the climate system is unequivocal (IPCC, 2007). Most of the globally observed increase in average temperatures since the mid-20th century is attributed to the anthropogenic emission of greenhouse gases. Since ca. 1850 the global atmospheric concentrations of greenhouse gases (i.e. carbon dioxide [CO_2], methane [CH_4], and nitrous oxide [N_2O]) have increased markedly as a result of human activities and now exceed pre-industrial values (IPCC, 2007). Due to the radiative forcing of these greenhouse gases, world surface temperatures increased by 0.74°C between 1906 and 2005, and are projected to rise by between 1.1 and 6.4°C by the end of the 21st century (IPCC, 2007). In northeastern North America, warming is projected to be somewhere between 3-4°C and precipitation is projected to increase by 10-20% by the end of the 21st century (IPCC, 2007).

This increase in atmospheric CO_2 concentration and the concomitant warming and modification of water regimes will, in all likelihood, influence plant physiology

(Keeling et al., 1996; Myneni et al., 1997), phenology (Raulier and Bernier, 2000; Delbart et al., 2008), growth (Huang et al., 2007; Brassard et al., 2009), and thus modify the future range and dynamics of many plant species and ecosystems (Overpeck et al., 1991; Hansen et al., 2001; Neilson et al., 2005; McKenney et al., 2007). Changes in physiology, phenology, and distribution of individual plant species will inevitably alter competitive and other interactions between species, with consequent feedback to local abundance and community composition. Recent analyses of long-term data sets indicate that some North American tree species are already responding to recent anthropogenic climate change, particularly at the northern treeline of the boreal forest (Lloyd and Fastie, 2003; Gamache and Payette, 2005; Caccianiga and Payette, 2006). Current responses include *in situ* species conversion (i.e., the replacement of dominant species by subdominant species [Midgley et al. (2007)]) and species migration.

Because forest ecologists have been studying successional patterns since the pioneering works of Clements (1916) and Gleason (1926), the processes driving *in situ* conversion are relatively well understood. However, because it is a much slower process, migration is less well understood. Nevertheless, in order to understand species migration in response to climate change, ecologists rely (i) on paleoecological studies that relate past species migration to past changing climate, and (ii) on studies of invasive exotic species. While paleoecological studies reveal that at the end of the last glaciation plant species followed a poleward migration behind the retreating glacier (e.g. Davis, 1983; Jackson et al., 1997), studies of invasive exotic species reveal that species invasion (migration) rate is determined both by dispersal rate and population growth rate at the invasion (migration) front (Hastings et al., 2005).

Although temperature and precipitation are often considered the major factors determining plant species and ecosystem distribution, other factors such as dispersal ability, competition, predation, disturbance regime, and rate of genetic adaptation are also important. Although these factors have the potential to influence the success of species migration (e.g. McKenney et al., 2007), they are rarely included in models that simulate the effects of climate change on plant species migration, probably due to the difficulties of implementing these processes in simulation models. Similarly, although soil factors such as nutrient and water availability are known to influence seed germination, seedling survivorship and growth, and hence the probability of successful colonization of plant species, soils are often omitted in models simulating plant species migration. Iverson and colleagues (Iverson and Prasad, 1998, 2002; Iverson et al., 2008a, 2008b) recently published results from models simulating the range shift response of several North American tree species to climate change which included soil variables. Although soil variables were important predictors of species range shift in response to climate change, the authors did not offer any explanation as to how soil variables could facilitate or constrain tree species migration in response to projected climate change.

Considering that (1) projected climate change is expected to promote poleward migration of forest tree species, (2) upon migration, species are likely to encounter soil conditions different from their original locations and (3) soil factors influence tree species through effects on seed germination, seedling establishment, growth and reproduction, our objective is to demonstrate how soil factors could influence the migration of tree species in response to climate change across several biomes of northeastern North America (i.e. from the boreal forest to the tundra, and from the temperate forest to the boreal forest). First, we briefly review tree migration in response to past, recent, and projected climate change. Second, we review how soil factors currently limit tree establishment and growth, and species distribution. Finally, we review the potential responses of tree species to climate change, and how this response could be influenced by soil factors. Although this work focuses on the migration of trees in response to climate change in northeastern North America, results from studies carried out elsewhere in North America, in Europe and in Asia are used to support our hypotheses for responses in northeastern North America.

A1.4. Past, current, and future response of vegetation to climate change

A1.4.1. Response of boreal and temperate tree species to past global warming

Based on pollen and plant macrofossils (e.g. seeds, fruits, leaves, twigs and wood) preserved in sediments in wetlands, peatlands and lakes, several authors reported evidence of past migration of trees following the end of the last ice age about 12 000 years ago.

As early as 15 000 years ago, changes in biome and plant community composition began in what is now the southeastern U.S., where boreal species were replaced by hardwood species (Webb, 1988). As shown by several authors (e.g. Jackson et al., 1997; Williams et al., 2004), most of the tree species now found in the northeastern North American boreal and temperate forests were able to track the warming trend of the Holocene. While *Picea* spp. reached their current northern range limit about 3 000 to 5 000 years ago (Jackson et al., 1997; Williams et al., 2004), *Abies balsamea*, *Quercus* spp., and *Fagus grandifolia* reached southern Quebec around 10 000 BP, 7 000 BP and 6 000 BP, respectively (Muller and Richard, 2001; Williams et al., 2004). According to these records, tree species migrated at different rates, reinforcing Gleason’s (1926) idea of an individualistic view of plant succession and resulting chance combinations of species assemblages.

Although none of the paleoecological studies cited above mention soil factors or processes as having influenced tree establishment behind the retreating ice sheet, soil factors and processes most likely constrained seed germination and seedling establishment; this is supported by studies on both primary succession in areas where glaciers are currently retreating, such as Glacier Bay, Alaska (Chapin et al., 1994), and in areas devastated by recent volcanic eruptions, such as Mount St. Helens (del Moral and Wood, 1993). Both Chapin et al. (1994) and del Moral and Wood (1993) identified nutrient limitation to plant growth as a factor limiting colonization in early primary succession. As Walker and Syers (1976) pointed out, most newly deposited substrates, such as glacier deposits, are devoid of N, which is required for plant growth. In these "young" soils, N must therefore be obtained from the atmosphere by biological N fixation or atmospheric deposition. Thus, N-fixing species such as *Alnus* spp. and *Dryas* spp. may have been among the first plant species to colonize the newly available sites following the retreat of the North American ice sheet (Reiners et al., 1971), and their presence may have enhanced growth of associated species (Chapin et al., 1994). Therefore, tree establishment may well have followed that of N-fixing plant species by a few decades. However, studying the causes of primary succession at Glacier Bay, Alaska, Fastie (1995) showed that tree species were not necessarily preceded by N-fixing plants. Nevertheless, over time, N fixation and atmospheric deposition have increased the availability of N in the soil in sufficient amounts to allow the establishment of more N-demanding species (Stevens and Walker, 1970; Gorham et al., 1979).

Studying the influence of landscape structure and climate variability on the late Holocene migration of *Juniperus osteosperma* in the western U.S., Lyford et al. (2003) showed thatspecies migration was in part constrained by the distribution of suitable substrate. For *Juniperus,* suitable substrates consisted of coarse-textured soils, particularly in regions of resistant sandstones and coarse shales, and highly suitable surface materials consisted of rock outcrops and colluvial deposits.

Hence, these studies strongly suggest that soil factors and processes restricted tree migration through constraints on seedling establishment following the gradual retreat of the North American ice sheet during the Holocene.

A1.4.2. Impacts of recent global warming on boreal and temperate tree species

At the continental and subcontinental scales, the transition zones between adjacent biomes and vegetation communities are sensitive to climate variation (Goldblum and Rigg, 2005). In these zones, projected climate change could cause detectable shifts in species composition, whereas in the middle of broad forest zones such changes might not take place. Because northern treeline ecosystems (i.e. the transition zone between the boreal forest and the tundra) are sensitive to changes in climatic conditions, several authors have used these ecosystems as proxies of biotic change in response to global warming (e.g. Kullman, 2001, 2002; Gamache and Payette, 2004). Several studies showed that at the end of the Little Ice Age (ca. 1850), the northern treelines of North America and Eurasia began migrating poleward in response to warmer temperatures. In Canada, Payette and coworkers showed that the *Picea glauca* (Payette and Filion, 1985; Caccianiga and Payette, 2006) and *Picea mariana* treelines (Gamache and Payette 2005) expanded significantly northward during the last 100 years in response to recent climate warming. In Alaska, Lloyd and Fastie (2003) found similar results for *Picea glauca*, concluding that the recent shift in the location of the forest-tundra border was a response to recent warming. In Eurasia, Kharuk et al. (2005) showed that *Pinus sibirica* and *Betula* spp. were penetrating into a zone traditionally occupied by two larch species (*Larix gmelinii* and *Larix sibirica*) in response to climate change during the past three decades. Similarly, Kullman (2001, 2002) showed that treelines in the Swedish Scandes have responded to recent global warming with altitudinal and northward tree species invasion into the tundra.

While these latter studies focused on the transition at the treeline, few have specifically addressed the effects of recent climate change on the transition zones between forested areas, e.g. between boreal coniferous and mixedwood forests or between boreal mixedwood and temperate deciduous forests. Montane ecosystems provide an ideal environment for observing shifts in forest distribution in response to climate change because of steep climatic gradients across elevation. In many respects, these ecosystems are comparable to latitudinal climatic gradients, but with clear boundaries between forest types that may facilitate detection of range shifts (Diaz et al., 2003). In 2004, Beckage et al. (2008) resurveyed plots established in 1964 along elevation transects in the Green Mountains of Vermont, U.S.A., to examine whether a shift had occurred in the location of the transition zone between the northern hardwood and boreal forests. They found an increase in dominance of hardwood species and a concomitant decrease in boreal species within the transition zone. Using aerial photographs and satellite imagery, they found an estimated 91- to 119-m upslope shift in the upper limits of the northern hardwood-boreal transition zone from 1962 to 2005. This shift was consistent with a 1.1°C increase in annual temperature, and a 34% increase in precipitation. They concluded that the upslope shift they observed was the result of climate-driven shifts in competitive balance between hardwood and boreal species in the transition zone.

These observations of recent, directional shifts at the northern treelines are consistent with expectations of species migration in response to climate warming, and offer further support to the idea that tree species will in all likelihood migrate poleward in response to projected climate change. Once again, while it is known that soil factors influence plant development, and hence the likelihood of species range shift, soil factors are rarely explicitly discussed when explaining species recent range shifts. Nevertheless, Gamache and Payette (2005) suggested that at the microsite scale, the suitability of seedbed and seedling establishment substrate are important for successful range shift, and that suitable seedbeds and establishment substrates may vary from region to region. However, as suggested by Beckage et al. (2008), at a broader scale, soil factors may not represent major constraints for tree species range shift.

A1.4.3.Projected impacts of global warming on boreal and temperate tree species

Simulation models have been utilized extensively in recent years to forecast migration rates of tree species and to predict future forest composition. These models are most often based on the climate envelope approach that relates species distribution to an *a priori* selection of climatic variables that are indicators of underlying physiological or biophysical limits on species distribution. These simulations indicate that, in response to climate warming and changes in water balance, plant species and communities in the boreal and temperate forests are likely to experience longer growing seasons (Chuine et al., 2000; Goldblum and Rigg, 2005) and modified disturbance regimes (Flannigan et al., 2009; Jiang et al., 2009).

Further, simulations also anticipate significant shifts in plant species ranges in response to global warming. For instance, using general circulation models (GCM), Overpeck et al. (1991) predicted that climate change could lead to significant vegetation change. The array of the genera they simulated were likely to be displaced northward by at least 100 km, and in some cases (e.g. *Picea* spp.) by as much as 1 000 km. Their results suggest that *Picea* spp. and northern pine (i.e. *Pinus strobus, Pinus banksiana* and *Pinus resinosa*) populations in the eastern U.S. could decline in abundance because of a northward shift of their southern range limit. In parallel, southern oaks (*Quercus* spp.) and pine species are expected to move northward by as much as 500 km because of local drying. Thus, in the eastern U.S., areas now dominated by mixed conifer-hardwood forests could become increasingly deciduous. In addition, Overpeck et al.'s (1991) simulation indicates that the area now occupied by tundra vegetation would decrease where simulated warming favours the expansion of tree populations. These results support paleoecological observations that biome compositions will not remain constant as plant taxa respond individualistically to future climate change.

Similarly, McKenney et al. (2007) used GCMs and species current climatic envelopes to predict the potential impacts of climate change on the distribution of North American trees. They concluded that the mean centres of future climatic envelopes were predicted to shift northward by several degrees of latitude. Their simulation predicted that by the end of the 21st century the CE of most of species modeled would shift into northern Ontario and Quebec. For example, *Acer saccharum* CE is projected to shift north by about 1 000 km, and that of *Betula alleghaniensis* by about 900 km. Further, several of the species modeled (e.g. *Quercus palustris* and *Betula nigra*) are projected to expand their range into southern Canada by the end of the 21st century.

In the above-cited studies, assessments of future distribution change are based on the climate envelope approach. Although soil factors are of utmost importance to plant establishment and growth, and modelers recognize their potential to influence the success of plant migration and establishment, soil factors are often omitted from models simulating the effects of climate change on plant migration. Nevertheless, in a series of studies Iverson and Prasad (1998, 2002) and Iverson et al. (2008*a*, 2008*b*) used a set of soil variables (e.g. water-holding capacity, pH, permeability, texture, organic matter content) along with climate variables to predict the distribution of several tree species following climate change in the eastern U.S. Their results showed that several species now occurring in the temperate or boreal forests would show range expansion and/or shifts. For example, *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* were expected to migrate north, showing an important range decline in the eastern U.S., while some species (e.g. *Carya tomentosa*, *Celtis laevigata*, *Cercis canadensis* and *Diospyros virginiana*) currently absent in Canada or present only in southernmost Ontario could become established in eastern Canada in the near future. Their simulations showed that soil factors were important for species to achieve successful range shift; those most important were soil permeability rate (cm h^{-1}), organic matter content, pH, cation exchange capacity, percent clay and bulk density.

Although we recognize important methodological differences between the studies of Iverson and Prasad (1998) and McKenney et al. (2007), a thorough examination and comparison of both studies reveals the importance of soil constraints on the migratory potential of several species common to these studies. For instance, while the unconstrained migration scenario of McKenney et al (2007) predicts that by the end of the 21st century the center of the climatic envelope of *Carya cordiformis* will be located at 44.5°N and that of *Quercus rubra* at 48.7°N, the soil-constrained scenario of Iverson and Prasad (1998) predicts that the latitudinal optimum of *Carya cordiformis* will be located at 39.4°N, and that of *Quercus rubra* at 40.4°N. The differences in migratory potential between these two studies may reflect the constraints that soil conditions exert on species establishment, growth and reproduction.

A1.5. Soil limitations to plant growth and tree species distribution

The type of vegetation that characterizes a region depends on several environmental factors, among which soil is of the utmost importance. Soil can indeed influence plant community composition through differential effects on individual plant species. Texture, porosity, aeration, temperature, moisture and nutrient content are among the soil variables that can independently and/or in interaction influence plant development (Aber and Melillo, 1991; Marschner, 1995). Their relative importance may or may not vary throughout the life cycle of an individual plant, i.e. during the plant's germination, establishment, growth and reproduction phases. In Germany for instance, Ammer et al. (2002) showed that the establishment of *Fagus sylvatica* in *Picea abies* stands was constrained by seed germination that is limited by inadequate soil moisture. Soil temperature is also a primary factor limiting growth during early establishment. In Ontario and the Yukon respectively, Grossnickle (1988) and Danby and Hik (2007) showed that soil temperature places stress on *Picea glauca* seedlings by affecting soil water movement, gas exchange, and subsequent root growth. Once established, seedlings must acquire sufficient nutrients in order to survive, grow and reproduce. For instance, in Ontario and Saskatchewan, Fogal et al. (1999) showed that seed production of *Pinus banksiana* in seed orchards was positively influenced by the addition of fertilizer, while in Sweden, Karlsson and Örlander (2002) showed that nutrient status of *Pinus sylvestris* influenced cone and seed production. Therefore, several soil factors have the potential to influence plant growth and species' migration success in response to climate change, and therefore plant community composition.

Several authors studying exotic plant invasion showed that soil property modifications by invasive species influence their own invasion rate (Levine et al., 2006; Gòmez-Aparacio and Canham, 2008). Indeed, forest species, by producing organic compounds, can influence soil weathering rates and nutrient availability (Binkley and Giardina, 1998; Nezat et al., 2004). For instance, in British Columbia, Tuason and Arocena (2009) found that the rhizosphere of *Picea glauca* and *Abies lasiocarpa* had lower pH and higher exchangeable Ca^{2+} and K^{+} content than adjacent soils, and suggested that organic acids exuded by the tree's root system might have played a role in the modification of the properties of their rhizoshpere. Therefore, because of their ability to modify soil properties, some tree species may with time create soil conditions favourable to their establishment and persistence, and detrimental to other tree species (i.e. already established or migrating species).

Because it is beyond the scope of this synthesis, we will not provide any further details on the generally accepted influence of soil properties on plant growth.

Rather, we refer the readers to Aber and Mellilo (1991) and Marschner (1995) for a thorough discussion on this topic.

A1.6. Tree species responses to soil factors during climate change-induced migration

At the end of the last ice age, plant species migrating behind the retreating glacier established on uncolonized glacial deposits in a reorganizing environment. Over time, soils began to develop in response to climate, topography, and biological factors (i.e. plants and soil microorganisms), as did plant communities. Early in the colonization process, competition for habitat resources such as water and nutrients was probably negligible because of the scattered distribution of individual plants. With time, however, competitive interactions became more prominent, possibly having an important influence on species migration rate and community composition (Ravazzi, 2002).

In contrast, unless massive forest dieback occurs, species that will migrate in the boreal and temperate forests in response to climate change will have to establish on sites that are already colonized by plants, and may thus compete for habitat resources upon their establishment. These migrating species will also colonize soils that are already developed, and that may locally possess properties that delay or constrain their establishment. Consequently, in these recipient habitats, competitive interactions and soil properties may interact to influence the population growth of migrating species. Because it is beyond the scope of this synthesis, we will not provide details on the possible influence of competitive interactions on plant migration and establishment. We refer the readers to Scheller and Mladenoff (2008) for a discussion on this topic.

A1.6.1.Migration from the boreal forest to the tundra

As shown in a previous section, in both Eurasia and North America several tree species located at the treeline moved north in response to recent climate change. These recent invasions of the tundra may be indicative of the relatively high tolerance of boreal forest tree species to soil conditions found in the tundra, or that soils conditions in the tundra are closely similar to those found in the boreal forest. Nevertheless, locally species migration may be limited because of particular soil conditions.

First, species migration from the boreal forest to the tundra may be limited by waterlogged conditions and a small soil/humus volume for root exploitation. In areas where waterlogged conditions and low soil temperatures combine to slow soil development and reduce decomposition rates, the establishment of tree species unadapted to these conditions may be hindered (Anderson, 1991). Similarly, on rocky outcrops where soil is absent, the establishment of trees is unlikely.

Likewise, species migration could be limited by permafrost, which would prevent seedling establishment by limiting root development and penetration into the soil. Projected temperature increases, however, will likely lead to permafrost degradation, especially in regions where discontinuous permafrost prevails. In northern Canada, for instance, a warming of 4–5 °C could reduce the area underlain by discontinuous permafrost by up to 50% (Woo et al., 1992). As shown by Waelbroeck et al. (1997), the warming and melting of the permafrost are associated with an increase in N mineralization rates, and, as pointed out by Woo et al. (1992), the melting of the permafrost can create areas of improved drainage as a result of improved vertical movement of water through the soil. Consequently, plant species that are unable to establish on cold, poorly drained soils underlain by permafrost could expand as permafrost melts. Permafrost warming and melting have, therefore, the potential to facilitate plant species migration and to affect plant community composition.

For instance, at the arctic treeline in northwestern Alaska, Lloyd et al. (2003) showed that well-drained soils on steep banks sustain plant communities different from those found on adjacent level tundra underlain by permafrost. They also found that thaw-pond banks sustained a higher density of trees and shrub species, and that shrubs were taller on banks. Thaw-pond banks likely provided better microsites for growth than the tussock tundra that covered the more level terrain. According to Lloyd et al. (2003), it is therefore likely that the establishment of shrubs and trees in the tundra is constrained by a set of environmental factors, including both above ground and below ground conditions. In the tundra, the response of trees to climate warming could therefore be conditional upon the formation of well-drained microsites. Such microsites are likely to be restricted in extent, at least during the first stages of permafrost degradation, and thus the establishment of migrating tree species is likely to be delayed (Lloyd et al., 2003). Nevertheless, over time, as permafrost melts and soil conditions improve, the establishment of tree species could be facilitated and their migration accelerated.

Furthermore, where permafrost is non-existent or where the soil active layer is thick, the expected rise in summer temperatures at the transition zone between the tundra and the boreal forest could improve soil conditions, enhancing seed germination and seedling growth, ultimately causing a northward shift of treeline species. For example, in an Alaskan shrub tundra, Hobbie and Chapin (1998) found that the seed germination of three treeline species (*Betula papyrifera*, *Picea glauca* and *Populus tremuloides*) increased as a result of simulated global warming. Although the success of seed germination was attributed to increased air temperature, subsequent seedling growth depended on soil conditions, i.e. growth was reduced on nutrient-poor or cold and wet microsites, such as tussock or heath tundra.

Contrary to Hobbie and Chapin (1998), Barber et al. (2000) and Lloyd and Fastie (2002) observed a reduction in the growth rate of mature *Picea glauca* in response to warming. The latter authors attributed this growth reduction to drought stress. Although the planted seedlings of Barber et al. (2000) and Lloyd and Fastie (2002) were located further south, and were consequently more liable to drought than those planted by Hobbie and Chapin (1998), the contrasting responses to warming between early and late life stages of *Picea glauca* emphasize that the response of a tree to any given environmental factors may vary throughout its life cycle. This variable response could have repercussions on establishment, survival, and reproduction success. Thus, in the tundra and in the transition zone between the boreal forest and the tundra, soil factors will likely play an important role during tree development, following establishment in new habitats. The distribution range of a species could therefore potentially be constrained during a specific phase of its life cycle.

The preceding paragraphs show that in response to climate warming, current boreal tree species are likely to be capable to migrate northward where soil conditions allow, i.e. at or slightly north of the transition zone between the tundra and the boreal forest. However, as one moves further north, thin (or the absence of) mineral soil and organic matter, permafrost, and waterlogged conditions could prevent or delay the establishment of trees and the development of forests. Those species showing broad tolerance to soil conditions may not see their migration constrained by soil, and may therefore migrate poleward, following the warming trend. However, species having narrower tolerance to soil conditions could see their migration constrained by soil conditions during the first stages of global warming; constraints may subsequently diminish as soil properties change (in response to climate and biotic variables) and become favourable for their establishment and growth.

A1.6.2.Migration from the temperate to the boreal forest

In the boreal forest, high soil moisture and low temperature, and fire are the major factors controlling nutrient cycling and forest productivity (Van Cleve et al., 1983; Bonan and Shugart, 1989). In response to global warming, a combination of warmer soils and increased evapotranspiration may therefore enhance nutrient cycling and potentially increase forest productivity, allowing the establishment of more productive and nutrient-demanding southern tree species (e.g. *Acer saccharum*, *Fagus grandifolia*, *Quercus rubra* and *Tilia americana*). However, locally or regionally deep peat soils such as those found in the James Bay Lowlands (Quebec and Ontario) may not be as responsive to global warming as other types of soils, primarily because of their chemical composition and high water content. These deep organic soils may persist for a long time, despite otherwise favourable climate conditions for decomposition. Excluding regions where deep peat accumulation occurs, in response to altered climate, the establishment of tree species not currently present in the boreal forest should be possible where soil conditions are favourable, and the northern distribution limit of several temperate forest tree species could therefore move north.

For instance, in Ontario, studying sugar maple growth at the deciduous–boreal forest ecotone, Barras and Kellman (1998) found that *Acer saccharum* seedlings were of broad tolerance to forest floor depth and moss cover, and were able to establish in the boreal forest. The broad tolerance of *Acer saccharum* to soil conditions was confirmed by Kellman (2004) in a transplantation experiment where the species' establishment in the boreal forests was successful, at least at the germination and seedling growth stage. According to Goldblum and Rigg (2005), *Acer saccharum* has good potential for increased growth rates at the transition zone between the deciduous and boreal forests under predicted climate change. Thus, it appears that soil conditions found in the boreal forest will not constrain *Acer saccharum* germination and seedling establishment. Therefore, provided sufficient seed availability, projected increase in temperature and precipitation in northeastern North America could enhance the future status of *Acer saccharum* at its northern limit and facilitate its range expansion northward.

Further, several studies conducted in northeastern Canada have shown that broadleaf species such as *Populus tremuloides* can rapidly establish following harvesting in stands previously dominated by *Picea mariana* (Chen et al., 2009; Laquerre et al., 2009). The presence of *Populus tremuloides* in *Picea mariana* stands has been shown to induce changes in the soil macrofaunal community and to accelerate the rate of soil processes by having either direct or indirect influence on microbial activity (Légaré et al., 2005; Laganière et al., 2009, 2010). In turn, these modified soil conditions have the potential to favour the establishment of new species and consequently modify plant community composition (Légaré et al., 2001; Chávez and Macdonald, 2010), and allow for the persistence of a species within the current limit of its distribution range.

Therefore, the migration of temperate tree species within the area currently occupied by the boreal forest is probable where soil conditions allow. As shown for *Acer saccharum*, in response to climate change, improved soil conditions or broad tolerance to soil conditions may facilitate the migration and establishment, in the boreal forest, of tree species now typically occurring in the temperate forest. Other tree species, such as *Acer rubrum* and *Betula alleghaniensis*, for which distribution limits occur at or near the transition zone between the temperate and the boreal forest, could potentially become established in the boreal forest (Tremblay et al., 2002). Locally, however, properties of coniferous forest soils could hinder the establishment of species associated with base-rich soils, such as basswood (Burns and Honkala, 1990), or unable to withstand waterlogged conditions such as those found in the peaty soils of the James Bay Lowlands. Under these latter conditions, tree species migration is likely to be restricted or delayed. Because species respond differently to soil conditions, species showing broad tolerance to soil conditions could migrate poleward with the warming trend, whereas species showing narrower tolerance to soil conditions could see their migration delayed, at least during first stages of global warming. Nevertheless, as soil properties change (in response to climate and biotic variables) and become favourable for their establishment and growth, the migration of these species could proceed. We acknowledge that while some soil properties may change within a few years or a few decades (e.g. nutrient availability and surficial melting of the permafrost), other properties may change only over the course of centuries or millennia (e.g. soil texture and thickness of the organic layer).

A1.7. Synthesis

Since plant species distribution is under partial control of climate variables such as annual average temperature and precipitation regime, the projected climate change is expected to modify the distribution range of tree species. Furthermore, as soil factors and processes are partly determined by climate variables, climate change is also expected to alter soil properties. Because plant species are influenced by soil factors and processes, soil modifications in turn are likely to interact with altered climate variables to influence tree species migrational response. Hence, tree species' response to the projected climate change is likely to be complex.

We suggest that the migrational response of trees species to climate change, especially to global warming and to soil conditions, could fall into one of four broad categories (Figure A1.1). First, tree species migration could be fully constrained by unfavourable soil properties. Second, migration could be constrained by soil properties during the early stage of the projected temperature increase, and then be relieved later on as soil properties change (in response to climate change and biotic effects) and become favourable for seedling establishment and tree growth. Third, migration could proceed without soil constraints during the early stage of the temperature increase, and then be constrained subsequently as soils properties change (in response to climate change and biotic effects) and become detrimental to seedling establishment and tree growth. Fourth, migration could proceed without soil constraints for the full duration of the temperature increase. Because tree species are likely to respond individually to altered climate and soil conditions, the composition of tree communities is therefore expected to be modified.

Provided climate and genetic adaptations permit, for a given species soil factors should not represent a major constraint for the northward shift of populations located at the southern limit or at the centre of their distribution range. Because populations are already present, one can assume that the soils, at least locally, are suitable for the establishment of migrating populations. At some locations, however, unfavourable soil properties such as waterlogged conditions could preclude or slow down the establishment of migrating species that are poorly adapted to these conditions. For example, despite probable favourable climate envelopes, it is unlikely that *Acer saccharum* or *Betula alleghaniensis* will establish in the James Bay Lowlands, due to deep peat accumulation that creates waterlogged conditions unfavourable for their growth (Table A1.1). Similarly, the tundra, characterized by shallow or waterlogged soils and rocky outcrops, is unlikely to be rapidly colonized by deep tap-rooted species such as *Pinus banksiana*, despite more favourable climate conditions (Table A1.1). Table A1.1 illustrates potential soil constraints to the migration of selected species. For both short distances and long range dispersal, however, other factors such as disturbance regime, concurrent migration of associated pollinators and dispersers, and associated mycorrhizal fungi (e.g. in the boreal forest ericoid and ectomycorrhizal fungi have biochemical and physiological attributes that make them highly efficient at scavenging for organic N and P) and competition will also influence the migration and establishment of tree species in new habitats. Nevertheless, marginal populations could favour a rapid response to climate change.

Because the presence of soil is a prerequisite for tree establishment, the limited development of the soil profile may be an important factor constraining the establishment of trees in areas of the tundra where soils are poorly developed. As well, in some locations waterlogged conditions and permafrost may constrain tree establishment and therefore species migration. The importance of soil factors should thus be locally high in the tundra relative to other factors such as disturbance regime and competition. In contrast, in the boreal and temperate forests where soil profiles are well-developed, the importance of soil conditions for tree establishment should be lower relative to disturbance regime, competition and concurrent migration of associated pollinators and dispersers. Local soil conditions, such as waterlogged conditions, could also restrict species migration and establishment in the boreal forest.

Therefore, the migration of tree species is highly probable within the area currently occupied by the boreal and temperate forest, but will be restricted to the more favourable sites in the tundra (Gamache and Payette, 2005; Lloyd, 2005; Caccianiga and Payette, 2006; Lloyd et al., 2007). While the area covered by the boreal forest biome will in all likelihood decrease because of the northward expansion of the temperate forest biome, and constraints imposed by the tundra environment, the area covered by the temperate forest biome could remain the same, but show a poleward shift. In both biomes, the fate of individual species remains uncertain and is dependent upon their response to complex interactions among climate variables, soil factors and processes, genetic adaptations, modification of disturbance regime, competition, associated pollinators and dispersers, and associated soil microorganisms (e.g. mycorrhizae). Therefore, individual species are more likely to respond to climate change than an entire biome. Further, some species, such as

Betula nigra and *Quercus palustris,* which currently occur in the eastern U.S. only, may migrate to southeastern Canada in response to global warming. New plant species assemblages are therefore likely to emerge from climate change, which may pose new challenges to forest managers.

In conclusion, while climate change has the potential to improve soil conditions for plant growth, plants will also have to cope with soil properties that may hinder their establishment. These antagonistic forces could slow down the migration of some species in response to climate change. Despite the difficulties to reliably predict the fate of tree species communities in response to climate change, policy and management choices of the future will require an understanding of possible species responses to biotic and abiotic factors, including soil factors. Human assistance may also be needed if tree species are to realize their newly expanded, potential natural ranges.

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Tableau A.1.1. Selected North American tree species and potential soil constraints on their migrational response to climate change.

Species	Potential soil constraints
Abies balsamea	Low soil pH
Acer saccharum	Waterlogged conditions, low nutrient availability
Betula	Waterlogged conditions, low nutrient availability
Betula papyrifera	Waterlogged conditions
Carya cordiformis	Low nutrient availability
Carya ovata	Low nutrient availability
Fagus grandifolia	Waterlogged conditions, low nutrient availability
Faxinus americana	Low nutrient availability (especially N and Ca)
Fraxinus nigra	Dry soils, low nutrient availability
Picea glauca	Waterlogged conditions, permafrost
Pinus banksiana	Waterlogged conditions, alkaline soils, soil depth
Pinus resinosa	Waterlogged conditions, alkaline soils
Pinus strobus	Waterlogged conditions
Populus balsamifera	Waterlogged conditions, Low nutrient availability (especially Ca and Mg)
Populus tremuloides	Waterlogged conditions
Tilia americana	Low soil pH, low nutrient availability
Ulmus americana	Low nutrient availability

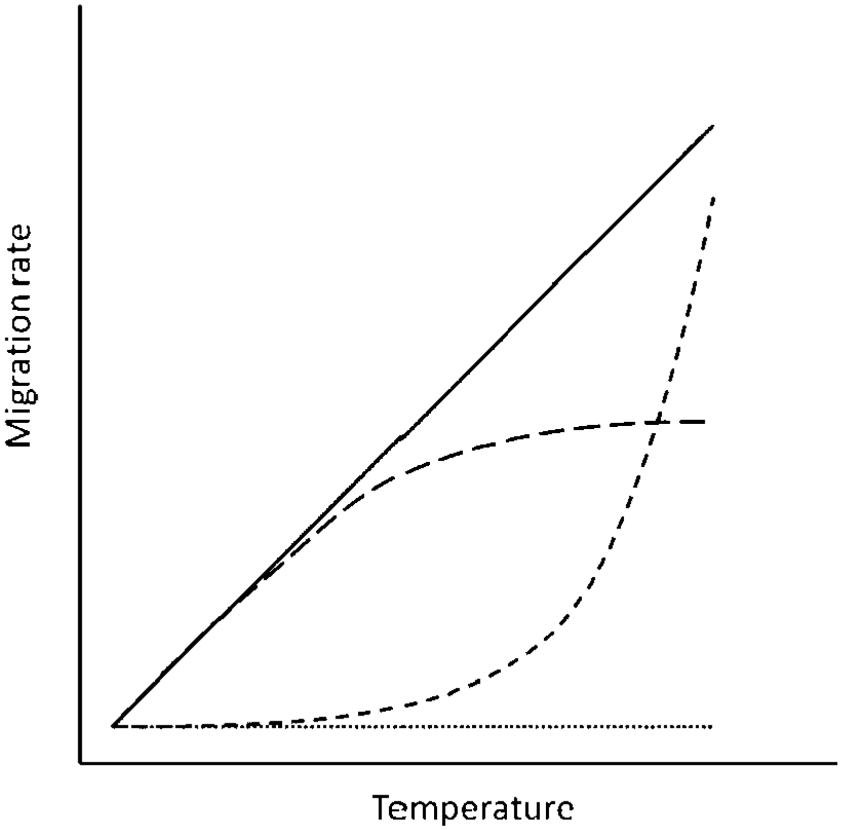

Figure A.1.1. Because tree species respond differently to climate variables and to soil properties, the migrational response of trees to climate change and soil properties could fall into one of four broad categories; (i) tree species migration could be fully constrained by soil properties (dotted line); (ii) migration could be constrained by soil properties during the early stage of the projected global warming, and then relieved later on as soil properties change (in response to climate change and biotic effects) and become favourable for seedling establishment and tree growth (short dashed line); (iii) migration could proceed without soil constraints during the early stage of the global warming, and then be constrained later on as soils properties change (in response to climate change and biotic effects) and become detrimental to seedling establishment and tree growth (long dashed line); (iv) migration could proceed without soil constraints during the full length of the global warming (solid line).