

UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

IMPACTS DES CONDITIONS PRÉ-RÉCOLTE SUR L'EFFICACITÉ DES TRAITEMENTS SYLVICOLES
DANS LA PESSIÈRE À MOUSSES DE LA CEINTURE D'ARGILE DU QUÉBEC

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE
EXTENSIONNÉE
DE
L'UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PAR
ESINAM KPODO

JUILLET 2014



BIBLIOTHÈQUE

Cégep de l'Abitibi-Témiscamingue
Université du Québec en Abitibi-Témiscamingue

Mise en garde

La bibliothèque du Cégep de l'Abitibi-Témiscamingue et de l'Université du Québec en Abitibi-Témiscamingue a obtenu l'autorisation de l'auteur de ce document afin de diffuser, dans un but non lucratif, une copie de son œuvre dans Depositum, site d'archives numériques, gratuit et accessible à tous.

L'auteur conserve néanmoins ses droits de propriété intellectuelle, dont son droit d'auteur, sur cette œuvre. Il est donc interdit de reproduire ou de publier en totalité ou en partie ce document sans l'autorisation de l'auteur.

Warning

The library of the Cégep de l'Abitibi-Témiscamingue and the Université du Québec en Abitibi-Témiscamingue obtained the permission of the author to use a copy of this document for non-profit purposes in order to put it in the open archives Depositum, which is free and accessible to all.

The author retains ownership of the copyright on this document. Neither the whole document, nor substantial extracts from it, may be printed or otherwise reproduced without the author's permission.

REMERCIEMENTS

I would like to express my deepest gratitude to Nicole Fenton and Yves Bergeron, my research director and co-director respectively, for given me the opportunity to undertake an MSc in Biology. To Nicole, I thank you for the immeasurable support, guidance and words of encouragement you gave me during my studies. You always had time for me and read my work countless times, and to Yves, I thank you for accepting me to be part of your family (Labo lym-lyr) and even with your tight schedules, you “squeezed” time to read through my work. I would also like to thank my committee members: David Paré, who allowed me to work in his laboratory at Canadian Forest Services (CFS), and Osvaldo Valeria for the advice you gave me one time or the other on my work.

I am also very grateful to the many people who helped me on the field and laboratory: Christine Allen, Pierre Paul Rocheleau, Julie Arseneault, Samuel Lafleche, Serge Rousseau and Gilles Villeneuve. Also, thanks to Marc Mazerolle for his help on statistical analysis and to Julien Moulinier for the English-French translation of my thesis. Special recognition is given to NSERC Industrial Chair UQAT-UQAM Sustainable Forest Management, Tembec Inc. NSERC CRD program and the Québec Ministry of Natural Resources for providing grants for the realization of this project.

Furthermore, I would like to thank all friends and office-mates who supported me in both good and bad times. You made my time at UQAT extremely enjoyable and absolutely unforgettable.

I am especially grateful to Kenneth (my soul mate) for his love, patience and words of encouragements especially in times when I was stressed out with work, and to my lovely son, Elorm, you are a wonderful gift to behold. I also thank my parents and brothers for their words of encouragement and prayers. Most of all, I would like to thank the LORD ALMIGHTY

whose mercies and grace has brought me this far. Indeed, YOU ARE MY STRENGTH AND MY FORTRESS.

TABLE DES MATIÈRES

LISTE DES FIGURES	v
LISTE DES TABLEAUX.....	vii
RÉSUMÉ	viii
CHAPITRE I	
INTRODUCTION GÉNÉRALE	1
1.1 Contexte.....	1
1.2 Revue de littérature.....	4
1.2.1 Composition du sous-couvert	5
1.2.2 Propriétés physiques et chimiques du sol	6
1.3 Objectif général.....	8
CHAPITRE II	
IMPACT OF PRE-HARVEST CONDITIONS ON DISTURBANCE SEVERITY OF DIFFERENT SILVICULTURAL TECHNIQUES IN THE BOREAL BLACK SPRUCE FORESTS.	10
2.1 Abstract.....	11
2.2 Résumé.....	12
2.3 Introduction.....	13
2.4 Materials and methods	16
2.4.1 Study area	16
2.4.3 Data collection.....	17
2.4.4 Nutrient Analysis.....	18
2.4.5 Microbial Activity	19
2.4.6 Statistical analyses.....	20
2.5 Results.....	22
2.5.1 Reduction of organic layer depth	22
2.5.2 Soil chemical properties.....	24
2.5.3 Understory composition response.....	24

2.6	Discussion.....	28
2.6.1	Impact of pre-harvest conditions on disturbance severity.....	28
2.6.2	Impact of mechanical site preparation on understory species.....	30
2.7	Management Implications.....	31
2.8	Conclusion.....	32
2.9	References.....	34
Appendix A: Results from model selection for change in organic layer depth and the exposure of different soil substrates. Only models $\Delta AIC_c < 4$ are presented with the number of parameters included (K), the second-order Akaike information criterion (AIC_c) and Akaike weight, N=565.		
		56
Appendix B: Mean (\pm SE) of soil chemical properties in different substrates under different site preparation techniques over time.....		
		57
Appendix C : Linear mixed models tested for factors affecting the change in the different soil chemical properties. Site was introduced into the model as random variable.		
		57
Appendix D: Summary of frequencies (presence or absence) of the different understory species before and after treatments. “Yes” indicates the presence of the species and “No” indicates species absence, N=565.		
		58
Appendix E: Model selection results for understory species cover (feather mosses, Sphagnum species, shrubs and grasses). Plots and sites were introduced into the model as random component. The bolded values are the values for competing models from the candidate models, N=565.....		
		59
CHAPITRE III		
	CONCLUSION GÉNÉRALE.....	61
	BIBLIOGRAPHIE.....	67

LISTE DES FIGURES

Figure	Page	
2.1	Map showing Clay Belt region of northwestern Quebec and northeastern Ontario. The location of the larger map in North America is indicated by the white box on the inset map.....	47
2.2	Map of study site indicating the nine blocks and treatments. “CT+Herse” indicates plow treatment; “CT+TTS” indicates disk trenching treatment and “CPRS” indicates harvest-only treatment.....	48
2.3	Effect of different silvicultural treatments and pre-harvest condition on organic layer. a) Comparison of mean (standard error) organic layer depth before and after treatments; b) Relationship between pre-harvest organic layer depth and organic layer reduction after treatments; c) Correlation between initial feather moss cover and organic layer reduction; d) Rate of decomposition and standard error under different treatments, N=433. Bars with different letters are significantly different, $p \leq 0.05$. “OL” indicates organic layer. In b and c, the dotted lines around each treatment represent their individual standard error.....	49
2.4	Relationship between the exposure of different soil layers following treatments and pre-harvest bryophyte species. a) Relationship between mesic layer exposure and pre-harvest feather moss cover after treatment; b) Correlation between mesic layer exposure and initial hollow Sphagnum cover in different treatments; c) Mean exposure (standard error) of humic layer in different silvicultural treatments. Bars with different letters are significantly different, $p \leq 0.05$ and d) Correlation between mineral soil exposure and initial feather moss cover, N=565. In a, b and d, the dotted lines represent the standard error.....	50
2.5	Mean change (standard error) in the total concentration of different elements in mesic layer under different treatments. Bars with different letters are significantly different, $p \leq 0.05$	51
2.6	Mean (\pm SE) of the cover of bryophyte species before and after different treatments, N=452. “Holl.” represents hollow whilst “Hum.” represents hummock.....	52

2.7	Mean (\pm SE) of different understory species cover before and after treatments, N=452.....	53
2.8	Mean change and standard error in the cover (%) of: a) <i>Ptilium crista-castrensis</i> ; b) Hollow Sphagnum species; c) <i>Vaccinum</i> species and d) <i>Carex</i> species after MSP. Bars with different letters are significantly different, $p \leq 0.05$	54

LISTE DES TABLEAUX

Tableau	Page
2.1 List of candidate models considered for the different dependent variables. List of candidate models considered for the different dependent variables during model selection. The dependent variables were modelled as a function of the pre-disturbance condition (initial OL depth, initial understory composition). The “+” indicates that the parameter was included whilst “:” indicates the interaction between two variables.....	39
2.2 Post-hoc comparison of plow and T26 on disturbance severity (organic layer reduction, rate of decomposition and soil layer exposure).....	41
2.3 Model averaged estimates for the exposure of soil layers, soil chemical properties in organic layers as well as soil nutrient availability. “:” indicates the interaction between two variables. 95% CI values that include zero have insignificant effects.....	41
2.4 Summary of statistics for the logistic regressions of understory plant species’ presence under MSP techniques.....	43
2.5 Post-hoc comparison of plow and T26 on the frequency of understory composition. Significant difference between MSP techniques on bryophyte effect.....	44
2.6 Summary of statistics for model average estimates (with SE and CI) for understory community. MSP techniques had no significant effect on the cover of these understory vegetation, N=565.....	45

RÉSUMÉ

Dans l'écosystème forestier, les perturbations naturelles telles que les feux ont une grande influence sur la composition et la structure de la forêt. La ceinture d'argile du Québec est caractérisée par des cycles de feux relativement longs qui facilitent le processus de paludification réduisant la productivité du site à long terme sans l'intervention humaine. Ce n'est que suite à des feux sévères que la couche organique peut être diminuée et que la productivité des sites puisse se rétablir. L'aménagement forestier dans la ceinture d'argile vise donc à utiliser des traitements sylvicoles qui perturbent fortement la couche de sol. Ces traitements sylvicoles consistent à assurer à long terme la continuité des fonctions écologiques de l'écosystème forestier. Néanmoins, l'impact d'une perturbation sur le sol ne dépend pas seulement de la sévérité de la perturbation, mais aussi des conditions pré-perturbation. Cette étude examine comment 1) les conditions pré-récolte influencent la sévérité des traitements sylvicoles et 2) comment la composition du sous-bois répond à ces traitements. L'étude a été effectuée dans la région de la ceinture d'argile dans neuf (9) blocs expérimentaux, chacun d'au moins 20 ha. La récolte a été suivie par deux techniques de préparation mécanique du sol (PMS). La herse forestière et le scarificateur T26 ont été assignés de façon aléatoire aux neuf sites traités. Le troisième traitement, qui a été perturbé uniquement par la récolte, a été considéré comme le témoin. Des données sur la composition et la couverture de plantes vasculaires et non vasculaires, ainsi que sur l'épaisseur des différentes couches de la matière organique (fibrique, mésique et humique) avant et après coupe, ainsi qu'après PMS ont été récoltées. Les résultats ont montré que l'épaisseur de la couche organique et l'abondance des bryophytes pré-récolte avaient une relation avec la proportion de la couche organique réduite par la PMS ainsi que l'exposition des différentes couches de sol. Par ailleurs, le taux de décomposition était plus élevé dans les sites traités par rapport aux sites témoins. Bien que la herse ait causé un plus gros changement dans les concentrations des éléments nutritifs du sol que le traitement du T26, la concentration de l'azote et du phosphore disponible aux plantes n'a pas affectée. En outre, la fréquence et l'abondance de la composition des bryophytes et des graminoides ont été plus affectées par la herse que par le T26. En revanche, l'abondance de *Kalmia angustifolia* L. et *Rhododendron groenlandicum* (Oeder) Kron & Judd n'a pas été affecté significativement différente entre les traitements. Cette étude suggère que même si les conditions pré-récolte ont affecté l'efficacité des traitements sylvicoles, les PMS ont pu créer plus de microsite de bonne qualité ainsi d'augmenter les taux de décomposition. En outre, il n'y avait pas de différence entre l'effet créé par les deux techniques de PMS suggérant que l'utilisation de l'une ou l'autre des techniques peut créer suffisamment de microsites favorables. Puisque l'objectif de ce projet est de réduire le taux de paludification et d'augmenter la productivité du site, des suivis seront nécessaires pour examiner à plus long terme l'effet des différents traitements sur la croissance des arbres, les éléments nutritifs et l'abondance des éricacées.

Mots clé : perturbation, conditions pré-récolte, sévérité, préparation mécanique des sols (PMS), matière organique.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Contexte

En Amérique du nord, la gestion des forêts publiques a progressivement évolué de la production de bois vers un aménagement basé sur la dynamique des écosystèmes. Le concept d'aménagement forestier écosystémique (AFE) a été développé dans le but de maintenir la santé et la capacité de résilience des écosystèmes en réduisant les différences entre les forêts naturelles et les forêts aménagées (Landres et al 1999; Gauthier et al. 2009). Selon Attiwill (1994) et Landres et al. (1999), l'intégrité des écosystèmes pourrait être maintenue à l'échelle du paysage en conservant les patrons de structure et de composition à l'intérieur de leur gamme de variabilité naturelle. À l'échelle du peuplement, l'aménagement écosystémique préconise l'utilisation de pratiques sylvicoles qui produisent des effets similaires à ceux créés par les perturbations naturelles (Seymour et Hunter 1999).

Une perturbation se définit comme toute altération de l'écosystème forestier ou de l'environnement physique par un agent naturel ou anthropique, qui affecte sa composition et sa structure (Pickett et White 1985). Les agents de perturbation naturelle tels que les épidémies d'insectes, les chablis et les pathogènes affectent principalement le couvert forestier, alors que les feux de forêt affectent à la fois le sol et le couvert forestier (Gauthier et al. 2009). Bien que la sévérité d'une perturbation influence l'effet post-perturbation, les conditions avant perturbation influencent aussi cet effet post-perturbation. Par exemple, le taux d'humidité, la masse volumique et la profondeur de la couche organique influencent le degré avec lequel un feu brûle le sol forestier (Miyanishi et Johnson 2002).

Le feu est le type de perturbation naturelle le plus documenté en forêt boréale nord-américaine, même si d'autres agents tels que les chablis et les épidémies d'insectes jouent un rôle important dans la dynamique forestière (Rowe et Scotter 1973; Bergeron et Harvey 1997).

Un feu sera caractérisé par une faible ou une forte sévérité dépendamment du total de couvert et de sous-couvert forestier qu'il aura consommé (Frelich et Reich 1998). Un feu de forte sévérité (durant lequel de nombreux arbres et une grande proportion de la couche organique sont brûlés) crée un environnement homogène avec des microsites de haute qualité qui sont nécessaires à l'établissement de la régénération et à la croissance d'espèces arborescentes telles que le peuplier faux-tremble (*Populus tremuloides* Michx.), le bouleau à papier (*Betula papyrifera* Marsh.), le pin gris (*Pinus banksiana* Lamb.) et l'épinette noire (*Picea mariana* (Mill.) BSP) (Greene et al. 1999; Simard et al. 2007). De plus, la combustion des racines d'éricacées durant un feu sévère entraîne une diminution du couvert en éricacées après le feu (Gauthier et al. 2009). Par conséquent, les feux sévères génèrent des peuplements denses et de structure équiennne qui ont une fermeture de la canopée assez rapide et un sous-couvert dominé par les mousses (*Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* Hedw. et *Ptilium crista-castrensis* (Hedw.) De Not.; Simard et al. 2007). Dans certaines régions, à mesure que les peuplements vieillissent, ces mousses sont graduellement remplacées par des espèces de sphaignes de début de succession (*Sphagnum capillifolium* (Ehrh.) Hedw., *Sphagnum russowii* Warnst., *Sphagnum girgensohnii* Russ., et *Sphagnum rubellum* Wils.). Au fil du temps, l'augmentation de l'épaisseur de la couche organique, la remontée de la nappe phréatique et l'ouverture des peuplements favorisent le remplacement des sphaignes de début de succession par des sphaignes de fin de succession (*Sphagnum magellanicum* Brid., *Sphagnum wulfianum* Girg., *Sphagnum angustifolium* (C. Jens.) Russ. et *Sphagnum fuscum* (Schimp.) Klingrr., Fenton et Bergeron 2006; Simard et al. 2007). Comparés aux feux de forte sévérité, les feux de faible sévérité laissent une quantité considérable de matière organique résiduelle et créent moins de microsites de haute qualité favorables à la germination des graines et à la croissance des semis (Simard et al. 2007). Les peuplements établis dans ces sites sont généralement plus ouverts, majoritairement composés d'arbres de petits diamètres (Lecomte et al. 2006), et ont un sous-couvert présentant une forte dominance d'espèces de sphaignes de début de succession par rapport à la couverture des mousses (Gauthier et al. 2009). De plus, les feux de faible sévérité favorisent la recolonisation par les éricacées dont les racines ne sont généralement pas brûlées lors de tels événements (Gauthier et al. 2009).

Des perturbations artificielles, telles que la récolte de bois (prélèvement d'une large proportion du couvert forestier par l'utilisation de machinerie), affectent principalement le couvert forestier et perturbent le sol dans une moindre mesure. Historiquement, la coupe à blanc a été presque exclusivement utilisée comme méthode de récolte en forêt boréale car on pensait qu'elle favorisait la régénération de l'épinette noire (Keenan et Kimmins 1993; McRae et al. 2001) et qu'elle créait des effets similaires à ceux générés par les feux (Johnson et al. 1998). Toutefois, certaines préoccupations ont été soulevées concernant les effets de la coupe à blanc sur les écosystèmes, entre autres, la destruction de la régénération préétablie, la perte d'habitat pour la faune et l'augmentation de l'érosion des sols (McRae et al. 2001; Lafleur et al. 2010). Ces préoccupations ont conduit à un changement dans les méthodes de récolte, passant de la coupe à blanc à la coupe avec protection de la régénération et des sols (CPRS). Actuellement, la CPRS est largement utilisée pour la récolte de bois au Québec. Toutefois, compte tenu que la CPRS a des effets négligeables sur le sol, en particulier parce qu'elle implique la circulation de la machinerie à l'intérieur de sentiers espacés. L'utilisation de ce traitement pourrait favoriser la paludification et le déclin de la productivité des peuplements à long terme dans certaines régions comme sur la ceinture d'argile du nord-ouest du Québec (Lavoie et al. 2005; Fenton et al. 2005; Simard et al. 2007).

La paludification résulte de la colonisation graduelle du sol forestier par des espèces de sphaignes. Les sphaignes, en possédant une forte capacité de rétention d'eau, entraînent une remontée de la nappe phréatique et une diminution de la température du sol. Ces conditions limitent l'activité des microbes du sol et restreint la croissance des arbres en réduisant la disponibilité des nutriments (Prescott et al. 2000; Fenton et al. 2005). Pour contrer l'engorgement du sol minéral, la zone d'enracinement des arbres migre du sol minéral vers la couche organique grâce au développement de racines adventives. Cette transition se déroule quand les cohortes d'arbres installées après un feu de forte sévérité commencent à mourir (donc entre 100 et 200 ans; Lecomte et al. 2006). Il existe deux types de processus de paludification : édaphique et successione. La paludification édaphique (aussi connue comme entourage de dépression humide; Payette et Rochefort 2001) est principalement contrôlée par la topographie. La paludification successione (en lien avec la succession forestière) se produit

normalement quand la formation de tourbières s'agglomère directement sur les sols mésiques. En absence de feu, la productivité forestière est réduite de 50 à 80% sur une période de 2350 ans (Simard et al. 2007). Cependant, la paludification successionnelle pourrait être inversée par des processus naturels tels que des feux de forêts, qui consomment la couche organique accumulée et améliorent les conditions de sols pour la croissance des végétaux. Par conséquent, en absence de feu de forêt, les traitements sylvicoles qui perturbent sévèrement la couche organique tels que la préparation de terrain pourrait être utilisés pour augmenter la productivité des sites.

1.2 Revue de littérature

La forêt boréale du nord est caractérisée par des cycles de feux courts qui façonnent la structure, la composition et la productivité à l'échelle du paysage et du peuplement (Kimmins 1994). Toutefois, certaines régions comme la ceinture d'argile ont un cycle de feux long, qui entraîne une perte de productivité des sites en raison d'une accumulation d'une épaisse couche de matière organique sur le sol forestier. Comme le principal objectif des gestionnaires forestiers est de maintenir et/ou augmenter de façon durable la productivité des forêts, l'accumulation de matériel sur le sol forestier est une menace pour la productivité des sites à long terme. Même si la productivité d'un site est déterminée par les propriétés du sol, elle pourrait être affectée par l'aménagement forestier. D'ailleurs, il y a un intérêt croissant pour l'intensification de pratiques sylvicoles qui améliorent la qualité du site, et qui permettront d'assurer la continuité à long terme des fonctions écologiques essentielles, de la santé et de la productivité des écosystèmes forestiers (Nyland 1996). Par conséquent, les traitements sylvicoles qui perturbent fortement la couche organique et le couvert forestier dans le but d'améliorer la productivité des forêts, ont des effets semblables à ceux d'un feu sévère, et sont donc souhaitables pour une gestion durable des forêts.

La préparation de terrain est un outil sylvicole utilisé pour perturber le sol forestier et ses horizons supérieurs afin de créer des conditions propices à une installation et une croissance efficaces de la régénération (Ryan et Sutherland 2001). Elle est généralement utilisée pour préparer ou modifier le sol, enlever les souches et les résidus de coupes, et réduire la compétition de la végétation indésirable. Elle peut être réalisée par des moyens mécaniques, donc utilisant de la machinerie, ou par des moyens chimiques, soit le brûlage dirigé (OMRN 1996). La préparation mécanique du sol (PMS) utilise de la machinerie afin d'améliorer la qualité d'un site (Sutherland et Foreman 1995). La PMS est largement utilisée en forêt boréale canadienne pour améliorer les conditions du sol telles que la température, l'humidité, l'aération et la fertilité (Sutton 1993; Sutherland et Foreman 2000). Elle a le potentiel de redistribuer les nutriments stockés dans la couche organique, les résidus de coupe et le sol minéral (Sutherland et Foreman 1995; Bock et Rees 2001). Une variété de microsites est produite par l'élimination, l'inversion et le mélange des couches organiques et minérales du sol (Örlander et al. 1990; von der Gönna 1992). Ainsi, les différentes techniques de préparation mécanique du sol conduisent à différentes perturbations du sol et différentes conséquences pour la productivité (Querejeta et al. 2001). La réponse de la végétation de sous-couvert à un traitement sylvicole dépend de la sévérité de la perturbation sur la couche organique (Haeussler et al. 1999; Roberts 2004; Roberts 2007).

1.2.22 Composition du sous-couvert

La végétation du sous-couvert forestier est la communauté végétale la plus diversifiée mais la moins bien comprises de la forêt boréale nord-américaine (Roberts 2004). Elle agit comme un moteur de la succession forestière (Nilsson et Wardle 2005) en influençant les flux d'énergie et en contrôlant en partie le microclimat forestier (Knops et al 1996). Le sous-couvert est composé de plantes vasculaires et non-vasculaire (les espèces de mousses et de sphaignes). Les mousses (principalement composées de *Pleurozium schreberi*, *Ptilium crista-castrensis* et *Hylocomium splendens*) forment une microtopographie composée de plateaux et de creux sur

le sol forestier (Shelter et al. 2008) alors que le regroupement des sphaignes en sphaignes de creux et en sphaignes de tapis sont basés sur leurs traits structurels (Turetsky et al. 2008). Les sphaignes de creux, la plupart appartenant à la section *Cuspidata*, développent des tiges robustes qui forment des tapis relativement productifs et espacés sur le sol forestier. À l'inverse, les sphaignes de tapis, généralement des espèces de la section *Acutifolia*, forment des pousses minuscules, qui se développent en coussins denses qui leur permettent de retenir l'eau. Elles sont aussi caractérisées par un plus faible taux de croissance que les sphaignes de creux (Gunnarson 2005; Rydin et al. 2006). Cette forte capacité de rétention d'eau abaisse la température du sol, qui à son tour restreint l'activité de la faune du sol et entraîne des taux de décomposition plus faibles que pour les mousses et les sphaignes de creux (Lang et al 2009). Toutefois, les mousses se décomposent plus rapidement que les sphaignes après perturbation (Lang et al. 2009).

Les changements observés dans la végétation de sous-couvert en réponse à la récolte et à la PMS en forêt boréale sont fortement contrôlés par la sévérité de la perturbation, avec d'autant plus de changements de la composition que la sévérité de la perturbation est grande (Haeussler et al. 1999; Roberts 2007). Par exemple, la coupe à blanc et la préparation de sites sont des perturbations de grande sévérité qui réduisent significativement la couverture des espèces de sous-couvert comparé à la CPRS (Sutherland et Foreman 2000; Lafleur et al. 2010). L'augmentation de la perturbation du sol suite à un feu ou une coupe favorise l'établissement des espèces de début de succession, particulièrement les espèces herbacées avec un statut nutritif foliaire élevé qui augmente la productivité du site (Whittle et al. 1997; Nguyen-Xuan et al. 2000; Bradbury 2004; Haeussler et Bergeron 2004; Wardle et Zackrisson 2005). Toutefois, des traitements très sévères peuvent aussi avoir un effet sur la biodiversité. Finalement, les perturbations d'intensité faible à modérée favorisent les espèces végétales existantes par rapport aux perturbations sévères qui éliminent les structures de reproduction végétative et favorisent les espèces provenant de l'extérieur du site (Haeussler et al. 2002).

1.2.23 Propriétés physiques et chimiques du sol

Généralement, la PMS améliore les propriétés physiques et chimiques du sol même si dans certains cas ces effets peuvent être négatifs. Les propriétés physiques qui peuvent être affectées incluent la température du sol, l'humidité saisonnière du sol, l'aération et la masse volumique alors que le pH du sol, la capacité d'échange cationique et la saturation sont les propriétés chimiques qui peuvent être impactées. La PMS peut effectivement diminuer la masse volumique du sol et augmenter son aération pour favoriser la croissance racinaire des végétaux (Montero 1994; Orlander et al. 1998). Une augmentation de l'aération diminue la conductivité thermique, causant une dissipation de la chaleur moins rapide, et donc une augmentation de la température (Attiwill et al. 1985). Cette augmentation de la température du sol stimule l'activité microbienne et la décomposition, et a pour effet d'augmenter le taux de photosynthèse net et la mobilisation des nutriments (Nordbog et al. 2003; MacKenzie et al. 2005). Les nutriments existent sous forme d'ions en solution dans le sol, par conséquent le taux d'absorption d'eau, affecté par la température du sol, est déterminant pour la quantité d'éléments nutritifs qui atteignent le système vasculaire des végétaux (Van Cleve et al. 1983). Des précédentes études ont montré que la préparation mécanique du sol affecte significativement la dynamique des nutriments (Schmidt et al. 1996; Lafleur et al. 2010), en particulier pour l'azote du sol. Les coupes à blanc comme les PMS sont associées à une augmentation de la minéralisation et de la nitrification de l'azote (Munson et al. 1993). Une augmentation de la nitrification augmente la disponibilité des ions hydrogène, qui remplacent les cations des complexes d'échanges du sol et entraînent à une lixiviation des cations. Bien que des précédentes études ont montré une augmentation du pH du sol et de la saturation après PMS (Schmidt et al. 1996; Bock and Van Rees 2002), d'autres travaux ont rapporté une diminution du N total et du C total, du rapport C/N, du NH₄-N, du N minéralisable (Schmidt et al. 1996) et de la disponibilité du P (Munson et al. 1993). Par conséquent, le degré de changement des propriétés du sol a tendance à augmenter avec la sévérité de la perturbation.

1.3 Objectif général

Les perturbations, naturelles ou artificielles, profitent à la production de bien forestiers en prévenant la succession forestière d'entrer en régression (Wardle 2009). Par conséquent, en l'absence prolongée de feux de forêts sévères, la préparation mécanique du sol pourrait être utilisée pour améliorer les conditions de sol et affecter la productivité du site. Bien que l'effet après perturbation dépende de la sévérité de la perturbation, il pourrait aussi être influencé par les conditions avant perturbation. Par exemple, la sévérité d'un feu est contrôlée par l'humidité du sol lors de la combustion (Miyaniishi and Johnson, 2002).

Cette étude vise à évaluer l'interaction entre les conditions avant récolte et la sévérité de la perturbation dans la région de la ceinture d'argile du nord-ouest du Québec. Trois traitements sylvicoles (CPRS, T26 et herse) qui diffèrent substantiellement dans la stratégie de perturbation du sol ont été comparés sur la base de leurs effets sur la profondeur de la couche organique et la composition des espèces du couvert et du sous-couvert. La génération de microsites favorables à la croissance des végétaux et les changements dans les propriétés chimiques ont aussi été comparées entre les trois types de traitements. Les données collectées avant et après perturbation ont permis de mieux comprendre les relations entre les conditions initiale avant récolte et les impacts des PMS, et entre l'ampleur des changements dans la profondeur de la couche organique et les propriétés chimiques du sol. Cette étude devrait donc permettre d'identifier les techniques les plus appropriées pour l'aménagement des forêts de la ceinture d'argile.

Le chapitre suivant de ce mémoire est un manuscrit qui sera soumis pour publication. Mon directeur et codirecteur, le Dr Yves Bergeron, professeur à l'UQAT et à l'UQAM et le Dre Nicole Fenton, professeure à l'UQAT, ont contribué à la réflexion sur les analyses et les résultats et orienté les grands axes de travail.

CHAPITRE II

IMPACT OF PRE-HARVEST CONDITIONS ON DISTURBANCE SEVERITY OF
DIFFERENT SILVICULTURAL TECHNIQUES IN THE BOREAL BLACK SPRUCE
FORESTS.

2.1 Abstract

In Canada, mechanical site preparation (MSP) is used to improve soil conditions in order to ensure the long-term continuity of essential ecological functions of the forest ecosystem. The impact of a disturbance event on soil is not only dependent on the severity of the disturbance event itself but also on the pre-disturbance site conditions. This study examined how 1) pre-harvest organic layer thickness and understory composition affected disturbance severity of different silvicultural treatments and 2) understory composition response to the different treatments employed. The study was carried out in the Clay Belt region of northwestern Quebec, in nine (9) blocks of approximately 20ha each. Three treatments that differ in the level of soil disturbance were contrasted: harvest-only (CPRS), disk-trenching (T26) and plowing. The thickness of the organic layer, the composition and cover of vascular and non-vascular plants, as well as the thickness of the different soil layers (fibric, mesic, humic) were assessed before and after harvesting and then after MSP. Results showed that the reduction in organic layer thickness was positively related to the pre-harvest organic layer depth and bryophyte composition. In addition, the rate of decomposition was higher in treated sites compared to the controls. Although plowing caused a greater negative change in the concentrations of carbon, nitrogen, phosphorus, and cation exchange capacity (CEC) than T26, it did not subsequently affect the concentration of available nitrogen and phosphorus. Furthermore, there was appreciable exposure of the different soil layers, which was dependent on the pre-disturbance bryophyte cover. Moreover, the frequency and abundance of bryophyte species and graminoids were more affected by the plowing treatment relative to the disk trencher. In contrast, the cover of *Kalmia angustifolia* L. and *Rhododendron groenlandicum* (Oeder) Kron & Judd were not significantly different among treatments. This study suggests that pre-harvest conditions affect the effectiveness of silvicultural techniques and must be taken into consideration when choosing a particular silvicultural practice.

Keywords: Pre-disturbance conditions, disturbance severity, mechanical site preparation (MSP), understory composition.

2.2 Résumé

Au Canada, la préparation mécanique du sol (PMS) est utilisée pour améliorer les conditions de sol afin d'assurer à long terme la continuité des fonctions écologiques de l'écosystème forestier. Le degré d'impact d'une perturbation sur le sol ne dépend pas seulement de la sévérité de la perturbation, mais aussi sur les conditions pré-perturbation. Cette étude examine comment 1) les conditions pré-récolte influencent la sévérité des différents traitements sylvicoles et 2) comment la composition du sous-bois répond à ces traitements sylvicoles. L'étude a été effectuée dans la région de la ceinture d'argile, dans neuf (9) blocs chacun des 20 ha de superficie. Trois traitements qui diffèrent par leur niveau de perturbation de sol ont été contrastés: la récolte seulement (contrôle), le scarificateur T26, et la herse forestière. Les données ont été récoltées sur la composition et la couverture de plantes vasculaires et non vasculaires, ainsi que sur l'épaisseur des différentes couches de la matière organique (fibrique, mésique et humique) avant et après coupe, ainsi qu'après PMS. Les résultats ont montré que l'épaisseur de la couche organique et l'abondance des bryophytes pré-récolte présentaient une relation positive avec la réduction de la proportion de la couche organique ayant subi une PMS ainsi que l'exposition des différentes couches du sol. Par ailleurs, le taux de décomposition était plus élevé dans les sites traités par rapport aux sites témoins. Bien que la herse ait causé un changement plus élevé dans les concentrations des éléments nutritifs du sol que le traitement du T26, il n'a pas affecté la disponibilité de l'azote et du phosphore. En outre, la fréquence et l'abondance de la composition de bryophytes et les graminoides ont été plus affectées par le traitement de la herse que par la scarification au T26. En revanche, l'abondance de *Kalmia angustifolia* L. et *Rhododendron groenlandicum* (Oeder) Kron & Judd n'était pas significativement différente entre les traitements. Cette étude suggère que les conditions pré-récolte affecte l'efficacité des techniques sylvicoles et doivent être prises en considération lors du choix d'une technique sylvicole.

Mot clé : Conditions pré-récolte, sévérité de perturbations, préparation mécanique du sol (PMS), composition du sous-bois.

2.3 Introduction

The North American boreal biome is driven by large-scale natural disturbances such as fire, although some regions like the Clay Belt have long fire cycles (Bergeron et al. 2004), resulting in the loss of productive sites due to the accumulation of a thick forest floor over the mineral soil. Most plant and animal species in the boreal forest are adapted to these frequent disturbances (Korpilahti and Kuuluvainen, 2002). As a result, knowledge of natural disturbance dynamics have been integrated into the management of the boreal forest at stand and landscape levels (Bergeron et al., 1999; Harvey et al. 2002). At the landscape level, having structural and compositional patterns within the natural range of variability produced under natural disturbance regimes implies the maintenance of ecosystem integrity (Landres et. al., 1999; Harvey et al., 2002). At the stand level, ecosystem management promotes the use of silvicultural practices to mimic natural stand dynamics, with the aim to maintain structural and biotic legacies of the pre-harvest stand (Franklin 1993; Seymour and Hunter 1999). In order to maintain long-term site productivity on the Clay Belt, management interventions should be geared toward mimicking high severity fire. The current harvesting practices carried out on the Clay Belt might mimic low severity fire that promotes paludification with consequences for site productivity (Lavoie et al. 2005).

Furthermore, the prolonged absence of high severity fires favours the proliferation of ericaceous shrubs in the understory vegetation. These ericaceous shrubs negatively affect the regeneration and growth of conifers through allelopathic effects (Thiffault et al. 2013). The process of paludification, as well as the detrimental effects of ericad species on site productivity, could be reversed by using silvicultural techniques such as site preparation techniques (controlled burning or mechanical site preparation) to considerably disturb the understory layer (Thiffault et al. 2013).

Mechanical site preparation is commonly used in North America to improve site conditions by reducing competing understory vegetation to increase tree growth. (Nilsson and Wardle 2005). There are five (5) commonly used MSP techniques: mounding, scalping,

mixing, disk trenching and plowing (von der Gonna, 1992), which create different degrees and types of soil disturbances. Plowing incorporate the organic layer into the underlying mineral soil (Boateng et al., 2006; Boateng et al., 2009) creating a homogeneous profile to mixing depth. Forest plow has a series of large steel blades joined to an axle, allowing them to disturb soil and results in about 100% exposure of the favourable soil layers (mesic, humic and mineral soil layer; von der Gonna 1992; Veal et al., 2002; Boateng et al., 2009) when pulled by skidders or crawling tractors. Disk trenching breaks up compacted soil and reduces hardwood competition. It results in a portion of both the mineral soil and forest floor being removed and deposited in berms next to the trench (MacKenzie, 1999). Disk trenching (T26) has two rotating, spring loaded toothed disks mounted on each side of the steel box frame of a skidder. The trenching (T26) produces three (3) microsites: trench, berm and hinge (von der Gonna 1992; White 2004) and disturbs part of the soil surface leading to about 48% exposure of the mesic and humic layers (von der Gonna 1992).

In order to determine the impact of soil disturbance by mechanical site preparation, a retrospective study was undertaken in the Clay Belt to compare the effect of season and harvest methods on soil properties (for details see Lafleur et al., 2010). The results of this study suggested that treatments associated with the highest level of organic layer disturbance created more high quality microsites and an understory composition similar to what was observed after high severity fire. Other studies have also reported how understory composition and soil properties respond to MSP in the boreal forest over the short and long term (Schmidt et al., 1996; Haeussler et al., 2002; Bock and Van Rees 2002; Boateng et al., 2009). However, these studies focused on the effect of site preparation techniques and harvest on understory species and organic layer depth using the residual cover as a measure of disturbance severity. Meanwhile, in order to determine the cover removed by disturbances owing to disturbance severity, it would be required to take measurement of understory species cover and organic layer depth before and after disturbance. This could be achieved by using the BACI approach (before, after, control and impact). In addition, it has been reported that variations in disturbance severity are dependent on site conditions such as forest floor depth (McInnis and

Roberts 1994; de Groot et al., 2009). Hence, the objectives addressed in this paper were to investigate;

- The effect of pre-harvest conditions (organic layer depth and understory species composition) on disturbance severity during soil disturbance. Disturbance severity is qualified as the change in organic layer depth, rate of decomposition and change in soil chemical properties as well as the exposure of different soil layers among treatments.
- The effect of disturbance severity created by the silvicultural techniques on, bryophyte and vascular plant survival and regeneration.

For the first objective, it was hypothesised that; 1) MSP treated sites will have higher disturbance severity compared to the harvest-only (CPRS) sites. However, of the two techniques, plowing will have greater disturbance severity compared to T26; 2) Proportion of organic layer reduction and percent soil exposure will be dependent on pre-harvest organic layer depth and bryophyte composition. Thus, thinner pre-disturbance organic layer sites will be more severely disturbed compared to thicker organic layer sites.

For the second objective, it was postulated that; 1) MSP treated sites will have lower understory cover, particularly, *Sphagnum* and ericad species compared to harvest-only sites; 2) Higher establishment of both pioneer vascular and pioneer bryophyte species in MSP sites compared to only harvest sites. Nevertheless, of the two MSP techniques, plow will greatly reduce the cover of mosses and ericaceous shrubs and favour the establishment of early successional plants (grasses) whilst T26 will have higher understory species survival.

2.4 Materials and methods

2.4.1 Study area

The study was carried out in sites with an organic layer that varied in depth between 20 and 60cm. Located in the Clay Belt region of northwestern Quebec, it is within the western black spruce (*Picea Mariana* (Mill)) – feather moss bioclimatic domain (Figure 2.1; Saucier et al. 2009). This region is covered by a fine textured clay deposit left by proglacial lakes Barlow and Ojibway (Vincent and Hardy, 1977). The mean annual temperature from 1971 to 2000 was 0.1°C; the average annual precipitation was 892mm, with 35% falling during the growing season (Joutel weather station; Environment Canada 2009). The cumulative annual degree-days (> 5°C) was 1249, with frost occasionally occurring during the growing season. Before harvest, the sites were dominated by black spruce and the shrub cover was dominated by Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd) and sheep laurel (*Kalmia angustifolia* L.) whereas the forest floor was covered by hollow sphagna (*S. magellanicum* Brid.; *S. fallax sensu lato* H.Klinggr.) and hummock sphagna (*S. russowii* Warnst.; *S. capillifolium* (Ehrh.) Hedw.; *S. fuscum* (Schimp.) Klinggr.; *S. rubellum* Wils.) and feather mosses (mainly *Pleurozium schreberi* (Brid.) Mitt. and *Ptilium crista-castrensis* (Hedw.) De Not.). Stands in this area are prone to paludification because of the cold and humid climate, low topographic relief, and poorly drained clay soil coupled with an increasing fire cycle (Fenton and Bergeron 2011).

2.4.2 Sampling design and site preparation

The study site was selected during the spring of 2009, and in the summer of 2009, nine (9) cut blocks, each of approximately 20ha, were established. Within each cut block, fifteen (15) circular plots (each 400m² in size) were established in such a way to ensure that the maximum variability in the depth of the organic layer was captured within each block, as estimated from Radarsat data (Beaudoin et al. 2012; Figure 2.2). The center of the 400m² plot

and the position of four (4) 1m x 1m quadrats that were installed systematically at 20m diagonally from the center were marked using differential global positioning system (DGPS) with a precision of +/-1m. The same sampling method was used before and after harvest (2010, 2011) and after site preparation (2012). During the autumn of 2010, the area was harvested using careful logging (CPRS) after which the plots and quadrats were re-established. In October 2011, two MSP techniques: disk trenching (T26) and forest plow were employed on three replicate blocks each. The blocks were assigned a treatment type in such a way that the variability in depth of the organic layer present across the nine sites was represented in each treatment type. A DGPS was installed on the machinery to determine the number of times the machine passes over a specific plot as a measure of disturbance intensity. Plots were re-established after the MSP treatment using the DGPS points.

2.4.3 Data collection

The BACI approach was employed in this study. It requires data on two types of sites; one corresponding to the control site and the other to the impacted site (Smith et al. 1993). These data are collected before the impact begins as well as after. Thus, when there is data or information before an impact, the test is referred to as before- after control-impact. In analysis, such data are treated as independent samples and compared using a two-way sample test. Any difference found in the analysis is attributed to the activity. However to account for problems associated with natural changes (i.e. not as a result of the disturbance event), the impacted site is compared to a control site. In this study, the site considered as control were not further disturbed by any of the MSP techniques after harvesting (CPRS).

The composition and cover of overstory and understory plant species of the forest stands within each plot were described before harvest. For *Sphagnum* species, due to the differences in the structural traits, they were grouped into two groups: hollow *Sphagnum* and hummock *Sphagnum* species during analysis. A soil pit was dug at the center of each plot from which total organic layer depth, thickness of the different layers of organic layer (fibric, mesic and

humic) were measured and samples taken for nutritive analyses. The different organic layers were differentiated based on the degree of decomposition on the von Post scale (Soil classification group, 1998). Regeneration (sapling stage) abundance as well as the composition (and cover) of the understory species (vascular and mosses) were visually evaluated in the four 1m x 1m quadrats that were systematically installed within the 400m² plots. Samples of bryophyte species were collected in the field for identification in the lab. Also the total organic layer depth for each quadrat was measured at the four (4) corners of each of the quadrats by inserting a meter rule through the organic layer to the mineral soil. The mean depth of the four corners of the quadrat was used to represent the depth of the organic layer in that particular quadrat. Quadrat level assessment permitted the determination of the impact of disturbances on individual species and colonies of understory plants. The above measurements were taken before and after harvest and then, after mechanical site preparation. In addition to the above data, residual tree stems as well as the horizontal exposure of the different soil substrates were measured after MSP treatment.

2.4.4 Nutrient Analysis

In assessing the impact of the different treatments on nutrient availability, two approaches were used: chemical extraction and ion exchange resins (IER).

For chemical extraction, the samples taken from the organic layers in the soil pit were placed in ziplock bags, transported to the laboratory and frozen for further analysis. Prior to analysis, all samples were air-dried at 30°C for 48hr, and then passed through 6mm mesh sieve. Sub-samples of each substrate were ground for the determination of total carbon and nitrogen. Total nitrogen and carbon contents were measured by dry combustion in LECO CNS-2000 (LECO Corporation, USA). Substrates' pH was determined in distilled water and calcium chloride (CaCl₂) using a 2:1 slurry of 0.01 mol/L CaCl₂. The slurry was left to stand for 30 min, and pH was measured on a Fischer Scientific pH meter (Hendershot et al. 1993). Available phosphorus was extracted using Bray 2 solution as an extractant (Bray and Kurtz 1945) and measured

colourimetrically. The absorbance of the compound was measured at 882 nm in a spectrophotometer that is directly proportional to the amount of phosphorus extracted from the organic layer. Exchangeable base cations (Ca, Mg, Na, K, Al, Fe, Mn) were extracted and measured at an inductively coupled plasma (ICP) atomic absorption and spectrometer after standard extraction with ammonium acetate (van Groenigen et al. 2003). All soil analysis were carried out at Canadian Forest Services, NRCan, Quebec.

The IER approach was used because of its sensitivity to changing field conditions and because it provides an accurate measure of mineralizable N in situ. A mixed-bed resin (charged with H⁺ and OH⁻ ions) was obtained from JT Baker Laboratory Inc. and prepared by adding approximately 10 g of resin to 5 cm × 5 cm nylon bags. The bags were first rinsed in deionized water for 24 h, loaded with 1 mol/L NaCl (25 mL per bag) for 24 h, and rinsed in deionized water again for 24 h (Krause and Ramlal 1987; MacKenzie and Schmidt 2005). The bags were then buried at a depth of 10-15cm in the central quadrat of ten (10) plots that were randomly selected from each site from September, 2012 to August, 2013. The amount of nutrient ions absorbed at the end of the incubation gives an estimate of the rate of supply of plant nutrients (Huang and Schoenau 1997). After retrieval, the concentration of the nutrient ions were extracted using the same procedure as described above.

2.4.5 Microbial Activity

In order to determine the effect of the different silvicultural treatments on microbial activity, the rate of decomposition was compared among treatments using the cotton strip method (Latter and Howson, 1977; Latter and Walton 1988) and still remain in use (Correll et al. 1997; Treonis et al., 2002). A 100% unbleached cotton cloth was cut into strips (5cmx5cm). Cotton is composed of 95% cellulose which becomes decomposable by microbes when buried in soils. Strips were autoclaved at 121°C for 20 min to prevent the introduction of foreign microorganism. Four (4) strips were individually inserted in the center quadrat of ten (10) randomly selected plots per site. They were inserted at a depth of 10-15cm and removed after

7, 14, 21 and 28 days in order to determine the loss in tensile strength (LTS) due to decomposition. On each retrieval date, a different strip with the same dimension and with the same pre-treatment condition was inserted into the soil and removed immediately to serve as a control. After retrieval, strips were gently washed in water and dried for 48hrs at room temperature. In the laboratory, strips were placed in a tensiometer and subjected to an increasing load until breakage. The load required to break up the strip is a measure of the tensile strength of the strip.

The loss in tensile strength (LTS) was calculated as;

$$LTS(\text{kg}) = TS_{\text{control}} - TS_{\text{buried strip}}$$

where LTS is a measure of soil microbial activity, TS_{control} is the tensile strength of the control strip, $TS_{\text{buried strip}}$ is the tensile strength of the buried strip. The rate of decay (RD) was calculated using the function derived by Hill et. al. (1985):

$$RD = \left(\frac{LTS}{TS_{\text{buried strip}}} \right)^{\frac{1}{3}} * \left(\frac{365}{t} \right)$$

Where t is the incubation time in days. This allows for comparison between sites. Approximately 8% of the strips were too decomposed to be measured; hence their RD was standardized to 100% and included in the analysis.

2.4.6 Statistical analyses

All statistical analyses were carried out in R freeware (v. 2.15.2, R development Core Team 2012). A significance level of $\alpha=5\%$ was used. Square-root transformation was carried out on soil layer exposure (mesic, humic and minerals soil) to meet the assumptions of homoscedasticity and normality. In instances where treatment effect was significant, a post-hoc linear contrast was used to compare treatments to assess whether they are statistically different from each other.

A paired t-test was performed on the depth of organic layer to determine whether treatments caused a significant difference in the mean value of the change in organic layer depth, exposure of different soil layers, rate of decomposition and change in soil chemical properties). Subsequently, the relationships between dependent variables (change in organic layer depth and the exposure of soil layers) and the various explanatory variables (pre-harvest organic layer depth and pre-harvest understory species) were tested using linear mixed model analyses. Linear mixed model with the function lme was used for the estimations. Variability among sites and plots were considered as the random effects to avoid pseudo-replication. Each model represented a biological hypothesis (Table 2.1). The interaction between fixed effects and covariates in the candidate models along with the null model were also included in the set of models. Model selection was done by comparing the Akaike information criteria for small sample size (AICc; Burnham and Anderson 2002). Model fit was evaluated using Pearson's correlation. Model average estimates were also computed for variables in models having delta AICc <4, using the AICcmodavg package (Mazerolle 2013). Furthermore, differences in the rate of decomposition among treatments were tested using mixed models; time was considered as the random variable. In addition, the impact of silvicultural techniques on soil chemical properties was analysed by comparing the concentration of the different soil properties before and after soil disturbance in the substrates. The change observed in the concentration was related to treatment and organic layer depth using a mixed model. Here, site was considered as a random variable. A null model was also considered. The concentration of available nitrogen and phosphorus was also analysed with mixed models in order to account for the variability within sites.

The influence of silvicultural techniques on understory species presence was analysed using logistic regression by relating the frequency of the understory species to a particular silvicultural treatment. Generalised linear models (GLM) with the logit function were employed because of the binary nature (presence or absence) of the response variable. The change in the cover of understory species before and after soil disturbance was also compared. Subsequently, the difference observed in the cover of each species was related to treatment and organic layer thickness before harvest using a linear mixed model with sites and plots as

random variables. Interactions, as well as a null model, were included in the candidate models. Model selection was completed by comparing the Akaike information criteria for small sample size (AICc). Model estimates were calculated for variables in models having $\Delta AICc < 4$.

2.5 Results

2.5.1 Reduction of organic layer depth

The depth of organic layer was reduced compared to pre-harvest organic layer depth in the different treatments after soil disturbance ($p < 0.001$, $t = 26.85$, $df = 564$; Figure 2.3a). This reduction in organic layer depth was influenced by the pre-harvest organic layer depth and by bryophyte composition, as indicated by model selection ($AICc = 4130.67$, $Weight = 1$; Appendix A). The proportion of the organic layer reduced was positively related to pre-harvest organic layer depth (Figure 2.3b) and feather moss cover (Figure 2.3c). The effect of MSP treatment on organic layer reduction was significantly different from harvest-only sites (estimate = 2.46, $se = 0.67$, $p = 0.01$). Even though there was no significant difference among MSP treatments ($p = 0.21$; Table 2.2), T26 seemed to have reduced the organic layer thickness 1.6 times more than forest plow. *Sphagnum* species composition had no significant effect on the reduction of the organic layer.

The rate of decomposition of cotton, which was examined over 28 days, was higher in MSP treated sites relative to harvest-only sites (Figure 2.3d). However, there was no significant difference between the two MSP techniques ($p = 0.98$; Table 2.2).

After mechanical site preparation, the mean exposure (in percent) of the different soil layers at harvest-only sites were 1.6 ± 0.5 for mesic layer, 1.7 ± 0.8 for humic layer and 3.7 ± 1.3 for mineral soil. Meanwhile, for plow treated sites, the mean exposure for mesic, humic layers and mineral soil were 6.9 ± 1.2 , 9.9 ± 1.6 and 9.9 ± 1.7 respectively, whereas in T26 treated sites,

the mean exposure was 6.9 ± 0.9 , 7.8 ± 1.2 and 24.9 ± 2.1 for mesic, humic and mineral soil respectively.

Results from model selection showed that model 1 was the most parsimonious in explaining the variability in the exposure of the mesic layer (AICc= 2337.94, Weight=0.99; Appendix A) among candidate models in Table 2.1. The exposure of the mesic layer was positively correlated with pre-treatment cover of hollow *Sphagnum* and feather moss (Figure 2.4a, b). Although, T26 seemed to have exposed a higher proportion of the mesic layer, it was not significantly different from that exposed by plow ($p=0.87$, $se=0.16$; Table 2.3).

In contrast to the mesic layer, four (4) models were plausible in explaining the variability in the exposure of humic layer as indicated by model selection. However, the model with the treatment factor was 5.2 times more parsimonious than the next best model (model 7), which included the interaction between treatment and pre-disturbance organic layer (0.52/0.1; Appendix A). Model averaged estimates calculated for the four selected models revealed only a significant effect of treatment on the exposure of the humic layer (Figure 2.4c; Table 2.3). Despite that plow seemed to expose more humic layer, there was no difference among MSP treatments (Table 2.2).

Results indicated that the model with treatment, pre-treatment feather moss cover and the interaction between treatment and feather moss cover ranked high among candidate models in explaining exposure of the mineral soil. Both treatment and feather moss cover had a significant positive effect on mineral soil exposure (Figure 2.4d), with T26 exposing 1.4 times more mineral soil than plow. However, the effect created by T26 is dependent on the cover of feather moss as indicated by the interaction term in the linear mixed model (Table 2.3).

2.5.2 Soil chemical properties

The concentrations of carbon, nitrogen, phosphorus and CEC increased for all treatments after soil disturbance in all soil layers compared to their respective concentrations at the pre-harvest level (Appendix B). In the mesic layer, the change in the concentrations of carbon, nitrogen and CEC were significantly influenced by plow treatment compared to T26 that had a non-significant effect (Figure 2.5). On the other hand, phosphorus was neither influenced by treatments (plow and T26) nor by pre-harvest organic layer thickness.

In contrast, for the humic layer, the variability in the increment of the concentrations of carbon, nitrogen, CEC was not significantly impacted by either treatment. However, the change in phosphorus concentration was positively influenced by T26, while plow had a non-significant positive effect (model averaging; Table 2.3).

Estimations of seasonal availability of nutrients by IER gave contrasting results to those for extractable nutrients. Neither plow nor T26 had a significant effect on the seasonal availability of NH_4 ($p=0.88$ and $p=0.14$) or NO_3 ($p=0.81$ and $p=0.12$ respectively; Table 2.3) as estimated by IER. Although, the concentration of available nitrogen was not impacted by MSP techniques, T26 seemed to have lower concentrations of available nitrogen than plow. In comparison, the concentration of available P was significantly reduced at T26 treated sites ($p=0.017$) relative to plow sites, which had no significant effect on P concentration ($p=0.86$).

2.5.3 Understory composition response

Feather moss

MSP technique had an effect on the presence-absence of feather mosses (ie. *Pleurozium schreberi* and *Ptilium crista-castrensis*; Appendix D). The frequency of feather mosses was significantly reduced in MSP treated sites compared to sites with harvest only (Table 2.4). Even though, the presence of *P. schreberi* was significantly impacted by the two MSP techniques,

these techniques were not statistically different from each other. On the other hand, there was a greater significant effect of plow on the presence of *Ptilium crista-castrensis* compared to T26 ($p=0.01$, $se=0.52$; Table 2.5)

The mean abundance of *P. schreberi* in plow and T26 treated sites was $7.5\pm 1.3\%$ and $7.7\pm 1.2\%$ respectively compared to $10.7\pm 1.3\%$ in the harvest-only site. Similarly, the mean cover of *Ptilium crista-castrensis* was $1.9\pm 0.6\%$; $0.1\pm 0.1\%$ and $3.4\pm 0.8\%$ in plow, T26 and harvest-only sites respectively. It was however observed that compared to the pre-treatment cover, the abundance of *P. schreberi* and *Ptilium crista-castrensis* was reduced after soil disturbance in all treatments (Figure 2.6a and b). However, the reduction observed in *P. schreberi* was not influenced by treatment type (model averaging; Table 2.6). On the other hand, *Ptilium crista-castrensis* cover was less reduced by plow compared to T26, which had a non-significant positive effect (model averaged estimates; Figure 2.8).

Sphagnum species

The presence or absence of *Sphagnum* species was influenced by mechanical site preparation (Table 2.4). Plow had a significant positive effect on the frequency of hummock *Sphagnum* species, while T26 had a non-significant negative effect ($p<0.001$ and $p=0.55$ respectively; Table 2.4). Likewise, the frequency of hollow *Sphagnum* species was significantly affected by plow (estimate=0.92, $p=0.01$) contrary to T26, which had no effect on the frequency of hollow *Sphagnum* species (estimate=-0.03, $p=0.95$; Table 2.4). Of the two MSP techniques, the effect created by plow on the presence of both hollow and hummock *Sphagnum* was significantly different from the effect created by T26 ($p=0.01$, $se=0.18$ and $p<0.001$, $se=0.15$ for hollow and hummock *Sphagnum* respectively; Table 2.5)

Hollow *Sphagnum* mean cover was also reduced from 4.5 ± 0.6 to 1.0 ± 0.3 in plow treated sites; from 2.7 ± 0.5 to 0.5 ± 0.2 in T26 treated sites and from 1.0 ± 0.3 to 0.3 ± 0.2 in harvest-only sites after harvest and site preparation (Figure 2.6c) and this reduction was best explained by two competing models; 2 and 3 (Appendix E). The pre-harvest organic layer (model 2) was the

best with an evidence ratio of 1.9 over the interaction model (model 3). Nevertheless, both plow and the pre-harvest organic layer depth had significant positive effects on the reduction in abundance of hollow *Sphagnum* (model averaging; Figure 2.8).

Meanwhile for hummock *Sphagnum* species, the variability observed in its change in cover from 2.7 ± 0.5 to 2.9 ± 0.5 ; 2.5 ± 0.5 to 0.9 ± 0.3 and 2.4 ± 0.5 to 1.1 ± 0.3 in plow, T26 and harvest-only sites respectively (Figure 2.6d) was best explained by the interaction between treatment and pre-harvest organic layer as well as the pre-harvest organic layer. However, the model including the interaction term was the best having an evidence ratio of 3 over the model with only pre-harvest organic layer. The effect of treatment on the reduction of hummock *Sphagnum* was dependent on the depth of the pre-harvest organic layer (Table 2.6).

Ericaceous shrubs

Contrary to mosses, the presence or absence of ericaceous shrubs (*R. groenlandicum*, *K. angustifolia* and *Vaccinium* species) was independent of MSP technique used (Table 2.4). However, shrub cover was related to various factors. The reduction in *K. angustifolia* cover after disturbance (Figure 2.7a) was observed to be influenced by the interaction between treatment and pre-harvest organic layer, having a significant negative effect with T26 and no significant effect with plow (Table 2.6). However, for *R. groenlandicum* species cover, its reduction was positively correlated to pre-harvest organic layer depth (Table 2.6).

Regarding change in *Vaccinium* cover, two (2) models were selected ($\Delta AIC_c < 4$), including the treatment and the null models, but the most parsimonious was the treatment model (model 1) having an evidence ratio of 2.5 relative to null model. Model- average estimates showed that T26 highly reduced the cover of *Vaccinium* species relative to plow (Figure 2.8c).

Graminoid species

The frequency of the cover of graminoids was dependent on the type of MSP technique used with plow having a slightly greater effect than T26 (estimate=0.57 and 0.51 respectively; Table 2.4).

The mean abundance of *Carex* species increased after harvest and mechanical site preparation from 0.04(\pm 0.03) to 3.06(\pm 0.54) in plow site, from 0.006(\pm 0.004) to 1.62(\pm 0.29) in T26 site and from 0.15(\pm 0.08) to 1.39(\pm 0.34) in harvest-only site (Figure 2.7d). This variability observed in the increase in graminoids cover was best explained by three good models: treatment, null model and pre-harvest organic layer model. However, the model with treatment factor was 2.5 times more parsimonious than the null model (Appendix E). The abundance of graminoids was more enhanced at plow treated sites (model averaging; Figure 2.8d) compared to T26 treated sites, and the effect created by T26 was not different from the control.

2.6 Discussion

2.6.1 Impact of pre-harvest conditions on disturbance severity

Results show that the depth of organic layer and the abundance of feather moss cover before harvesting, along with site preparation, had significant effects on the reduction of the organic layer. There was a correlation between organic layer reduction and pre-harvest organic layer thickness (Fig. 2b), this supports our premise that pre-disturbance site conditions have a major effect on the thickness of the post-disturbance organic layer. This is the first study to report the influence of pre-harvest conditions on post-treatment organic layer depth as well as to quantify the change in organic layer depth as a measure of disturbance severity. However, to the extent that post-disturbance organic layer thickness is a measure of disturbance severity, these findings agree with those of McInnis and Roberts, (1994) who reported that variation in disturbance severity is dependent on site conditions. de Groot et al. (2009) also found pre-burn forest floor depth to be an important predictor of the amount of forest floor consumed during a fire event for upland forest.

The higher reduction rate in organic layer depth associated with higher initial cover of feather mosses is likely due to the structural characteristics and the rapid decomposition of this type of moss. Feather moss forms flat or hollow micro-topography on the forest floor (Shetler et al. 2008) that could be easily disrupted by a disturbance event. In addition, *Ptilium crista-castrensis* (a type of feather moss) develops wefts of loose shoots that can be easily disturbed. Feather mosses have been reported to have higher decomposition rates relative to *Sphagnum* mosses (Lang et al. 2009) and so areas with higher abundance of feather mosses probably decompose faster resulting in a greater reduction in organic layer depth. The reduction in organic layer thickness associated with high feather moss abundance probably led to the exposure of favourable soil substrates (mesic and mineral soil), which is an important process in enhancing site productivity.

Mechanical site preparation techniques fundamentally differed in the way soils were disturbed. Consequently, T26 exposed more mineral soil than plow, but, no major differences between the site preparation techniques were observed for the exposure of mesic and humic layers. The mesic layer and mineral soil are considered good microsites for black spruce growth (Lafleur et al., 2011). However the high clay in the mineral soil of the Clay Belt results in desiccation of these substrates during dry periods or waterlogging during prolonged wet conditions (Lavoie et al. 2007) and it is therefore considered a bad growth substrate in this area. The insignificant differences between the techniques in exposing mesic layers thus indicate that both treatments were effective at creating good microsites for plant growth. The higher exposure of favourable soil layers should support vigorous regeneration of tree species. The results further demonstrate that feather mosses and hollow *Sphagnum* species facilitated the exposure of the mesic layer, an observation that could be attributed to the structure of these bryophytes. For instance, hollow *Sphagnum* species are easily disrupted because of the development of loose shoots on the forest floor (Gunnarson 2005). This re-enforces the importance of pre-disturbance conditions on post-disturbance outcomes.

Disruption of the organic layer by mechanical site preparation was expected to modify soil temperature and moisture with implications for decomposition. Mallik and Hu (1997) demonstrated that the mixing of the organic layer and mineral soil improves soil conditions that lead to an increase in microbial population. Despite the short time period (10 months) after mechanical site preparation, the rate of decomposition increased under the two mechanical site preparation techniques considered in this study, suggesting an improvement in soil conditions. The lack of substantial differences in decomposition rates between sites treated with the two techniques indicates that the trenches and hinges of T26 created a microclimate that promoted the activity of organic matter decomposing organisms similar to conditions created in plow treated sites. Although, an insignificant difference in the rate of decomposition was observed between treatments, there were major differences in the change in the concentrations of soil chemical properties. Plow caused a greater change in the concentrations of carbon, nitrogen and phosphorus compared to T26, probably because of the differences in disturbance strategy.

The greater change in the concentration of the different soil chemical properties in plow treated sites did not, however, subsequently influence the concentration of available nitrogen and phosphorus. This is probably because nitrogen might not have been mineralised in treated sites because of the short time period after MSP treatment. Although neither plow nor T26 had an impact on the availability of nitrogen, T26 sites seemed to have lower concentrations of available $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ than plow sites. The lower concentrations of available nitrogen in T26 sites might be related to the higher exposure of mineral soil, resulting in excessively increased N-mineralisation leading to nitrogen loss through leaching. In contrast, the concentration of available phosphorus was reduced at T26 treated sites. Reduction in nutrient concentration following site preparation has been reported by some earlier studies. For instance, Schmidt et al. (1996) found a reduction in the concentration of available nitrogen and phosphorus 15 months after harvest and site preparation in Alberta. The lower availability of nitrogen and phosphorus concentration is considered a negative impact of the T26 treatment on the productivity of the site.

2.6.2 Impact of mechanical site preparation on understory species

This study found that mechanical site preparation led to changes in the cover of mosses (*Ptilium crista-castrensis* and *Sphagnum* species), *Carex* spp. and *Vaccinium* spp. but did not substantially affect the cover of *K. angustifolia* and *R. groenlandicum*. T26 had little impact on bryophyte composition compared to plowing. The cover of feather mosses was initially reduced by harvesting, which changed the microclimate by exposing them directly to sunlight. Subsequently, higher disturbance severity associated with the plow, further reduced the cover of hollow *Sphagnum* species by a low percentage. In addition, there was a higher abundance of graminoids species in plow treated sites compared to T26 sites. This could be related to the differences in disturbance severity, with plow creating more disturbed substrates to support the establishment of early successional plants relative to T26. This agrees with the findings of Roberts and Zhu (2002) who observed higher cover of graminoids by the second year after

clear cutting with site preparation compared to only clear cutting in the Acadian forest region. Nevertheless, with the exception of *Vaccinum* spp., which were significantly reduced by T26, the cover of ericaceous shrubs (*K. angustifolia* and *R. groenlandicum*) did not respond to mechanical site preparation. These results were inconsistent with the findings of Prevost (1996) who observed that disk trenching negatively impacted the cover of *Kalmia* spp. in black spruce forests. This might be due to the differences in the depth of the organic layer. The organic layer depth is relatively thin, enabling the disks to penetrate deeper into the organic layer and destroy vegetative structures of *Kalmia* spp. However, in this study, the thick organic layer impacted negatively on the effectiveness of the machinery for ericaceous shrubs. This study revealed that plow, rather than disk trenching, is more appropriate in managing *Sphagnum* species and *Ptilium crista-castrensis* prone areas especially given that *Sphagnum* species and ericaceous shrubs are particularly undesirable as far as site productivity is concerned.

2.7 Management Implications

As the maintenance of site productivity is of primary concern to forest management, the use of mechanical site preparation technique over a large proportion of the harvested area resulted in the reduction in the depth of organic layer as well as the abundance of hollow *Sphagnum*. *Sphagnum* mosses produce recalcitrant litters that decompose slowly, this coupled with its high water retention ability, increases soil moisture and lowers soil temperature, inhibiting decomposition, which results in the accumulation of thick organic soil layers. The reduction in these two variables led to the creation of i) good regeneration seedbed and ii) favourable microsites to support tree growth. Also, there was substantial increase in the rate of decomposition in disturbed sites compared to harvest-only sites. Furthermore, considering that the reduction in organic layer depth, change in decomposition rate, and exposure of the different soil layers were similar for both treatments, management should consider further criteria e.g. cost implications and the creation microsites in selecting between the two

machineries for site preparation. Plow however, seems to be an important mechanical site preparation technique in terms of its effect on hollow *Sphagnum* species.

2.8 Conclusion

This study showed that initial organic layer depth should be considered when selecting a site preparation technique. Despite the thick organic layer in some sites, mechanical site preparation techniques were able to reduce organic layer thickness and expose favourable microsites. Additionally, regardless of MSP technique, disruption of the organic layer enhanced soil conditions, showing that both plow and disc trenching are appropriate tools in this regard. Furthermore on the Clay Belt, since an increase in the cover of *Sphagnum* mosses and ericaceous shrubs have detrimental effects on the growth of black spruce, MSP should be used to reduce these plant species and the plow was particularly effective at reducing hollow *Sphagnum* species compared to disk trenching (T26).

The impact of MSP techniques on understory composition (and cover) and the concentration of soil chemical properties were assessed ten (10) months after mechanical site preparation. These results should therefore be considered as short-term effects. In order to choose the appropriate technique in managing the Clay Belt, longer-term observations will be necessary to determine how these techniques influenced soil properties, plant growth (in terms of their height and diameter growth) and ericaceous shrub cover.

Acknowledgements

We would like to acknowledge Christine Allen, Peter Paul Rocheleau, Julie Arseneault and Samuel Lafleche for their assistance in the field, Serge Rousseau (of Canadian Forest Services) for laboratory assistance and Marc Mazerolle for his statistical advice. We also thank Tembec and the Ministry of Natural Resources, Quebec for their valuable partnership. Funding for this project was provided by the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management and NSERC cooperative partnership program with Tembec.

2.9 References

- Bergeron, J-F., Grondin, P. and Blouin, J. 1999. Rapport de classification écologique du sous-domaine bioclimatique de la pessière à mousses de l'ouest. Ministères des Ressources naturelles du Québec.
- Bergeron, Y., Gauthier, S., Flannigan, M. and Kafka, V. 2004. Fire regimes at the transition between mixed-wood and coniferous boreal forest in northwestern Quebec. *Ecology*. **85**: 1916-1932.
- Boateng, J.O., Heineman, J.L., McClarnon, J. and Bedford, L. 2006. Twenty year responses of white spruce to mechanical site preparation and early chemical release in the boreal region of northeastern British Columbia. *Canadian Journal of Forest Research*. **36**: 2386-2399.
- Boateng, J.O., Heineman, J.L., Bedford, L., Harper, G.J. and Nemecek, L.F.A. 2009. Long-term effects of site preparation and postplanting vegetation control on *Picea glauca* survival, growth and predicted yield in boreal British Columbia. *Scandinavian Journal of Forest Research*. **24**: 111-129.
- Bock, M. D. and Van Rees, K.C. J. 2002. Mechanical site preparation impacts on soil properties and vegetation communities in the Northwest Territories. *Canadian Journal of Forest Research*. **32**: 1381-1392.
- Bray, R.H. and Kurtz, L.T. 1945. Determination of total, organic, and available forms of phosphorus in soils. *Soil Science*. **59**: 39-46.
- Burnham, K.P. and Anderson, D.R. 2002. Model selection and multi-model inference: a practical information-theoretical approach. Second edition. Springer-Verlag, New York.
- Correll, R.L., Harch, B.D., Kirkby, C.A., O'Brien, K. and Pankhurst, C.E. 1997. Statistical analysis of reduction in tensile strength of cotton strips as a measure of soil microbial activity. *Journal of Microbiological Methods*. **31**: 9-17.
- de Groot, W.J., Pritchard, J. and Lynham, T.J. 2009. Forest floor fuel consumption and carbon emissions in Canadian boreal forest fires. *Canadian Journal of Forest Research*. **39**: 367-382.
- Environment Canada. 2009. Canadian climate normals 1971–2000. Available from <http://www.climate.weatheroffice.ec.gc.ca>.
- Fenton, N. J. and Bergeron, Y. 2011. Dynamic old-growth forests? A case study of boreal black spruce forest bryophytes. *Silva Fennica*. **45**: 983-994.

- Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems or landscapes. *Ecological Applications*. **3**: 202-205.
- Gunnarsson, U. 2005. Global patterns of Sphagnum productivity. *Journal of Bryology*. **27**: 269-279.
- Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y. and Kranabetter, J.M. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. *Silva Fennica*. **36**: 307-327.
- Harvey, B.D., Leduc, A., Gauthier, S. and Bergeron, Y. 2002. Stand-landscape integration in natural disturbance based management of the southern boreal forest. *Forest Ecology and Management*. **155**: 369-385.
- Hendershot, W.H., Lalande, H. and Duquette, M. 1993. Ion exchange and exchangeable cations. *In*: Carter, M. R. and Gregorich, E.G. 2008 (eds). *Soil sampling and methods of analysis*. Second edition. CRC Press, Boca Raton. p. 197-206.
- Hill, M.O., Latter, P.M., and Bancroft, G. 1985. A standard curve for inter-site comparison of cellulose degradation using cotton strip method. *Canadian Journal of Soil Science*. **65**: 609-619.
- Huang, W.Z. and Schoenau, J.J. 1997. Seasonal and spatial variation in soil nitrogen and phosphorus supply rates in the boreal aspen forest. *Canadian Journal of Soil Science*. **77**: 597-612.
- Korpilahti, E. and Kuuluvainen, T. (Eds) 2002. *Disturbance dynamics in boreal forests: defining the ecological basis of restoration and management of biodiversity*. *Silva Fennica*. **36**: 1-447.
- Krause, H.H and Ramlal, D. 1987. In situ nutrient extraction by resin from forested, clear-cut and site-prepared soil. *Canadian Journal of Soil Science*. **67**: 943-952.
- Lafleur, B., Pare, D., Fenton, N. and Bergeron, Y. 2010. Do harvest methods and soil type impact the regeneration and growth of black spruce stands in northwestern Québec. *Canadian Journal of Forest Research*. **40**: 1843-1851.
- Lafleur, B., Paré, D., Fenton, N.J. and Bergeron, Y. 2011. Growth of planted black spruce seedlings following mechanical site preparation in boreal forested peatlands with variable organic layer thickness: 5-years result. *Annals of Forest Science*. **68**: 1291-1302.
- Landres, P.B., Morgan, P. and Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Application*. **9**: 1179-1188.

- Lang, S., Cornelissen, J.H.C., Klahn, T., van Logtestijn, R.S.P., Broekman, R., Schweikert, W., and Aerts, R. 2009. An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. *Journal of Ecology*. 97: 886-900.
- Latter, P.M. and Howson, G. 1977. The use of cotton strips to indicate cellulose decomposition in the field. *Pedobiologia*. 17: 145-155.
- Latter, P.M. and Walton, D.W.H. 1988. The cotton strip assay for cellulose decomposition studies in soil: history of the assay and development. *In*: Harrison, A.F., Latter, P.M., Walton, D.W.H. (Eds.). *Cotton Strip Assay: An Index of Decomposition*. Institute of Terrestrial Ecology, Cumbria, UK. p. 7-10.
- Lavoie, M., Paré, D., Fenton, N., Groot, A. and Taylor, K. 2005. Paludification and management of forested peatlands in Canada: a literature review. *Environmental Review*. 13: 21-50.
- Lavoie, M., Paré, D. and Bergeron Y. 2007. Relationships between microsite type and the growth and nutrition of young black spruce on post-disturbed low-land black spruce sites in eastern Canada. *Canadian Journal of Forest Research*. 37: 62-73.
- MacKenzie, M.D. 1999. The effect of mechanical site preparation on soil properties, nutrient dynamics and crop-tree growth: tenth year results from two sites in northern British Columbia, M.Sc. Thesis, Department of Geography, Simon Fraser University, Burnaby, BC. p. 117.
- MacKenzie, M.D., Schmidt, M.G. and Bedford, L. 2005. Soil microclimate and nitrogen availability 10 years after mechanical site preparation in northern British Columbia. *Canadian Journal of Forest Research*. 35: 1854-1866.
- Mallik, A.U and Hu, D. 1997. Soil respiration following site preparation treatments in boreal mixedwood forest. *Forest Ecology and Management*. 97: 265-275.
- Mazerolle, M.J. 2013. AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c). RPackage, Version 1.33.
<http://cran.rproject.org/web/packages/AICcmodavg/index.html>.
- McInnis, B.G. and Roberts, M.R. 1994. The effects of full-tree and tree-length harvests on natural regeneration. *Northern Journal of Applied Forestry*. 11: 131-137.
- Prevost, M. 1997. Effects of scarification on seedbed coverage and natural regeneration after a group seed tree cutting in a black spruce (*Picea mariana*) stand. *Forest Ecology and Management*. 94: 219-231.

- Roberts, M.R., and Zhu, L. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous – deciduous forest in New Brunswick, Canada. *Forest Ecology and Management*. **155**: 17-31.
- R Development Core Team, 2012. nlme: linear and nonlinear mixed effects models. <http://cran.rproject.org/package=nlme>, R package version 2.15.3.
- Saucier, J.P., Robitaille, A., and Grondin, P. 2009. Cadre bioclimatique du Québec. In R. Doucet & M. Côté (Eds.), *Manuel de foresterie, second ed.* (p. 186-205). Québec, QC: Ordre des ingénieurs forestiers du Québec, Éditions Multimondes.
- Seymour, R.S. and Hunter, M.L. Jr. 1999. Principles of ecological forestry. In *Managing biodiversity in forest ecosystems. Edited by M.L. Hunter, Jr.* Cambridge University Press, Cambridge. p. 22-61.
- Shetler, G., Turetsky, M.R., Kane, E. and Kasischke, E. 2008. Sphagnum mosses limit total carbon consumption during fire in Alaskan black spruce forests. *Canadian Journal of Forest Research*. **38**: 2328-2336.
- Smith, E.P., Orvos, D.R. and Cairns, J.J. 1993. Impact Assessment using the Before-After-Control-Impact (BACI) model: concerns and comments. *Canadian Journal of Fisheries and Aquatic Sciences*. **50**: 627-637.
- Soil Classification Working Group. 1998. The Canadian system of soil classification. Third edition. Agriculture and Agri-Food Canada Publication 1646, NRC Research Press, Ottawa, Canada.
- Thiffault, N., Fenton, N. J., Munson, A. D., Hébert, F., Fournier, R. A., Valeria, O., Robert L. Bradley, R. L., Bergeron, Y., Grondin, P., Paré, D. and Joannis, G. 2013. Managing Understory Vegetation for Maintaining Productivity in Black Spruce Forests: A Synthesis within a Multi-Scale Research Model. *Forests*. **4**: 613-631.
- Treonis, A.M., Wall, D. H. and Virginia, R.A. 2002. Field and microcosm studies of decomposition and soil biota in a cold desert soil. *Ecosystems*. **5**: 159-170.
- van Groenigen, J.W., Mutters, C.S., Horwath, W.R. and van Kessel, C. 2003. NIR and DRIFT-MIR spectrometry of soils for predicting soil and crop parameters in a flooded field. *Plant and Soil* **250**: 155-165.
- Veal, M.W., Taylor, S. E., Rummer, R.B., and Raper, R.L. 2002. Evaluation of site preparation plow energy requirements. Council on Forest Engineering (COFE) Conference Proceedings: “A Global Perspective” Auburn, June 16-20.
- Vincent, J. and Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois, *Géographie physique et Quaternaire*. **31**: 357-372.

von der Gonna, M.A. 1992. Fundamentals of mechanical site preparation. Canada-B.C. Partnership Agreement on Forest Resource Development: FRDA II. Forestry Canada and B.C. Ministry of Forests, Victoria. FRDA Rep. No. 178.

White, L.L., Zak, D.R. and Barnes, B.V. 2004. Biomass accumulation and soil nitrogen availability in an 87-year-old *Populus grandidentata* chronosequence. *Forest Ecology and Management*. 191: 121–127.

Table 2.1: List of candidate models considered for the different dependent variables during model selection. The dependent variables were modelled as a function of the pre-disturbance condition (initial OL depth, initial understory composition). The “+” indicates that the parameter was included whilst “:” indicates the interaction between two variables.

Model names	Models
<i>Change in organic layer depth</i>	
Mod 1	Treatment+ OL (before)+ <i>Sphagnum</i> + feather mosses
Mod 2	Treatment+ OL (before)+ Treatment : OL (before)
Mod 3	OL (before)
Mod 4	Null
Mod 5	Treatment
Mod 6	<i>Sphagnum</i>
Mod 7	Treatment+ <i>Sphagnum</i> + Treatment: <i>Sphagnum</i>
Mod 8	Feather mosses
Mod 9	Treatment+ feather mosses+ Treatment: feather mosses
<i>Mesic layer exposure</i>	
Mod 1	Treatment + OL(before)+ <i>Sphagnum</i> + feather moss+ <i>K. angustifolia</i> + <i>R. groenlandicum</i> + <i>D. polysetum</i>
Mod 2	Treatment + feather moss + Treatment : feather moss
Mod 3	Feather moss + <i>D. polysetum</i>
Mod 4	Treatment + <i>Sphagnum</i> + Treatment : <i>Sphagnum</i>
Mod 5	Treatment
Mod 6	Treatment + <i>K. angustifolia</i> + <i>R. groenlandicum</i> + Treatment : <i>K. angustifolia</i> + Treatment : <i>R. groenlandicum</i>
Mod 7	Treatment + <i>D. polysetum</i> + Treatment : <i>D. polysetum</i> <i>K. angustifolia</i> + <i>R. groenlandicum</i>
Mod 8	<i>Sphagnum</i>
Mod 9	Treatment+ OL(before)+ Treatment : OL(before)
Mod 10	Null

Mod 11 OL(before)

Humic layer exposure

Mod 1 Treatment + OL(before)+ *Sphagnum* + feathermoss+ *K. angustifolia*
+ *R. groenlandicum* + *D. polysetum*

Mod 2 Treatment + feather moss + Treatment : feather moss

Mod 3 Feather moss + *D. polysetum*

Mod 4 Treatment + *Sphagnum* + Treatment : *Sphagnum*

Mod 5 Treatment

Mod 6 *Sphagnum*

Mod 7 Treatment+ OL(before)+ Treatment : OL(before)

Mod 8 Null

Mod 9 OL(before)

Mineral soil exposure

Mod 1 Treatment + OL(before)+ *Sphagnum* + feather moss+ *K. angustifolia*
+ *R. groenlandicum* + *D. polysetum*

Mod 2 Treatment + feather moss + Treatment : feather moss

Mod 3 Treatment + *Sphagnum* + Treatment : *Sphagnum*

Mod 4 Treatment

Mod 5 Treatment + *K. angustifolia* + *R. groenlandicum* + Treatment : *K. angustifolia* + Treatment : *R. groenlandicum*

Mod 6 *Sphagnum*

Mod 7 Treatment+ OL(before)+ Treatment : OL(before)

Mod 8 Null

Mod 9 OL(before)

Table 2.2: Post-hoc comparison of plow and T26 on disturbance severity (organic layer reduction, rate of decomposition and soil layer exposure).

Variable	Value	SE	t-value	p-value
Organic layer reduction	1.6	1.15	1.41	0.210
Rate of decomposition	-0.006	0.2	-0.03	0.980
Exposure of soil layers				
Mesic layer	0.03	0.18	0.16	0.870
Humic layer	-0.09	0.23	-0.41	0.700
Mineral soil	1.02	0.22	4.61	0.004

Table 2.3: Model averaged estimates for the exposure of soil layers, soil chemical properties in organic layers as well as soil nutrient availability. “:” indicates the interaction between two variables. 95% CI values that include zero have insignificant effects.

Variables	Substrate type	Variables	Estimate	SE	95% CI	
					lower limit	Upper limit
<i>Mesic layer</i>						
Plow			0.95	0.23	0.49	1.40
T26			0.97	0.22	0.53	1.40
<i>Humic layer</i>						
Plow			1.32	0.37	0.60	2.04
T26			1.13	0.36	0.42	1.84
<i>Mineral soil</i>						
Plow			1.32	0.37	0.60	2.04
T26			2.99	0.35	2.29	3.68

Plow: feathermoss			-0.02	0.03	-0.07	0.03	
T26 : feather moss			0.09	0.02	0.05	0.13	
<i>Soil properties</i>							
C_{total} (%)	Mesic	Plow	-14.76	5.56	-25.66	-3.85	
		T26	-0.34	5.26	-10.64	9.97	
		OL (before)	0.15	0.36	-0.55	0.85	
	Humic	Plow	5.12	10.09	-14.65	24.90	
		T26	5.14	10.59	-15.62	25.90	
		OL (before)	0.23	0.14	-0.05	0.5	
	N_{total} (%)	Mesic	Plow	-0.54	0.19	-0.91	-0.18
			T26	-0.1	0.18	-0.45	0.25
			OL (before)	0.001	0.003	-0.005	0.006
Humic		Plow	-0.11	0.2	-0.51	0.29	
		T26	0.22	0.21	-0.2	0.63	
		OL (before)	0.004	0.003	-0.003	0.01	
P (mg kg ⁻¹)		Mesic	Plow	-45.08	30.85	-105.55	15.38
			T26	14.18	29.07	-42.8	71.16
			OL (before)	1.09	1.5	-1.85	4.02
	Humic						

		Plow	0.06	27.38	-53.6	53.71
		T26	58.74	28.56	2.77	114.71
		OL (before)	-0.23	0.47	-1.16	0.69
<i>CEC (cmolkg⁻¹)</i>	Mesic	Plow	-23.78	8.58	-40.59	-6.97
		T26	3	8.08	-12.84	18.84
		OL (before)	-0.2	0.42	-0.67	0.97
	Humic	Plow	-11	18.83	-47.91	25.9
		T26	30.96	19.76	-7.78	69.7
		OL (before)	0.13	0.33	-0.52	0.77
<i>Available nutrients</i>	<i>NH₄ (mg/kg)</i>	Plow	-2.13	13.59	-28.76	24.5
		T26	-22.46	13.09	-48.12	3.2
<i>NO₃ (mg/kg)</i>	Plow	-51.28	204.22	-451.54	348.98	
	T26	-291.35	155.54	-596.2	13.5	
<i>P (mg/kg)</i>	Plow	2.32	10.0	-17.28	21.91	
	T26	-23.45	9.64	-42.34	-4.57	

Table 2.4: Summary of statistics for the logistic regressions of understory plant species' presence under MSP techniques.

Plant species	SP technique	Estimate	SE	P-value
<i>P. schreberi</i>	<u>Plow</u>	-0.55	0.22	0.01
	<u>T26</u>	-0.53	0.21	0.01

<i>P. crista-castrensis</i>	<u>Plow</u>	-1.15	0.35	0.001
	<u>T26</u>	-3.78	1.02	<0.001
<i>Sphagnum</i> (hollow)	<u>Plow</u>	0.92	0.37	0.01
	<u>T26</u>	-0.028	0.42	0.95
<i>Sphagnum</i> (hummock)	<u>Plow</u>	1.1	0.29	<0.001
	<u>T26</u>	-0.2	0.34	0.55
<i>K. angustifolia</i>	<u>Plow</u>	-0.12	0.3	0.7
	<u>T26</u>	-0.03	0.29	0.92
<i>R. groenlandicum</i>	<u>Plow</u>	0.1	0.25	0.69
	<u>T26</u>	0.17	0.24	0.48
<i>Vaccinium</i> sp.	<u>Plow</u>	-0.37	0.25	0.14
	<u>T26</u>	0.23	0.23	0.33
<i>Carex</i> sp.	<u>Plow</u>	0.57	0.25	0.019
	<u>T26</u>	0.51	0.24	0.035

Table 2.5: Post-hoc comparison of plow and T26 on the frequency of understory composition. Significant difference between MSP techniques on bryophyte effect.

Variable	Value	SE	p-value
<i>P. schreberi</i>	0.01	0.11	0.900
<i>Ptilium crista-castrensis</i>	-1.31	0.52	0.010
Hollow <i>Sphagnum</i>	-0.5	0.18	0.010
Hummock <i>Sphagnum</i>	-0.65	0.15	<0.001
Graminoids	-0.03	0.11	0.790

Table 2.6: Summary of statistics for model average estimates (with SE and CI) for understory community. MSP techniques had no significant effect on the cover of these understory vegetation, N=565.

Variable	Estimate	SE	95% CI	
			Lower limit	Upper limit
<i>P. schreberi</i>				
OL (before)	-0.16	0.09	-0.35	0.02
Plow	-2.78	7.86	-18.19	12.62
T26	6.72	7.79	-8.54	21.98
<i>Hollow Sphagnum</i>				
Plow	2.37	0.86	0.69	4.06
T26	1.12	0.85	-0.55	2.78
OL (before)	0.04	0.01	0.02	0.07
Plow : OL (before)	0.01	0.03	-0.06	0.07
T26 : OL (before)	0.03	0.04	-0.04	0.1
<i>Hummock Sphagnum</i>				
Plow	-0.55	1.29	-3.07	1.97
T26	0.97	1.27	-1.53	3.46
OL (before)	0.06	0.02	0.03	0.1
Plow: OL (before)	-0.11	0.04	-0.19	-0.02
T26 : OL (before)	0.0	0.05	-0.09	0.1
<i>Kalmia angustifolia</i>				
Plow	1.66	1.18	-0.65	3.97
T26	-0.22	1.17	-2.5	2.07
OL (before)	0	0.02	-0.04	0.03
Plow : OL (before)	-0.06	0.04	-0.14	0.03
T26 : OL (before)	-0.16	0.05	-0.25	-0.07
<i>Rhododendron groenlandicum</i>				
Plow	1.29	1.25	-1.17	3.75
T26	2.38	1.23	-0.03	4.8
OL (before)	0.09	0.03	0.04	0.14
Plow : OL (before)	-0.06	0.07	-0.2	0.07

T26 : OL (before)	0.09	0.07	-0.06	0.23
-------------------	------	------	-------	------



Figure 2.1: Map showing Clay Belt region of northwestern Quebec and northeastern Ontario. The location of the larger map in North America is indicated by the white box on the inset map.

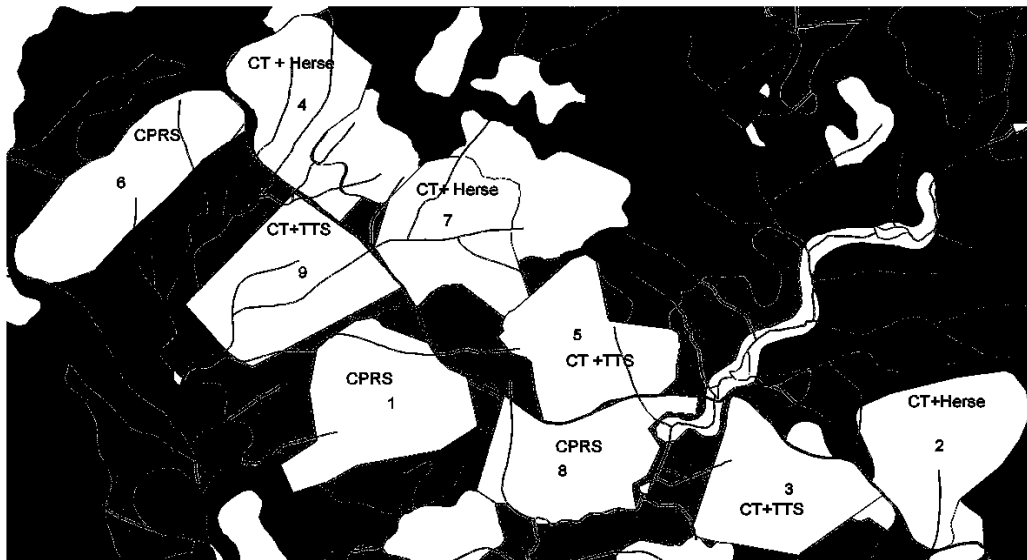


Figure 2.2: Map of study site indicating the nine blocks and treatments. “CT+Herse” indicates plow treatment; “CT+TTS” indicates disk trenching treatment and “CPRS” indicates harvest-only treatment.

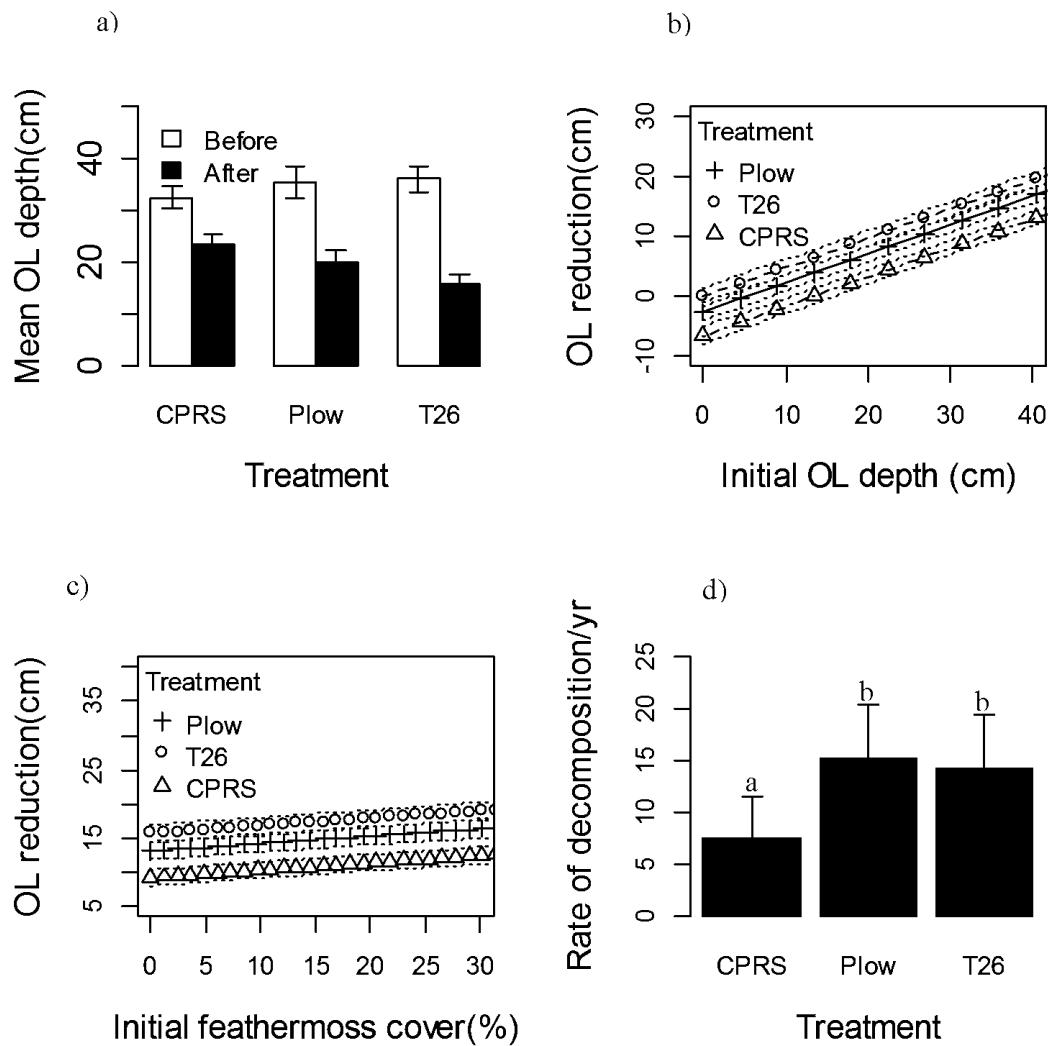


Figure 2.3: Effect of different silvicultural treatments and pre-harvest condition on organic layer. a) Comparison of mean (standard error) organic layer depth before and after treatments; b) Relationship between pre-harvest organic layer depth and organic layer reduction after treatments; c) Correlation between initial feather moss cover and organic layer reduction; d) Rate of decomposition and standard error under different treatments, $N=433$. Bars with different letters are significantly different, $p \leq 0.05$. “OL” indicates organic layer. In b and c, the dotted lines around each treatment represent their individual standard error.

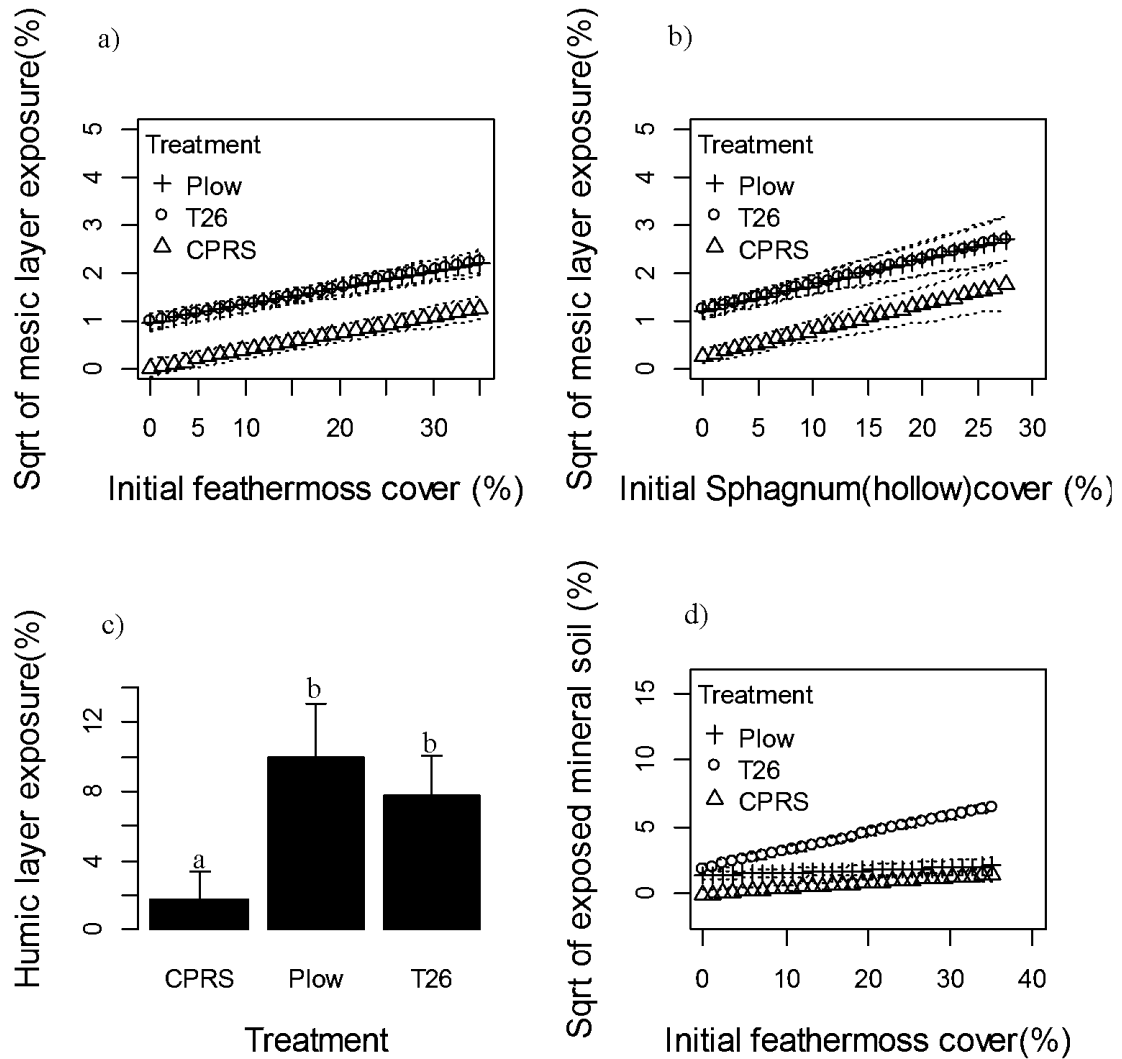


Figure 2.4: Relationship between the exposure of different soil layers following treatments and pre-harvest bryophyte species. a) Relationship between mesic layer exposure and pre-harvest feather moss cover after treatment; b) Correlation between mesic layer exposure and initial hollow *Sphagnum* cover in different treatments; c) Mean exposure (standard error) of humic layer in different silvicultural treatments. Bars with different letters are significantly different, $p \leq 0.05$ and d) Correlation between mineral soil exposure and initial feather moss cover, $N=565$. In a, b and d, the dotted lines represent the standard error.

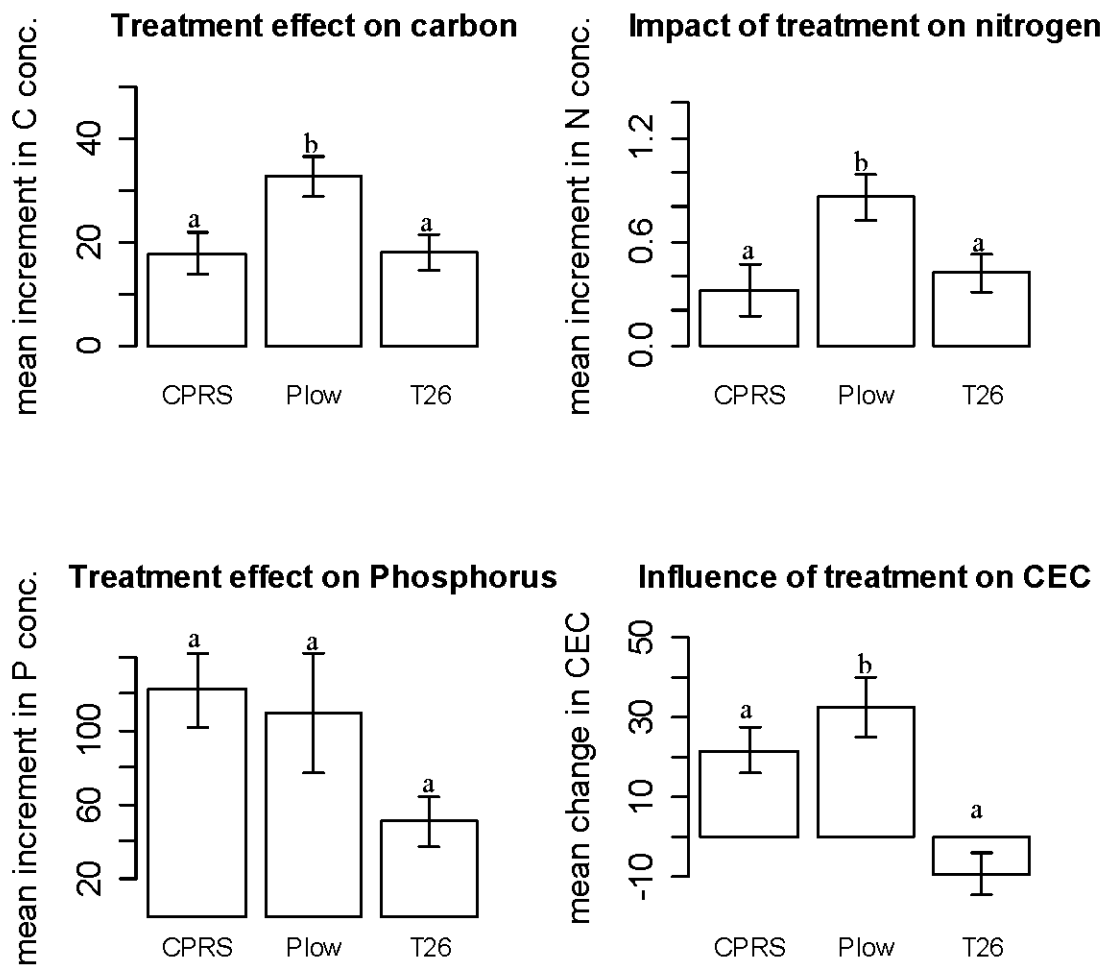


Figure 2.5: Mean change (standard error) in the total concentration of different elements in mesic layer under different treatments. Bars with different letters are significantly different, $p \leq 0.05$

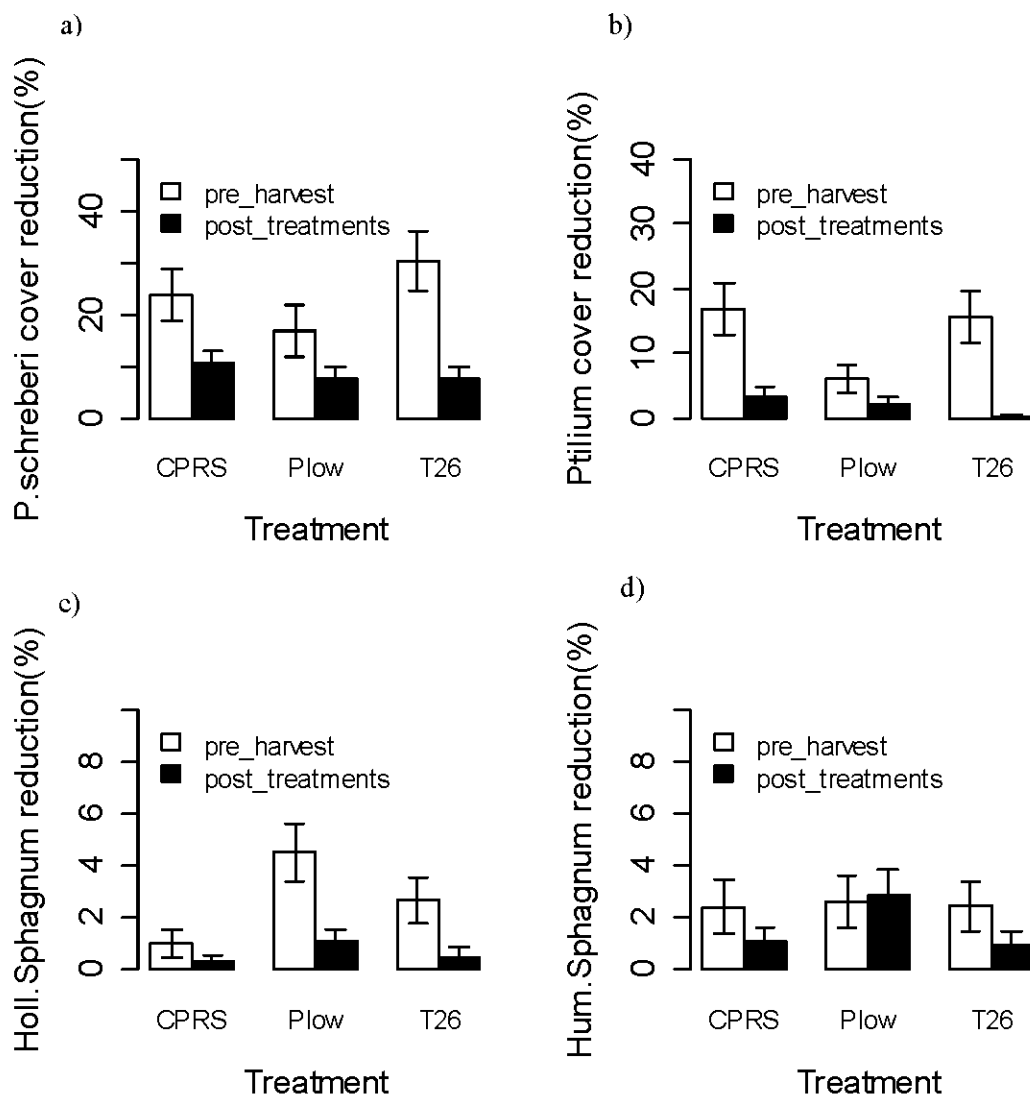


Figure 2.6: Mean (\pm SE) of the cover of bryophyte species before and after different treatments, N=452. "Holl." represents hollow whilst "Hum." represents hummock.

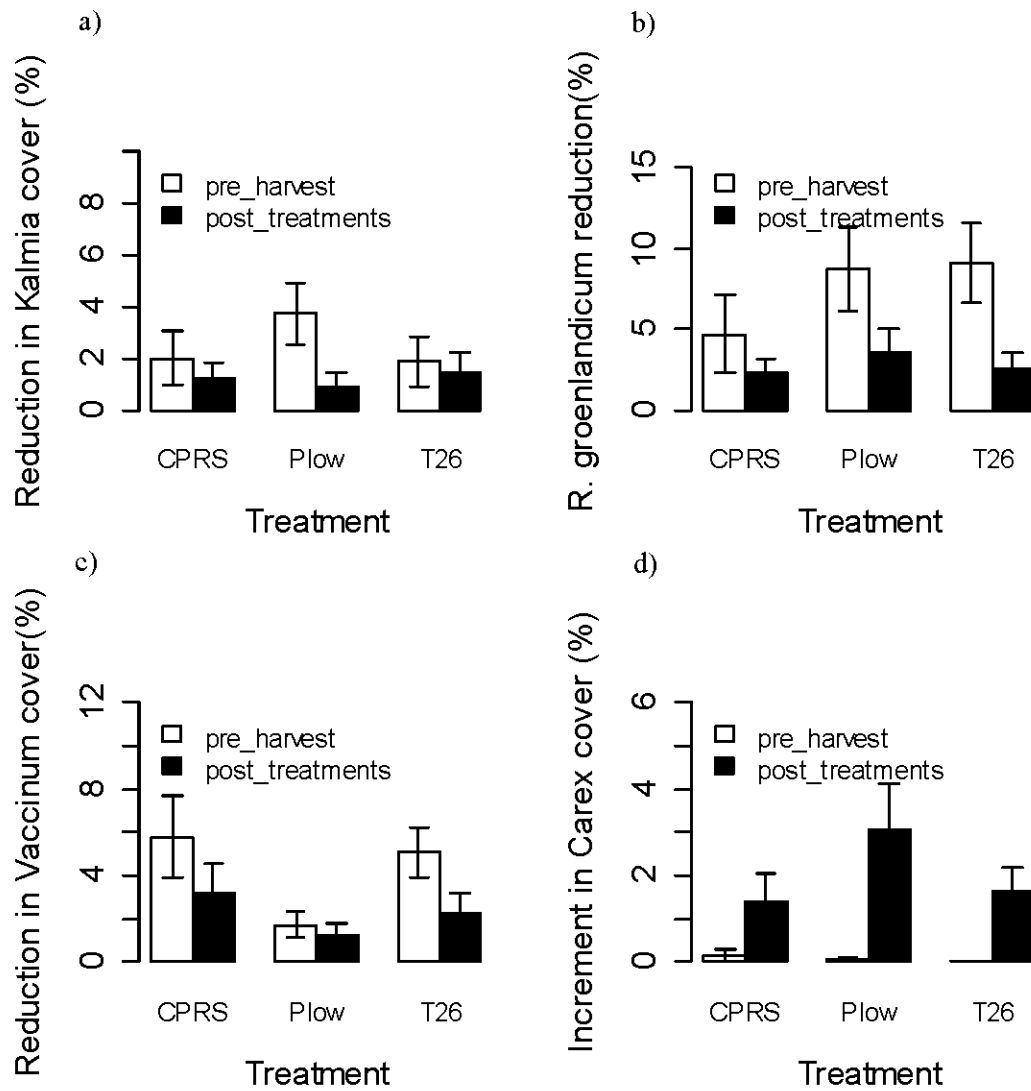


Figure 2.7: Mean (\pm SE) of different understory species cover before and after treatments, N=452.

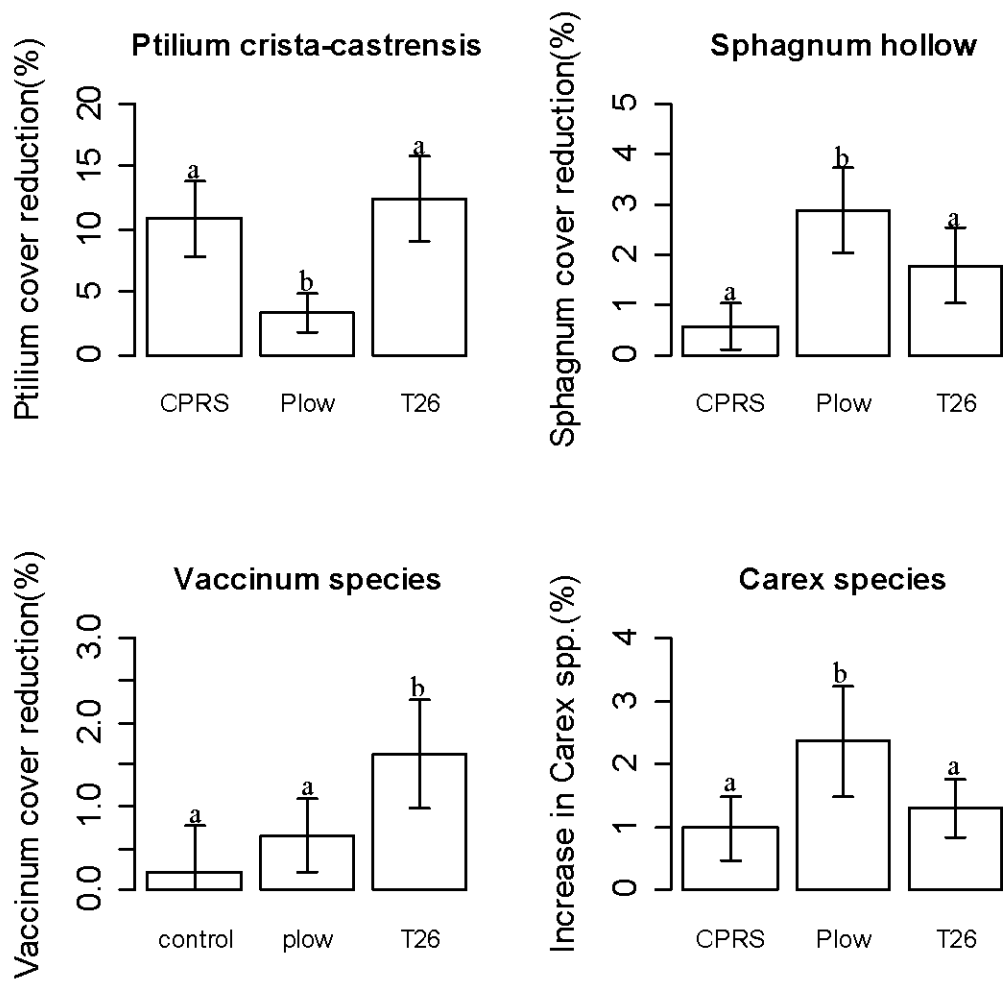


Figure 2.8: Mean change and standard error in the cover (%) of: a) *Ptilium crista-castrensis*; b) Hollow *Sphagnum* species; c) *Vaccinum* species and d) *Carex* species after MSP. Bars with different letters are significantly different, $p \leq 0.05$.

APPENDICES

Appendix A: Results from model selection for change in organic layer depth and the exposure of different soil substrates. Only models $\Delta AIC_c < 4$ are presented with the number of parameters included (K), the second-order Akaike information criterion (AIC_c) and Akaike weight, $N=565$.

Model names	Explanatory variables	No. of parameters (K)	AIC_c	Weight
<i>Change in organic layer depth</i>				
Mod 1	Treatment+ OL (before)+ Sphagnum+ feather moss	10	4130.67	1
<i>Mesic layer exposure</i>				
Mod 1	Treatment + OL(before)+ <i>Sphagnum</i> + feather moss+ <i>K. angustifolia</i> + <i>R. groenlandicum</i> + <i>D. polysetum</i>	13	2337.94	0.99
<i>Humic layer exposure</i>				
Mod 5	Treatment	6	2510.56	0.52
Mod 7	Treatment+ OL(before)+ Treatment : OL(before)	9	2513.82	0.1
Mod 4	Treatment + <i>Sphagnum</i> + Treatment : <i>Sphagnum</i>	12	2513.94	0.1
Mod 2	Treatment + feather moss + Treatment : feather moss	9	2514.56	0.07
<i>Mineral soil exposure</i>				
Mod 2	Treatment + feather moss + Treatment : feather moss	9	2711.27	1

Appendix B: Mean (\pm SE) of soil chemical properties in different substrates under different site preparation techniques over time.

Soil properties	Substrate type	Plow		T26		Control (CPRS)	
		Before	After	Before	After	Before	After
C_{total} (%)	Mesic	12.73 (4.08)	40.8 (2.11)	23.0 (3.13)	41.04 (1.65)	21.44 (4.61)	39.2 (2.66)
	Humic	15.66 (6.77)	27.03 (3.5)	19.97 (5.86)	23.34 (3.24)	5.96 (4.41)	22.46 (2.25)
N_{total} (%)	Mesic	0.36 (0.09)	1.15 (0.09)	0.64 (0.09)	1.05 (0.05)	0.74 (0.16)	1.06 (0.08)
	Humic	0.39 (0.12)	1.13 (0.09)	0.68 (0.16)	0.89 (0.08)	0.36 (0.17)	0.86 (0.07)
P ($mg\ kg^{-1}$)	Mesic	43.09 (16.11)	149.49 (25.98)	36.77 (7.27)	92.45 (7.47)	40.13 (9.38)	109.98 (13.99)
	Humic	27.0 (11.17)	136.38 (15.31)	32.89 (9.38)	95.25 (18.02)	19.63 (7.2)	141.47 (20.20)
CEC	Mesic	30.17 (2.19)	47.48 (6.56)	41.73 (4.44)	33.84 (2.42)	35.99 (3.23)	31.10 (4.0)
	Humic	30.78 (3.41)	63.53 (13.5)	39.97 (5.19)	29.65 (1.46)	27.24 (1.51)	48.99 (20.97)

Appendix C : Linear mixed models tested for factors affecting the change in the different soil chemical properties. Site was introduced into the model as random variable.

Model names	Explanatory variables	C		N		P		CEC	
		AICc	Wt	AICc	Wt	AICc	Wt	AICc	Wt
	<i>Mesic layer</i>								
Mod 1	Treatment	435.02	0.62	90.89	0.68	611.68	0.29	481.11	0.58

Mod 4	Null	436.07	0.27	93.43	0.19	610.59	0.50	482.35	0.31
Mod 3	OL (before)	438.92	0.10	95.78	0.06	612.42	0.20	484.59	0.10
Mod 2	Treatment*OL (before)	442.03	0.02	95.65	0.06	618.29	0.01	488.98	0.01
<i>Humic layer</i>									
Mod 1	Treatment	187.69	0.02	30.73	0.11	223.80	0.09	212.48	0.19
Mod 4	Null	181.03	0.62	26.9	0.74	220.23	0.53	209.98	0.63
Mod 3	OL (before)	182.42	0.32	30.04	0.15	220.85	0.39	212.51	0.18
Mod 2	Treatment*OL (before)	199.17	0.00	41.70	0.00	236.74	0.00	224.26	0.00

Appendix D: Summary of frequencies (presence or absence) of the different understory species before and after treatments. “Yes” indicates the presence of the species and “No” indicates species absence, N=565.

Understory species	Plow				T26				Control			
	Before		After		Before		After		Before		After	
	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No
<i>P. schreberi</i>	54	90	56	88	85	71	64	92	81	71	85	67
<i>P.crista-castrensis</i>	47	97	12	132	83	73	1	155	90	62	34	118
<i>Sphagnum</i> (hollow)	61	83	26	118	48	108	12	144	25	127	12	140
<i>Sphagnum</i> (hummock)	38	106	47	97	33	123	17	139	33	119	21	131
<i>Kalmia</i> <i>angustifolia</i>	44	100	24	120	24	132	28	128	27	125	28	124
<i>Rhododendron</i> <i>groenlandicum</i>	59	85	42	102	63	93	48	108	48	104	41	111
<i>Vaccinum sp.</i>	61	83	34	110	85	71	58	98	52	100	49	103
<i>Carex sp.</i>	5	139	54	90	2	154	56	100	4	148	38	114

Appendix E: Model selection results for understory species cover (feather mosses, Sphagnum species, shrubs and grasses). Plots and sites were introduced into the model as random component. The bolded values are the values for competing models from the candidate models, N=565.

Model names	Explanatory variables	AICc	Wt	AICc	Wt
			<i>P. schreberi</i>		<i>P. crista-cristensis</i>
Mod 3	Treatment + OL (before) + Treatment : OL(before)	5465.00	0.03	4961.24	0.69
Mod 2	OL (before)	5459.18	0.53	4965.55	0.08
Mod 4	Null	5460.04	0.35	4967.10	0.04
Mod 1	Treatment	5462.73	0.09	4963.81	0.19
			<i>Sphagnum</i> (hollow)		<i>Sphagnum</i> (hummock)
Mod 3	Treatment + OL (before) + Treatment : OL(before)	3371.67	0.33	3713.44	0.25
Mod 2	OL (before)	3370.31	0.64	3725.57	0.00
Mod 4	Null	3378.62	0.01	3722.82	0.00
Mod 1	Treatment	3377.05	0.02	3711.22	0.75
			<i>K. angustifolia</i>		<i>R. groenlandicum</i>
Mod 3	Treatment + OL (before) + Treatment : OL(before)	3603.57	0.83	4350.23	0.62
Mod 2	OL (before)	3609.94	0.03	4351.26	0.37
Mod 4	Null	3607.96	0.09	4358.95	0.01
Mod 1	Treatment	3609.42	0.04	4360.10	0.00
			<i>Vaccinium</i> species		<i>Carex</i> species
Mod 3	Treatment + OL (before) + Treatment : OL(before)	3944.31	0.07	3283.59	0.06
Mod 2	OL (before)	3943.16	0.12	3281.78	0.16
Mod 4	Null	3941.94	0.23	3281.12	0.22

Mod 1	Treatment	3940.11	0.57	3279.25	0.56
-------	-----------	---------	------	---------	------

CHAPITRE III

CONCLUSION GÉNÉRALE

Les feux de forêt, principale perturbation en forêt boréale, modifient considérablement les conditions de sol qui affectent la composition et la structure des peuplements forestiers. Les feux de forte sévérité, qui consomment la quasi-totalité de la couche organique, libèrent des nutriments de la couche organique pour les végétaux (Prescott et al. 2000) et augmentent ainsi la productivité forestière. À l'inverse, les feux peu sévères laissent une épaisse couche organique résiduelle qui limite l'accès au sol minéral aux semis nouvellement établis (Simard et al. 2007). Ces feux de faible sévérité sont susceptibles d'accélérer le processus de paludification. Toutefois, la diminution de la fréquence des feux dans les forêts de la pessière noire à mousses, observée au cours des 300 dernières années (Bergeron et al. 2004), a le potentiel de changer des écosystèmes forestiers productifs en sites improductifs par paludification. Des études antérieures ont suggéré que les pratiques de récolte actuelles (CPRS) sont de nature à favoriser la paludification due à une perturbation insuffisante du sol (Lavoie et al. 2005; Fenton et al. 2005). Dans une tentative de contrôle du processus de paludification et d'amélioration de la qualité du site, des études sur la sévérité des feux et les traitements sylvicoles ont suggéré que le brassage de la couche organique est nécessaire au maintien et à la restauration des peuplements sujets à la paludification (Fenton et al. 2005; Simard et al. 2007; Lafleur et al. 2011).

Dans ce contexte, ce projet avait pour principaux objectifs de 1) déterminer comment les conditions avant récolte ont influencé la sévérité de trois techniques sylvicoles, mais aussi de définir quelles techniques 2a) a réduit la profondeur de la couche organique ainsi que la couverture des espèces de sous-bois (en particulier les espèces de sphaignes et d'éricacées) et 2b) a exposé des couches de sol favorables et a augmenté la disponibilité des nutriments.

Les résultats ont montré que la réduction de l'épaisseur de la couche organique était positivement influencée par la profondeur de la couche organique avant récolte et la couverture en mousses. Une plus grande réduction de la couche organique sur les sites les plus épais indique l'influence de l'épaisseur de la couche organique avant perturbation sur l'épaisseur de la couche organique après perturbation. Ce résultat confirme les résultats d'études antérieures qui montraient que l'effet créé par une perturbation (telle que l'abattage ou le feu) dépend des conditions de site avant la perturbation, telles que le taux d'humidité et la profondeur de la couche organique (McInnis et Roberts 1994; Miyanishi et Johnson 2002). Des études précédentes qui ont examiné la sévérité de la perturbation par PMS sur la profondeur de couche organique et sur la composition du sous-couvert forestier ont utilisé la profondeur de la couche organique et le recouvrement de la végétation en sous-couvert comme mesure de la sévérité de la perturbation (Haeussler et al. 2002; Boateng et al. 2009). La présente étude est la première à évaluer les changements dans la profondeur de la couche organique et le recouvrement des espèces en sous-couvert comme mesure de la sévérité de la perturbation et à rapporter les effets des conditions avant perturbation sur l'efficacité des techniques sylvicoles.

L'épaisseur de la couche organique avant perturbation n'a pas été la seule condition initiale qui a influencé la sévérité de la perturbation. Une corrélation positive entre la réduction de profondeur de la couche organique et le recouvrement en mousses avant la récolte a été observée. Ceci pourrait être lié au taux de décomposition de ce type d'espèces de bryophytes. Des taux de décomposition plus élevés pour les mousses (Lang et al. 2009) auraient pu faciliter la réduction de l'épaisseur de la couche organique. Une plus forte réduction de l'épaisseur de la couche organique dans les sites traités par PMS a conduit à une plus grande exposition des couches de sol plus favorables, comparativement aux sites uniquement récoltés par CPRS. Malgré cela, l'exposition des différentes couches du sol suite aux différentes interventions sylvicoles a aussi été influencée par le recouvrement initial en mousses et en sphaignes de creux. Ceci pourrait être dû à leurs traits fonctionnels. Les mousses et les sphaignes de creux forment des tapis lâches sur le sol forestier (Shelter et al. 2008) qui pourrait facilement s'arracher à la moindre perturbation et exposer des couches sol plus favorables.

L'importante épaisseur de la couche organique dans les sites uniquement récoltés devrait tendre à réduire la productivité des peuplements à cause de l'inaccessibilité au sol minéral et aux nutriments pour les nouveaux semis établis (Fenton et al. 2005). De plus, puisque la qualité des microsites est un facteur majeur qui influence l'établissement et la croissance des arbres (Lavoie et al. 2007; Lafleur et al. 2010), la faible exposition des couches de sol favorables dans les sites uniquement récoltés indique que la proportion de microsites de grande qualité produits est faible, et ne permettra qu'un faible recrutement d'arbres comparé aux sites traités par PMS. En termes de création de microsites favorables (exposition du sol minéral, couches mésiques et humiques), nos résultats corroborent ceux de Lafleur et al. (2011) qui ont aussi rapporté une plus grande exposition de couches de sol favorable après l'application de techniques de PMS. En termes de restauration ou de maintien la productivité des peuplements d'épinette noire paludifiés, ce résultat supporte l'intégration de PMS aux pratiques d'aménagement forestier. En comparant les deux techniques, la herse forestière a perturbé une plus grande proportion de la surface récoltée que la T26, mais il n'y avait pas de différence significative dans leurs effets sur la réduction de l'épaisseur de la couche organique, et sur l'exposition des couches mésique et humique. Ce résultat suggère donc que l'une ou l'autre ces techniques de PMS pourraient être utilisées.

En forêt boréale, la croissance des arbres est influencée par la disponibilité des nutriments (Bonan et Shugart 1989). En seulement dix (10) mois après l'application des traitements de PMS, il y a eu une augmentation de l'activité microbienne du sol qui a conduit à une augmentation du taux de décomposition. Bien que la température et l'humidité du sol n'aient pas été directement mesurées dans cette étude, l'augmentation de la décomposition implique une sensible amélioration des conditions de température et d'humidité du sol. Wardle et al. (2004) ont fait des observations similaires sur les taux de décomposition après une perturbation du sol. Bien que le taux de décomposition n'était pas différent entre les deux techniques, les sites traités par la herse forestière semblaient avoir des taux de décomposition plus élevés, générant une plus grande variation dans la concentration en carbone, en azote, en phosphore et en CEC que les sites traités par la T26. Ceci s'explique parce que la herse forestière a engendré une perturbation du sol supérieure à la T26, en termes de superficie et de

stratégie de perturbation du sol (von der Gonna, 1992). Toutefois, les grands changements de concentration dans les propriétés chimiques du sol des sites traités par la herse forestière n'ont pas influencé la disponibilité du NH_4 , NH_3 et du phosphore. Ce résultat pourrait être dû au fait que la minéralisation de l'azote n'avait pas augmenté au moment de la collecte des données mais qu'elle l'aurait été probablement plus à un stade ultérieur de la composition de la couche organique. En revanche, la T26 a réduit de manière significative la disponibilité du phosphore. D'ailleurs, Schmidt et al. (1996) ont rapporté une baisse de concentration en phosphore disponible au cours de la saison de végétation suivant la préparation mécanique du site. Ces résultats suggèrent que dans des régions comme celle de la ceinture d'argile, qui sont sujettes à la paludification, la PMS est capable d'augmenter la température et l'humidité du sol, et de façon subséquente, le taux de décomposition, dans les couches organiques de surface comme dans les couches profondes.

La composition du couvert et du sous-couvert forestier influencent aussi fortement la régénération et la croissance de l'épinette noire en forêt boréale. La végétation de sous-couvert incluait certaines espèces d'éricacées (*Kalmia angustifolia* and *Rhododendron groenlandicum*) et de sphaignes. Les éricacées sont connues pour avoir des stratégies de régénération efficaces ainsi que des effets allélopathiques sur la croissance et l'établissement des semis d'arbres (Mallik 1995; Thiffault et al. 2013). L'augmentation du recouvrement en sphaignes limite la régénération des arbres en réduisant la température du sol et en restreignant l'activité des micro-organismes du sol. L'augmentation du recouvrement en éricacées et en sphaignes peut convertir des sites forestiers productifs en sites improductifs. Les résultats de cette étude suggèrent qu'entre les deux traitements les deux techniques de PMS, le traitement par la herse forestière a eu un effet plus préjudiciable sur la fréquence et l'abondance des sphaignes comparativement au traitement de la T26. Newmaster et Bell (2002) ont fait des observations similaires sur l'abondance des bryophytes. Bien que par rapport aux sites uniquement récoltés (CPRS), la PMS a engendré un brassage de la couche organique sur une large proportion de la superficie récoltée, du point de vue statistique, elle n'a pas significativement réduit le taux de recouvrement des éricacées. Ces résultats contredisent ceux de Prévost (1996) qui ont observé un effet significatif négatif de la PMS sur le taux de recouvrement de *Kalmia angustifolia* dans

la forêt boréale du Québec. Cette différence pourrait être due au fait que leur sites avaient une couche organique relativement mince par rapport aux sites de la présente étude, permettant aux disques de la machinerie de pénétrer plus profondément dans la couche organique et de détruire les organes reproducteurs des espèces de *Kalmia*. Ces résultats suggèrent que l'aménagement forestier dans la ceinture d'argile devrait favoriser l'utilisation de la herse forestière plutôt que la T26, à cause de son effet sur l'abondance des sphaignes. D'ailleurs, pour réduire le taux de recouvrement en éricacées dans la ceinture d'argile, des traitements plus sévères de PMS devraient être utilisés.

En conclusion, la production durable de bois est un objectif clé de l'aménagement forestier et il est nécessaire de maintenir la productivité d'un site afin d'atteindre cet objectif. La préparation mécanique du sol a été utilisée pour améliorer les conditions de sol dans la ceinture d'argile à des fins d'augmenter la productivité des sites. Bien que la période entre la préparation de terrain et la collecte des données ait été courte, les résultats de cette étude suggèrent que, indépendamment du type de traitement sylvicole utilisé, son efficacité sera affectée par la profondeur la couche organique avant traitement et par le taux de recouvrement des espèces de bryophytes. Toutefois, il n'y avait pas de différence entre les deux techniques de PMS, en termes d'effets sur la réduction de la couche organique et l'exposition de couches favorables du sol. Si un choix devait s'opérer entre ces deux techniques, au regard de la technique la plus appropriée pour l'aménagement dans la ceinture d'argile, la herse forestière devrait être plus utilisée que la T26. Ceci est dû à la capacité de la herse forestière à réduire le recouvrement en sphaignes, étant donné que ces espèces de bryophytes sont indésirables quand la productivité du site est concernée. Toutefois, ces résultats sont à considérer comme les effets des traitements à court terme. Par conséquent, les propriétés chimiques du sol, le taux de recouvrement des espèces du sous-couvert (en particulier la couverture en éricacées et en sphaignes) et la croissance des arbres devraient être suivis en continu sur un plus long terme.

BIBLIOGRAPHIE

- Attiwill, P.M., Turvey, N.D. et Adams, M.A. 1985. Effects of mound-cultivation (bedding) on concentration and conservation of nutrients in a sandy podzol. *Forest Ecology and Management*. **11**: 97-110.
- Attiwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management*. **63**: 247-300.
- Bergeron, Y. et Brian, H. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. *Forest Ecology and Management*. **92**: 235-242.
- Bergeron, Y., Gauthier, S., Flannigan, M. et Kafka, V. 2004. Fire regimes at the transition between mixed-wood and coniferous boreal forest in northwestern Quebec. *Ecology*. **85**: 1916-1932.
- Bock, M.D. et Van Rees, K.C.J. 2002. Mechanical site preparation impacts on soil properties and vegetation communities in the Northwest Territories. *Canadian Journal of Forest Research*. **32**: 1381-1392.
- Boateng, J.O., Heineman, J.L., Bedford, L., Harper, G.J. et Nemec, L.F.A., 2009. Long-term effects of site preparation and postplanting vegetation control on *Picea glauca* survival, growth and predicted yield in boreal British Columbia. *Scandinavian Journal of Forest Research*. **24**: 111-129.
- Bonan, G.B. et Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. *Annual Review of Ecological Systematics*. **20**: 1-28.
- Bradbury, S. 2004. Understory plant communities in boreal cutblocks with different sizes and numbers of residual tree patches. *Canadian Journal of Forest Research*. **34**: 1220-1227.
- Fenton, N., Lecomte, N., Legare, S. et Bergeron, Y. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. *Forest Ecology and Management*. **213**: 151-159.
- Fenton, N.J. et Bergeron, Y. 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. *Journal of Vegetation Science*. **17**: 65-76.
- Fenton, N.J. et Bergeron, Y. 2011. Dynamic old-growth forests? A case study of boreal black spruce forest bryophytes. *Silva Fennica*. **45**: 983-994.

- Frelich, L.E. et Reich, P.B. 1998. Disturbance severity and threshold responses in the boreal forest. *Conservation Ecology*. **2**: 7.
- Gauthier, S., Vaillancourt, M-A., Leduc, A., De Grand pré, L., Kneeshaw, D., Morin, H., Drapeau, P. and Bergeron, Y. 2009. Ecosystem management in the boreal forest. p. 256-266.
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. et Simard, M.-J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research*. **29**: 824-839.
- Gunnarsson, U. 2005. Global patterns of Sphagnum productivity. *Journal of Bryology*. **27**: 269-279.
- Haeussler, S., Bedford, L., Boateng, J.O. et MacKinnon, A. 1999. Plant community responses to mechanical site preparation in northern interior British Columbia. *Canadian Journal of Forest Research*. **29**: 1084-1100.
- Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y. et Kranabetter, J.M. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. *Silva Fennica*. **36**: 307-327.
- Haeussler, S. et Bergeron, Y. 2004. Range of variability in boreal aspen plant communities after wildfire and clear-cutting. *Canadian Journal of Forest Research*. **34**: 274-288.
- Johnson, E.A., Miyanishi, K. et Weir, J.M.H. 1998. Wildfires in the western Canadian boreal forest: Landscape patterns and ecosystem management. *Journal of Vegetation Science*. **9**: 603-610.
- Keenan, R. J. et Kimmins, J. P. 1993. The ecological effects of clear-cutting. *Environmental Reviews*. **1**: 121-144.
- Kimmins, J.P. 1994. Identifying key processes affecting long-term site productivity. *In*: Dyck, E.J., Cole, D.W. et Comerford, N.B. (eds). *Impacts of forest harvesting on long-term site productivity*. Chapman and Hall, New York. p. 119-150.
- Knops, J.M.H., Nash, T.H. et Schlesinger, W.H. 1996. The influence of epiphytic lichens on the nutrient cycling of an oak woodland. *Ecological Monographs*. **66**: 159-179.
- Lafleur, B., Paré, D., Fenton, N. et Bergeron, Y. 2010. Do harvest methods and soil type impact the regeneration and growth of black spruce stands in northwestern Québec. *Canadian Journal of Forest Research*. **40**: 1843-1851.
- Lafleur, B., Paré, D., Fenton, N.J. et Bergeron, Y. 2011. Growth of planted black spruce seedlings following mechanical site preparation in boreal forested peatlands with

- variable organic layer thickness: 5-years result. *Annals of Forest Science*. **68**: 1291-1302.
- Landres, P.B., Morgan, P. et Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Application*. **9**: 1179-1188.
- Lang, S., Cornelissen, J.H.C., Klahn, T., van Logtestijn, R.S.P., Broekman, R., Schweikert, W. et Aerts, R. 2009. An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. *Journal of Ecology*. **97**: 886-900.
- Lavoie, M., Paré, D., Fenton, N., Groot, A. et Taylor, K. 2005. Paludification and management of forested peatlands in Canada: a literature review. *Environmental Review*. **13**: 21-50.
- Lecomte, N., Simard, M. et Bergeron, Y. 2006. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Quebec, Canada. *Ecoscience*. **13**: 152-163.
- MacKenzie, M.D., Schmidt, M.G. et Bedford, L. 2005. Soil microclimate and nitrogen availability 10 years after mechanical site preparation in northern British Columbia. *Canadian Journal of Forest Research*. **35**: 1854-1866.
- Mallik, A.U. 1995. Conversion of temperate forests into heaths: Role of ecosystem disturbance and ericaceous plants. *Environmental Management*. **19**: 675-684.
- McInnis, B.G. and Roberts, M.R. 1994. The effects of full-tree and tree-length harvests on natural regeneration. *Northern Journal of Applied Forestry*. **11**: 131-137.
- McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T. et Woodley, S. 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environmental Review*. **9**: 223-260.
- Miyaniishi, K. et Johnson, E.A. 2002. Process and patterns of duff consumption in the mixed wood boreal forest. *Canadian Journal of Forest Research*. **32**: 1285-1295.
- Montero, J.A. 1994. Evaluation of mechanical site preparation impacts on physical soil properties of three boreal mixed-wood sites. MSc thesis. University of Alberta. Edmonton, AB.
- Munson, A.D., Margolis, H.A. et Brand, D.G. 1993. Intensive silvicultural treatment: impacts on soil fertility and planted conifer response. *Soil Science Society of America Journal*. **57**: 246-255.

- Newmaster, S.G. et Bell, F.W. 2002. The effects of silvicultural disturbances on cryptogam diversity in the boreal-mixed wood forest. *Canadian Journal of Forest Research*. **32**: 38-51
- Nguyen-Xuan, T., Bergeron, Y., Simard, D., Fyles, J.W. et Paré, D. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. *Canadian Journal of Forest Research*. **30**: 1353-1364.
- Nilsson, M.C. et Wardle, D.A. 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*. **3**: 421-428.
- Nordborg, F., Nilsson, U. et Örlander, G. 2003. Effects of different soil treatments on growth and net nitrogen uptake of newly planted *Picea abies* (L.) Karst. seedlings. *Forest Ecology and Management*. **180**: 571-582.
- Nyland, R.D. 1996. *Silviculture: Concepts and applications*. McGraw Hill, New York.
- Örlander, G., Gemmel, P. et Hunt, J. 1990. Site preparation: a Swedish overview. FRDA Report 105. B.C. Ministry of Forestry and Lands, Victoria, British Columbia.
- Örlander, G., Hallsby, G., Gemmel, P. et Wilhelmsson, C. 1998. Inverting improves establishment of *Pinus contorta* and *Picea abies*—10-year results from a site preparation trial in northern Sweden. *Scandinavian Journal of Forest Research*. **13**: 160-168.
- Payette, S. et Rochefort, L.(eds.) 2001. *Écologie des tourbières du Québec-Labrador*, Presse de l'Université Laval, Québec, Québec, Canada.
- Pickett, S.T.A., et White, P.S.(eds). 1985. Patch dynamics: a synthesis. *In: The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Fla. p. 371-383.
- Prescott, C.E., Maynard, D.G. et Laiho, R. 2000. Humus in northern forests: friend or foe? *Forest Ecology and Management*. **133**: 23-36.
- Prevost, M. 1997. Effects of scarification on seedbed coverage and natural regeneration after a group seed tree cutting in a black spruce (*Picea mariana*) stand. *Forest Ecology and Management*. **94**: 219-231.
- Querejeta, J., Roldan, A., Albadelejo, J. et Castillo, V. 2001. Soil water availability improved by site preparation in a *Pinus halepensis* afforestation under semi-arid climate. *Forest Ecology and Management*. **149**: 115-128.

- Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany*. **82**, 1273-1283.
- Roberts, M.R. 2007. A conceptual model to characterize disturbance severity in forest harvests. *Forest Ecology and Management*. **242**: 58–64.
- Rowe, J.S. et Scotter, G.W. 1973. Fire in the boreal forest. *Quaternary Research*. **3**: 444-464.
- Ryans, M. et Sutherland, B. 2001. Site preparation – mechanical. *In*: R.G. Wagner and S.J. Colombo (eds.). *Regenerating the Canadian Forest: Principles and Practice for Ontario*. Fitzhenry & Whiteside, Markham, ON. p. 177-199. .
- Rydin, H., Gunnarsson, U. et Sundberg, S. 2006. The role of *Sphagnum* in peatland development and persistence, in: *Boreal peatland ecosystems*, edited by: Wieder, R.K. et Vitt, D.H., *Ecological Studies Series*, Springer Verlag, Berlin. p. 47-65.
- Schmidt, M.G., Macdonald, S.E. et Rothwell, R.L., 1996. Impacts of harvesting and mechanical site preparation on soil chemical properties of mixed-wood boreal forest sites in Alberta. *Canadian Journal of Soil Science*. **76**: 531-540.
- Seymour, R.S. et Hunter, M.L., Jr. 1999. Principles of ecological forestry. *In*: *Managing biodiversity in forest ecosystems*. Edited by M.L. Hunter, Jr. Cambridge University Press, Cambridge. p. 22-61.
- Shetler, G., Turetsky, M.R., Kane, E. et Kasischke, E. 2008. Sphagnum mosses limit total carbon consumption during fire in Alaskan black spruce forests. *Canadian Journal of Forest Research*. **38**: 2328-2336.
- Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y. et Paré, D. 2007. Forest productivity decline caused by successional paludification of boreal soils. *Ecological Application*. **17**: 1619-1637.
- Sutherland, B.J. et Foreman, F.F. 1995. Guide to the use of mechanical site preparation equipment in northwestern Ontario. Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, Ont. NODA/NFP Report. 4113.
- Sutherland, B. et Foreman, F.F. 2000. Black spruce and vegetation response to chemical and mechanical site preparation on a boreal mixed wood site. *Canadian Journal of Forest Research*. **30**: 1561-1570.
- Sutton, R.F. 1993. Mounding site preparation: A review of European and North American experience. *New Forests*. **7**: 151-192.
- Thiffault, N., Fenton, N. J., Munson, A. D., Hébert, F., Fournier, R. A., Valeria, O., Robert L. Bradley, R. L., Bergeron, Y., Grondin, P., Paré, D. et Joanisse, G. 2013. Managing

Understory Vegetation for Maintaining Productivity in Black Spruce Forests: A Synthesis within a Multi-Scale Research Model. *Forests*. **4**: 613-631.

- Turetsky, M.R., Crow, S.E., Evans, R.J., Vitt, D.H. et Wieder, R.K. 2008. Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *Journal of Ecology*. **96**: 1297-1305.
- Van Cleve, K., Oliver, L. et Scilientner, R. 1983. Productivity and nutrient cycling in taiga forest ecosystems. *Canadian Journal of Forest Research*. **13**: 747-766.
- von der Gönna, M.A. 1992. Fundamentals of mechanical site preparation. Forestry Canada, Pacific Forestry Centre and B.C. Ministry of Forests, Victoria, B.C. Forest Resource Development Agreement Report. 178.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. et Wall, D.H. 2004. Ecological linkages between aboveground and belowground biota. *Science* **304**: 1629-1633.
- Wardle, D.A. et Zackrisson, O. 2005. Effects of species and functional group loss on island ecosystem properties. *Nature*. **435**: 806–810.
- Wardle, D.A. 2009. Aboveground and belowground consequences of long-term forest retrogression in the timeframe of millennia and beyond. *In: Old-Growth Forests*. Springer Berlin Heidelberg. p. 193-209.
- Whittle, C.A., Duchesne, L.C. et Needham, T. 1997. The impact of broadcast burning and fire severity on species composition and abundance of surface vegetation in a jack pine (*Pinus banksiana*) clear-cut. *Forest Ecology and Management*. **94**: 141-148.