UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

RÔLE DE LA STRATE DES MOUSSES ET LICHENS DANS L'ÉTABLISSEMENT ET LE MAINTIEN DE MILIEUX OUVERTS STABLES EN FORÊT BORÉALE

THÈSE
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AVANT-PROPOS

Le corps de cette thèse est composé de cinq articles scientifiques rédigés en anglais et publiés ou destinés à la publication dans des journaux avec comité de lecture. La thèse comporte également une introduction et une conclusion générales rédigées en français.

Chapitre II. Pacé M., Fenton N.J., Paré D. & Bergeron Y. 2017. Ground layer composition affects tree fine root biomass and soil nutrient availability in jack pine and black spruce forests under extreme drainage conditions. *Canadian Journal of Forest Research*, 47:433-444.

Chapitre III. Pacé M., Fenton N.J., Paré D., Stefani F.O.P., Massicotte H.B., Tackaberry L.E. & Bergeron Y. Lichens contribute to open woodland stability in the boreal forest through detrimental effects on pine growth and root ectomycorrhizal status. Article en préparation pour soumission à *Journal of Vegetation Science*.

Chapitre IV. Pacé M., Fenton N.J., Paré D. & Bergeron Y. Differential effects of feather mosses and *Sphagnum* spp. on black spruce germination and growth. Article en préparation pour soumission à *Forest Ecology and Management.*

Chapitre V. Pacé M., Fenton N.J., Paré D. & Bergeron Y. Differential effects of lichen, *Sphagnum* spp. and feather moss leachates on jack pine and black spruce growth. Article en préparation pour soumission à *Plant and Soil.*

Chapitre VI. Pacé M., Barrette M., Fenton N.J., Paré D. & Bergeron Y. Ground layer composition may limit the positive impact of precommercial thinning on boreal stand productivity. Article accepté pour publication dans *Forest Science*.

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LISTE DES ABRÉVIATIONS, SIGLES ET ACRONYMES

AICc	Corrected Aikake information criterion
A.I.D.	Azote inorganique dissous
BA	Basal area
CEF	Centre d'étude de la forêt
CRSNG	Conseil de recherches en sciences naturelles et en génie
DBH/dbh	Diameter at breast height
Dens	Density
Df	Degree of freedom
dNTP	Deoxynucleotide
D.I.N.	Dissolved inorganic nitrogen
DRF	Direction de la recherche forestière
EPC	Eclaircie pré-commerciale
FRQNT	Fonds de recherche du Québec – Nature et technologies
HPLC	High performance liquid chromatography
ICP	Inductively coupled plasma
IRF	Institut de recherche sur les forêts
IRME	Institut de recherche en mines et environnement
ITS	Internal transcribed spacer
JP	Jack pine
MCF	Modélisation de la complexité de la forêt

PCR	Polymerase chain reaction
MFFP	Ministère des forêts, de la faune et des parcs du Québec
MRNF	Ministère des ressources naturelles et de la faune
MT	Merchantable trees
NCBI	National center for biotechnology information
NSERC	Natural science and engineering research council of Canada
OES	Optical emission spectrometer
OTU	Operational taxonomic unit
PCT	Precommercial thinning
SE	Standard error
TEI	Thinning efficiency index
UNBC	University of Northern British Columbia
Ø	Diameter

RÉSUMÉ

En forêt boréale, les accidents de régénération peuvent mener à l'établissement de deux types de milieux ouverts stables : des landes à lichens sur les sites à drainage excessif et des tourbières à sphaignes sur les sites sujets à l'entourbement. Dans les deux cas, l'ouverture à long-terme de la station forestière s'accompagne d'une modification de la composition de la strate des mousses et lichens. Les mousses hypnacées (e.g. *Pleurozium schreberi* (Brid.) Mitt.) sont remplacées par les lichens (*Cladonia* spp.) sur les sites fortement drainés, par les sphaignes (*Sphagnum* spp.) sur les sites faiblement drainés.

Dans la mesure où elle affecte les conditions physico-chimiques et biologiques du sol forestier, la composition de la strate des mousses et lichens contribue à la structuration de la communauté végétale forestière par la facilitation ou non de la régénération des plantes vasculaires. Le rôle de la strate des mousses et lichens dans le déficit de régénération menant à l'établissement et/ou au maintien de milieux ouverts stables est souvent suggéré bien que peu démontré expérimentalement, et les mécanismes sous-jacents restent à identifier. Cette thèse vise à (i) déterminer les effets différentiels des mousses hypnacées, des lichens et des sphaignes sur la régénération et les conditions de croissance du pin gris (*Pinus banksiana* Lamb.) et de l'épinette noire (*Picea mariana* [Mill.] B.S.P.), (ii) identifier les mécanismes à l'origine de ces effets, et (iii) évaluer les risques d'accidents de régénération liés à l'ouverture du couvert forestier par éclaircie pré-commerciale.

Comparé à l'absence de couvert au sol ou à la présence d'un couvert de mousses hypnacées, les lichens ont inhibé la croissance du pin gris à chacun des stades de développement analysés, c.-à-d. la croissance des plantules (0-6 mois), la croissance des jeunes plants (2 à 3 ans), ainsi que le développement racinaire fin d'arbres adultes (20-40 ans). D'après nos résultats, les effets du lichen sur la croissance du pin gris seraient liés non seulement à une disponibilité moindre des nutriments dans le sol forestier, mais aussi à l'existence d'interférences chimiques plus directes *via* l'émission de substances dans la solution du sol. La présence de lichens était également associée à une mycorhization moindre des racines de plantules, ce qui suggère un effet négatif des lichens sur la capacité du pin gris à prélever les éléments nutritifs dans le sol.

Nos résultats confirment que les sphaignes affectent moins l'établissement que la croissance de l'épinette noire. Bien que le défaut de croissance associé à la présence de sphaignes soit principalement lié à l'accumulation à long-terme d'une épaisse couche organique au sol, nos résultats indiquent qu'un couvert peu épais de sphaignes peut également avoir des effets à court-terme sur la disponibilité des nutriments et donc limiter le potentiel de croissance d'un peuplement forestier.

Compte-tenu des effets contrastés des différents types de couvert au sol sur la germination et la croissance ligneuse, il parait tout à fait probable que le remplacement des mousses hypnacées par les lichens ou les sphaignes en cas d'ouverture du couvert forestier contribue à la dégradation des conditions de croissance du pin gris et de l'épinette noire. Nos résultats supportent donc l'hypothèse selon laquelle les changements qui s'opèrent dans la strate des mousses et lichens constituent un moteur de l'établissement et de la stabilisation des milieux ouverts en forêt boréale, en intervenant comme un facteur aggravant du déficit de régénération.

Les pratiques sylvicoles qui ouvrent le couvert forestier, telles que l'éclaircie pré-commerciale (EPC), sont susceptibles dans certaines conditions de favoriser l'expansion des lichens ou des sphaignes aux dépens des mousses hypnacées. Etant données les répercussions négatives de ces changements de composition sur la croissance ligneuse, nos résultats suggèrent que les sites fortement drainés à lichens et les sites à drainage lent avec un fort couvert initial en sphaignes ne devraient pas être ciblés dans la mesure où ils sont moins enclins à répondre favorablement à l'EPC et plus à risque de transiter vers un état de clairière ouverte stable. En améliorant notre compréhension des mécanismes sous-jacents aux effets des lichens et des sphaignes sur la croissance des arbres, les résultats de cette thèse offrent également des pistes intéressantes pour l'élaboration de techniques de restauration de la productivité forestière. Ils suggèrent notamment que la plantation et/ou l'ensemencement à forte densité contribuent à améliorer les conditions de croissance ligneuse en favorisant une refermeture rapide du couvert forestier.

Mots-clés : Lichen, mousse, régénération, pin gris, épinette noire.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 La strate des mousses et lichens dans les écosystèmes forestiers boréaux

En forêt boréale, le parterre forestier est principalement dominé par les mousses et les lichens terricoles. Ces organismes non vasculaires, bien que petits par la taille, sont susceptibles d'avoir des effets considérables sur le fonctionnement de l'écosystème en participant notamment à la structuration de la communauté forestière.

1.1.1 Particularités écologiques des mousses et des lichens terricoles

Dans le cadre de cette thèse, nous utiliserons le terme commun de mousse comme un synonyme de bryophyte, bien que taxonomiquement, le groupe des bryophytes *lato sensu* ne comprend pas uniquement le phylum des mousses mais également celui des Hépatiques et des Anthocérotes (Glime, 2013). Les bryophytes sont des organismes poïkilohydriques, c.-à-d. leur état d'hydratation dépend directement du taux d'humidité associé à leur environnement direct. De cette particularité nait la nécessité de développer une grande résistance à la dessiccation chez ces organismes qui restent dépendants de l'eau pour l'essentiel de leur métabolisme ainsi que pour leur reproduction. Les bryophytes étant dépourvues de trachéides, le mouvement de l'eau à l'interne y est plus lent et limité que chez les végétaux vasculaires. A ceci s'ajoute l'absence de racines qui ne leur permet pas une acquisition efficace de l'eau contenue dans le sol. Les rhizoïdes non-vasculaires présents chez la plupart des bryophytes sont principalement utiles au support et à l'acquisition des nutriments (Glime, 2013). Ils aident également à limiter la vitesse de dessiccation de la plante en cas de réduction de l'humidité aérienne ambiante (Glime, 2013), dans la mesure où ces organes sont situés sous la surface du sol et bénéficient d'un effet d'isolation thermique. Les bryophytes, qui se distinguent également des autres végétaux terrestres par la dominance de leur stade gamétophytique, forment un groupe d'une grande diversité spécifique largement distribué à l'échelle mondiale (Glime, 2013). Parmi les types de mousses présents dans la forêt boréale canadienne, deux seront distingués par la suite du fait de leurs particularités et de leurs effets contrastés sur le fonctionnement de l'écosystème forestier : le groupe des mousses hypnacées (dont la plus répandue en forêt boréale est *Pleurozium schreberi* (Brid.) Mitt.) et le groupe des sphaignes (*Sphagnum* spp.).

Les lichens terricoles du genre Cladonia, également connus sous le nom francisé de *cladonies*, sont très répandus en forêt boréale où ils forment des tapis de densité et d'épaisseur variables, notamment sur les sols forestiers bien drainés (Haughian and Burton, 2015). Bien que la taille et le port de ces organismes dans le tapis forestier leur donnent des allures de mousses, leurs caractéristiques physiologiques et leur origine taxonomique sont bien différentes de celles des végétaux. En effet, les cladonies sont des lichens, c.-à-d. des champignons en association symbiotique avec un ou plusieurs photobiontes, généralement des algues ou des cyanobactéries (Honegger, 1993 ; Crittenden, 2000 ; Spribille et al., 2016). Comme les bryophytes, les lichens terricoles sont poikilohydriques. Ils sont donc métaboliquement inactifs en cas de sécheresse, leur activité photosynthétique étant restreinte à des périodes intermittentes d'humidité suffisante (Crittenden, 2000). Les lichens terricoles se distinguent de la vaste majorité des autres lichens par leur croissance apicale et leur faible ancrage au substrat (Crittenden, 2000 ; Kytöviita et Crittenden, 2007). En vieillissant, la base du thalle qui devient sénescente continue de servir de support physique au développement vertical de la partie supérieure vivante du thalle. Ainsi, les tapis vieillissants de lichens terricoles sont constitués d'une couche supérieure vivante basée sur une assise inférieure de biomasse morte plus ou moins profonde (Crittenden, 2000). Ce caractère est d'ailleurs partagé avec plusieurs groupes de bryophytes qui tendent eux aussi à croître sur leurs propres nécromasses (Glime, 2013). Les lichens sont capables de se reproduire de manière sexuée et asexuée (mycobionte uniquement), ainsi que par fragmentation du thalle (Crittenden, 2000). La reproduction par fragmentation permet de conserver l'association entre les deux partenaires symbiotiques, c.-à-d. mycobionte et photobionte.

1.1.2 Influence de la strate des mousses et lichens sur les processus écosystémiques

La composition de la strate des mousses et lichens influence la dynamique du carbone en forêt boréale (Turetsky, 2003 ; Cornelissen et al., 2007), du fait de ses effets sur la productivité primaire (DeLucia et al., 2003 ; Bond-Lamberty et Gower, 2007) et la décomposition (Lang et al., 2009 ; Fenton et al., 2010). Par exemple, le remplacement des mousses hypnacées par les sphaignes tend à modifier l'équilibre entre productivité primaire et décomposition, et donc à favoriser l'accumulation progressive d'une épaisse couche organique sur le sol forestier (Fenton et al., 2005 ; Lavoie et al., 2005 ; Fenton et al., 2010). Le taux de décomposition des lichens tend quant à lui à être plus grand que celui des bryophytes (Lang et al., 2009). La couche de matière organique associée à ce type de couvert au sol est en général moins profonde que celle associée à un couvert de bryophytes (Haughian et Burton, 2014). La composition et la structure de la strate des mousses et lichens peut avoir des répercussions importantes sur les propriétés physico-chimiques du sol forestier (Turetsky, 2003 ; Cornelissen et al., 2007), dont, entre autres, le pH (Lavoie et al., 2005), l'humidité (Fleming et Mossa, 1994 ; Lafleur et Schreader, 1994), la température (Soudzilovskaia et al., 2013 ; Kayes, 2016) et l'oxygénation (Lavoie et al., 2005 ; Fenton et al., 2006). Ces modifications vont avoir un impact important sur la composition et l'activité des communautés microbiennes (Ohtonen et Väre, 1998 ; Sedia et Ehrenfeld, 2003 ; Lavoie et al., 2005) et donc sur la décomposition de la matière organique et la minéralisation des nutriments (Dioumaeva et al., 2003 ; Sedia et Ehrenfeld, 2006 ; Cornelissen et al., 2007). En limitant les amplitudes de variations thermiques du sol forestier et la fréquence des évènements de gel-dégel au cours de la saison, la présence d'un tapis muscinal intervient comme un mécanisme important de régulation de l'activité microbienne (Soudzilovskaia et al., 2010, 2013). Les lichens, dont l'effet de tampon thermique est moindre que celui des mousses hypnacées (Kayes, 2016), sont également connus pour réduire la température du sol et l'activité microbienne *via* leur forte réflectance des rayonnements solaires (Kershaw et Field, 1975 ; Bernier et al., 2011). La rétention d’eau par certaines mousses telles que la sphaigne peut également avoir des répercussions importantes sur l’activité microbienne et la décomposition (Lavoie et al., 2005), notamment lorsque la température est en-dessous du point de congélation (Dioumaeva et al., 2003).

La strate des mousses et lichens est un acteur important de la dynamique de l’azote en forêt boréale. Dans les peuplements matures où l’azote est particulièrement limitant, la fixation du diazote atmosphérique par plusieurs espèces de mousses entretenant une relation symbiotique avec des cyanobactéries constitue une part non négligeable du flux entrant d’azote dans l’écosystème (Cornelissen et al., 2007 ; Zackrisson et al., 2009 ; Stuiver et al., 2015). Dans certaines forêts, ce flux peut aller jusqu’à 2 kg N/ha/an et égaler la quantité d’azote provenant des dépôts atmosphériques (Zackrisson et al., 2009). Parmi les mousses concernées, on compte *Pleurozium schreberi*, espèce largement répandue en forêt boréale, ainsi que les genres *Hylocomium* et *Sphagnum*. La fixation de l’azote par les mousses est utilisée en complément des autres apports (principalement les dépôts atmosphériques) et dépend de la disponibilité de cet élément dans le milieu environnant. Certains lichens terricoles, dont *Stereocaulon* spp., sont également capables de fixer l’azote atmosphérique (Crittenden, 2000).

Les mousses et lichens produisent une litière généralement pauvre en nutriments et peu décomposable (Lang et al., 2009), en raison notamment de leur forte capacité à recycler l’azote de manière interne (Crittenden, 2000 ; Lindo et Gonzalez, 2010). Ainsi, ils ont pour effet d’immobiliser les éléments nutritifs, dont l’azote, en les rendant moins accessibles pour les autres plantes (Startsev et Lieffers, 2006 ; Augusto et al., 2015). Cet effet est favorisé par la formation d’un tapis continu à l’interface sol-atmosphère qui permet l’interception et la séquestration par les mousses et lichens des élements nutritifs provenant des dépôts solides atmosphériques (Crittenden, 2000 ; Liu et al., 2013). La présence de sites d’échanges très actifs au niveau des feuilles de mousse favorise la fixation des nutriments (Glime, 2017a, b). Ces derniers sont ensuite stockés à différents niveaux de la plante, fixés sur des membranes, à l’intérieur des parois végétales, ou bien stockés dans les vacuoles (Glime, 2017c). Les éléments prisonniers des tissus muscinaux ou lichéniques (N, P, K, Ca, Mg etc.) ne sont plus disponibles pour la végétation avoisinante à moins d'être remis en circulation par le processus de décomposition. Chapin et al. (1987) ont également mis en évidence le rôle essentiel des mousses dans l'acquisition et l'accumulation du phosphore. La capacité des sphaignes et des mousses hypnacées à assimiler cet élément par transport actif étant bien plus grande que celles des racines fines d'épinette (*Picea* spp.), son transfert depuis la litière muscinale vers les arbres *via* les hyphes mycorhiziens constituerait une source importante de phosphore pour les arbres (Chapin et al., 1987).

1.1.3 La strate des mousses et lichens structure la communauté végétale forestière

Compte-tenu de ses effets sur les conditions physico-chimiques et biologiques du sol forestier, la composition de la strate des mousses et lichens joue un rôle clé dans la structuration de la communauté végétale forestière en devenir *via* différents niveaux de facilitation et/ou d'inhibition de la régénération des plantes vasculaires (Malmer et al., 2003 ; Nilsson et Wardle, 2005 ; Gornall et al., 2011 ; Turetsky et al., 2012). En effet, les caractéristiques de la végétation au sol déterminent la disponibilité des microsites favorables à la germination (Ohlson et Zackrisson, 1992 ; Groot et Adams, 1994 ; Camill et al., 2010 ; Soudzilovskaia et al., 2010) et les conditions de croissance des jeunes arbres (Mallik, 2003 ; Lavoie et al., 2007a, 2007b ; Thiffault et al., 2013 ; Kayes, 2016). Les effets de la strate des mousses et lichens peuvent être positifs ou négatifs pour les plantes vasculaires voisines (Cornelissen et al., 2007 ; Soudzilovskaia et al., 2010), dépendamment notamment de l'épaisseur du tapis muscinal (Gornall et al., 2011) ou lichénique. Par exemple, une strate muscinale d'épaisseur modérée (10 - 20 cm) tend à maintenir une humidité favorable au développement des plantes vasculaires (Hesketh et al., 2009 ; Gornall et al., 2011) et à limiter les dommages du gel sur les racines en jouant un rôle de tampon thermique (Soudzilovskaia et al., 2013). Au contraire, l'accumulation d'une épaisse couche fibrique d'origine muscinale réduit la température du sol et la disponibilité des nutriments (Gornall et al., 2011), et favorise la rétention de l’eau dans le sol organique, ce qui a pour effet de retarder le dégel du sol et donc de raccourcir la saison de croissance pour les plantes vasculaires (Gornall et al., 2007). Ainsi, l’accumulation d’une épaisse couche de matière organique sur le sol forestier est connue pour avoir un effet négatif sur l’établissement (Fleming et Mossa, 1994 ; Greene et al., 2007) et la croissance des arbres (Lecomte et al., 2006 ; Simard et al., 2009 ; Lafleur et al., 2016). Les lichens sont en général associés à une couche organique moins profonde (Haughian et Burton, 2014), mais leur effet d’albédo retarde le réchauffement du sol et donc la saison de croissance, ce qui a pour effet de ralentir la croissance des arbres (Kershaw, 1977). Les jeunes plantules peuvent également être affectées par certaines mousses et lichens en termes de compétition pour la lumière (Stuiver et al., 2014), ou peuvent être littéralement recouvertes par des mousses à croissance verticale rapide notamment dans les tourbières (Groot et Adams, 1994 ; Camill et al., 2010). L’existence d’effets plus directs tels que l’émission de composés allélopathiques et/ou antibiotiques a également été suggérée pour plusieurs espèces de bryophytes et lichens (Brown et Mikola, 1974 ; Crittenden, 2000 ; Michel et al., 2010 ; Molnár et Farkas, 2010 ; Chiapusio et al., 2013), bien que cette hypothèse reste controversée (Stark et al., 2007 ; Kytöviita et Stark, 2009). En effet, la plupart des études ayant suggéré l’existence de processus allélopathiques et/ou antibiotiques se sont appuyées sur des extraits de tissus végétaux (Sedia et Ehrenfeld, 2003 ; Molnàr et Farkas, 2010). Or, il reste à démontrer que ces substances présentes dans les tissus végétaux se retrouvent dans la solution du sol et ce en quantité suffisante pour avoir les effets observés au laboratoire. Ceci va dépendre entre autres de la solubilité et de la dégradation de ces composés en conditions naturelles.

L’influence de la strate des mousses et lichens étant la plus importante à la surface du sol forestier, les modifications qu’elle induit sur les conditions microclimatiques du sol auront un impact direct plus important sur la germination et la croissance des jeunes arbres en régénération que sur la croissance des arbres adultes. Cependant, la dépendance des arbres adultes vis-à-vis de leur réseau racinaire fin pour ce qui est de l'acquisition des nutriments et/ou de l'eau (Brassard et al., 2009) est susceptible de les rendre eux aussi vulnérables à l'influence des mousses et des lichens sur le sol forestier. Certaines essences telles que le pin gris (*Pinus banksiana* Lamb.) sont souvent dotées d'une racine pivot (Ressources naturelles Canada, 2017) qui leur permet de prélever l'eau en profondeur et les préserve du stress hydrique sur les substrats peu aptes à retenir l'eau en surface (Hébert et al., 2006). Cependant, ces essences restent dépendantes de leur réseau racinaire fin pour l'acquisition des nutriments. Dans les écosystèmes forestiers boréaux, les dépôts atmosphériques constituent la principale source de nutriments. C'est pourquoi la plupart des éléments nutritifs sont plus disponibles à la surface du sol, ce qui oblige l'arbre, même adulte, à se doter d'un réseau racinaire fin efficace principalement localisé à la surface du sol forestier (Noguchi et al., 2012). L'efficacité de ce réseau racinaire fin est optimisée par une surface d'échanges maximisée (Taskinen et al., 2003) et par des associations symbiotiques avec des champignons mycorhiziens (Hinsinger et al., 2009).

En résumé, la strate des mousses et lichens joue un rôle crucial dans le fonctionnement des écosystèmes forestiers boréaux, notamment parce qu'elle est à la base du patron de régénération de l'ensemble des plantes vasculaires qui seront menées à composer la communauté végétale en devenir (composition, densité, structure). De ce fait, certaines des espèces qui la composent peuvent être perçues comme des espèces ingénieures dans la mesure où elles sont susceptibles de modifier la vitesse et/ou la direction de la succession forestière (Malmer et al., 2003 ; Nilsson et Wardle, 2005 ; Royo et Carson, 2006 ; Gornall et al., 2011).

1.2 Établissement de milieux ouverts stables en forêt boréale

La forêt boréale canadienne couvre une superficie totale de 270 millions d'hectares (Brandt et al., 2013 ; Environnement Canada, 2016). Née de la dernière déglaciation, elle est structurée depuis 7000 ans par le climat et par plusieurs perturbations dont les feux de forêt, les épidémies d'insectes et les maladies (Brandt et al., 2013). Ces perturbations dont l'occurrence est en grande partie stochastique dans le temps et l'espace réinitialisent partiellement ou entièrement la succession forestière et engendrent une certaine hétérogénéité spatiale à l'échelle du paysage. Ainsi, loin d'être un territoire uniforme, la forêt boréale canadienne se présente sous la forme d'une mosaïque de peuplements à différents stades de la succession forestière.

La distribution spatiale de la végétation dépend du climat et de ses interactions avec le milieu physique (topographie, texture du sol, drainage), ainsi que de l'historique de perturbations. Au sein de la mosaïque forestière, certaines clairières ouvertes stables ne sont le résultat ni de contraintes climatiques, ni de contraintes du milieu physique, puisqu'elles se sont établies suite au recul de la forêt fermée. Ces accidents de régénération peuvent mener à l'établissement de deux types de milieux ouverts stables : (i) l'établissement de landes à lichens sur les sites où le drainage tend à être excessif ; (ii) l'établissement de tourbières à sphaignes sur les sites sujets à l'entourbement.

1.2.1 Établissement et stabilisation des landes à lichens

Au cours des 50 dernières années, la surface des landes à lichens ouvertes a rapidement augmenté dans la forêt boréale fermée de l'est canadien (Girard et al., 2008). Dans un grand nombre de cas, ces landes à lichens sont stables depuis plusieurs siècles (Morneau et Payette, 1989 ; Jasinski et Payette, 2005) et ne constituent donc pas un stade de la succession forestière menant à la formation d'une forêt fermée à mousses hypnacées (essentiellement *Pleurozium schreberii* (Brid.) Mitt.). Bien que certaines landes à lichens soient le fruit de contraintes climatiques et/ou édaphiques (Mansuy et al., 2012), d'autres se sont établies sur des sites anciennement occupés par des forêts fermées. Dans ce second cas, l'état de lande à lichens ouverte a été décrit comme un état stable alternatif de l'écosystème forestier (Jasinski et Payette, 2005 ; Côté et al., 2013). Plusieurs études suggèrent que cette transition serait le résultat de perturbations successives telles que le feu, la coupe et/ou les attaques d'insectes et de leurs interactions (Jasinski et Payette, 2005 ; Côté et al., 2013 ; DeLuca et al., 2013). Après perturbation, le basculement vers l'une ou l'autre des deux configurations stables de la communauté (forêt fermée ou clairière ouverte) dans un environnement supposé fixe est lié aux conditions initiales de la succession et à l'empreinte des évènements de dispersion et de colonisation sur l'assemblage de la communauté (Beisner et al., 2003). Dans le cas de l'établissement d'une lande à lichens, les perturbations seraient soit suffisamment rapprochées dans le temps (Payette et al., 2000 ; Payette et Delwaide, 2003), soit suffisamment sévères (Pinno et al., 2013) pour avoir un impact sur la production de graines et la capacité de régénération du peuplement (Figure 1.1).

Dans des conditions de drainage excessif, l'exposition directe aux rayonnements solaires et la sécheresse du substrat résultant de l'ouverture à long-terme du couvert forestier favorisent la formation d'un épais tapis de lichens (Boudreault et al., 2013 ; Haughian et Burton, 2014). Or, plusieurs études font état de potentiels effets négatifs de ce type de couvert au sol sur la germination (Wheeler et al., 2011 ; Kayes, 2016) et la croissance des arbres (Brown et Mikola, 1974 ; Hébert et al., 2006). Ainsi, il est possible que le lichen joue un rôle non négligeable dans le maintien de clairières ouvertes stables en forêt fermée (Morneau et Payette, 1989 ; Riverin et Gagnon, 1996), notamment *via* des mécanismes de rétrocontrôle positif liés à ses effets sur les conditions physico-chimiques et biologiques du sol (Sedia et Ehrenfeld, 2003, 2005, 2006). La présence d'un épais tapis de lichen serait non pas l'élément déclencheur de la transition vers une lande à lichens, mais un facteur aggravant du déficit de régénération qui pousserait le système vers un état ouvert différent de l'état de forêt fermée. Dans cette perspective, il participerait également au maintien de l'état ouvert stable en lui conférant une certaine inertie. Parmi les observations qui semblent soutenir cette hypothèse, Fauria et al. (2008) ont montré que la pâture du lichen par les rennes au nord-est de la forêt fenno-scandinave avait un effet positif sur la croissance des arbres, suggérant que le lichen constitue une barrière à la croissance ligneuse qui participe à la stabilisation de la clairière ouverte.

La probabilité d'un retour naturel d'une lande à lichens ouverte vers un état de forêt fermée est relativement mince. Elle repose premièrement sur un apport externe de graines viables, paramètre qui dépend de la proximité d'arbres semenciers et du hasard de la dispersion. A cette faible densité de graines s'ajoutent des conditions de germination et de croissance peu favorables pour les arbres en régénération, du fait de la présence d'un épais tapis de lichens et de l'absence de couvert forestier. La probabilité que des graines parviennent jusqu'à la station concernée et que les arbres s'établissent malgré les conditions peu favorables augmente avec le temps. Cependant, les conditions de croissance des arbres (disponibilité des nutriments) sont également susceptibles de se dégrader dans les clairières à lichens anciennes (Deluca et al., 2013), bien que l'occurrence d'un feu soit susceptible d'améliorer les conditions de croissance des arbres en supprimant le tapis de lichens et en favorisant une meilleure disponibilité des éléments nutritifs dans le sol forestier. La refermeture du couvert forestier sur ces sites est donc théoriquement possible même en l'absence d'intervention extérieure, bien qu'il s'agisse très probablement d'un processus très lent et incertain.

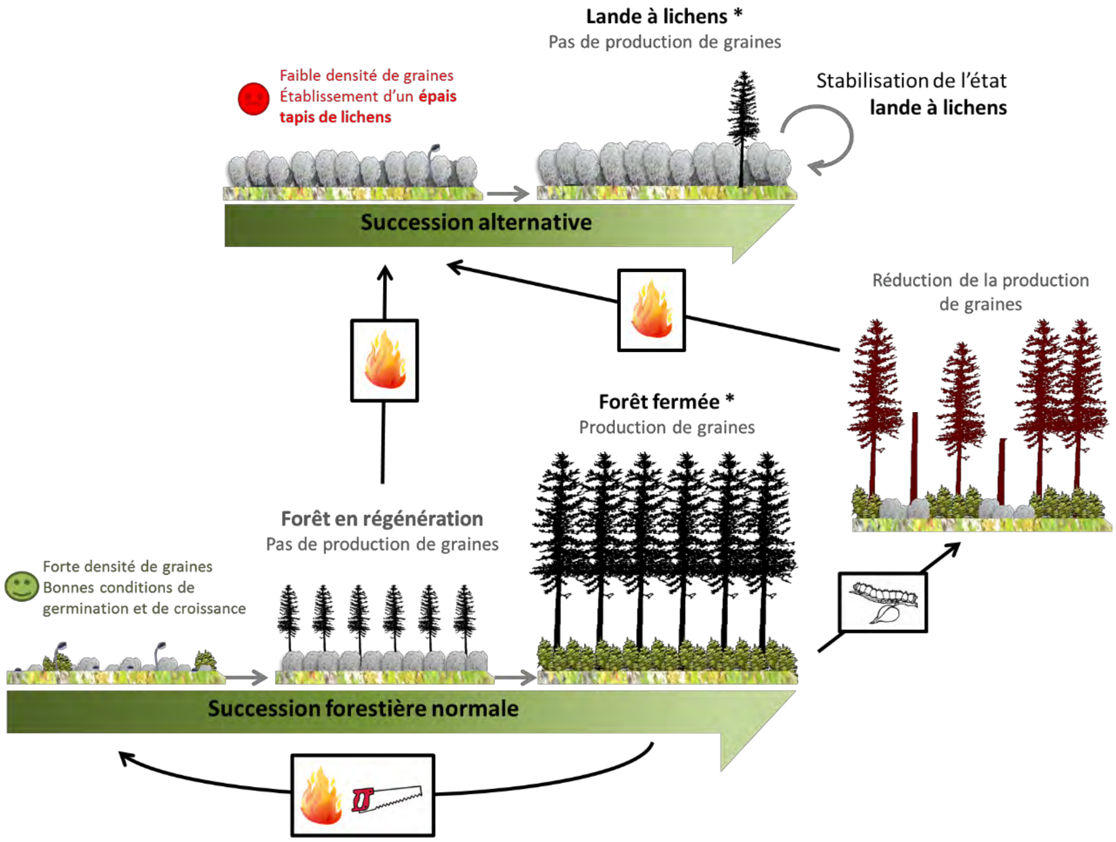

Figure 1.1 Établissement et maintien d'une lande à lichens. Les deux états alternatifs stables de l'écosystème forestier sont indiqués par un astérisque. Les transitions induites par des perturbations (feu, coupe, attaque d'insectes) sont représentées par des flèches noires, celles liées à la dynamique temporelle du peuplement par des flèches grises.

Les peuplements ayant subi une attaque d'insectes tendent à être moins résilients pour plusieurs raisons. D'abord, la défoliation des arbres affectés est associée à une réduction de leur capacité photosynthétique, ce qui va avoir un impact négatif indirect sur leur capacité de reproduction. Par ailleurs, certains insectes tels que la tordeuse des bourgeons de l’épinette s’attaquent également aux tissus reproducteurs (Greene et al., 1999). Les attaques d’insectes favorisent donc une réduction de la banque de graines à l’échelle du peuplement, ce qui tend à augmenter le risque d’accident de régénération en cas de feu subséquent. Par ailleurs, la défoliation par les insectes favorise la modification des conditions microclimatiques et l’augmentation de la disponibilité en lumière dans le sous-bois. De cette façon, elle est susceptible de favoriser la formation d’un épais tapis de lichens (Boudreault et al., 2013). L’apport rapide et ponctuel de matière organique relativement riche en carbone labile et en éléments nutrifs sur le sol forestier (feuilles et insectes) favorise une augmentation de la décomposition et de la disponibilité à court-terme des éléments nutritifs. Ceci peut conduire à plus long-terme à une redistribution des éléments nutritifs auparavant contenus dans les feuilles au profit de la végétation du sous-bois (Bastianelli, 2016).

1.2.2 Formation des tourbières à sphaignes

En forêt boréale, la formation de tourbières par paludification est étroitement associée à des conditions de faible drainage. La paludification édaphique (*sensu* Simard et al., 2007) qualifie l’entourbement des sites rendus subhydriques à hydriques du fait de leurs conditions topographiques ou édaphiques (Simard et al., 2007, 2009). L’autre type de paludification, la paludification successionnelle, dépend moins des conditions physiques du site que de processus endogènes liés à la dynamique de l’écosystème forestier. Dans la pessière noire à mousses de l’ouest du Québec, elle est le résultat naturel de la succession forestière (Lavoie et al., 2007b ; Simard et al., 2007 ; Figure 1.2).

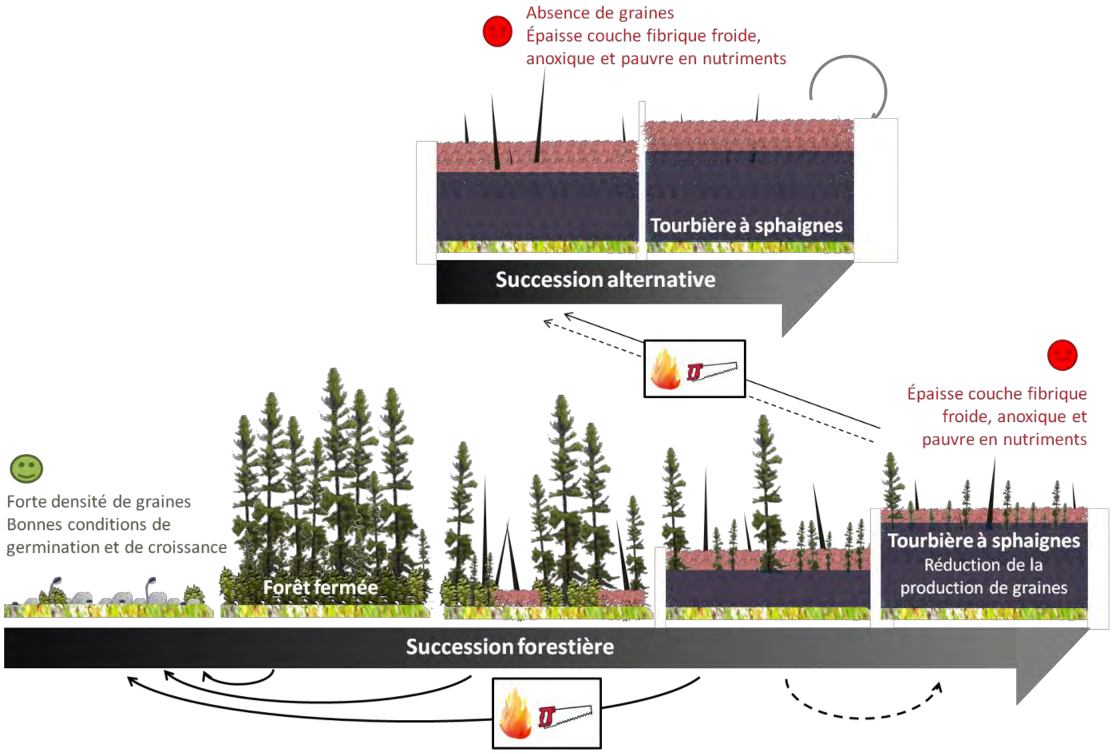

Figure 1.2 Établissement et maintien d'une tourbière à sphaignes. Les transitions induites par des perturbations de forte sévérité sont représentées par des flèches pleines (feu ou coupe perturbant fortement la couche organique). Les flèches en pointillés correspondent à des perturbations de faible sévérité qui n'affectent pas l'épaisseur de la couche organique (feu de surface, coupe avec protection de la régénération et des sols).

L'ouverture progressive du couvert forestier dans les peuplements vieillissants (Lecomte et al., 2006) tend à favoriser la colonisation du sous-bois par les sphaignes aux dépens des mousses hypnacées (Bisbee et al., 2001 ; Fenton et Bergeron, 2006). Les conséquences à long-terme de ce changement de composition sur l'ensemble de l'écosystème forestier sont relativement bien connues. Les sphaignes ayant une production primaire nette plus élevée (Bisbee et al., 2001 ; Swanson et Flanagan, 2001 ;

O'Connell et al., 2003) et un taux de décomposition plus faible (Lang et al., 2009 ; Fenton et al., 2010) que les mousses hypnacées, elles favorisent l'accumulation progressive de la matière organique et l'augmentation du niveau de la nappe phréatique (Fenton et al., 2005 ; Fenton et al., 2006). L'anaérobiose et la diminution de température qui en résultent réduisent le taux de décomposition et donc la disponibilité des nutriments pour le peuplement ligneux (Gower et al., 1996 ; Elliott-Fisk, 2000). Du fait de leur enracinement superficiel, les jeunes arbres issus de la régénération par graines sont particulièrement affectés par les conditions anoxiques et la faible disponibilité des nutriments dans la couche fibrique (Simard et al., 2007 ; Saint-Denis et al., 2010). Ce défaut de croissance de la régénération ligneuse est à l'origine de l'ouverture à long-terme du peuplement forestier. Dans la mesure où la sphaigne offre des conditions appropriées pour l'établissement des arbres (Chrosciewicz, 1976 ; Ohlson et Zackrisson, 1992 ; Groot et Adams, 1994 ; Hörnberg et al., 1997), la perte de productivité forestière à long-terme sur les sites sujets à la paludification résulterait plus d'un déficit de croissance ligneuse que d'un défaut de recrutement (Saint-Denis et al., 2010).

L'établissement d'une tourbière à sphaignes est rendu possible par l'absence prolongée de perturbations sévères du système. Plus la couche de matière organique au sol est épaisse, moins la station forestière paludifiée est sujette à permettre un feu suffisamment sévère pour retourner au stade productif (Terrier et al., 2014), et donc moins le site est susceptible de revenir à l'état initial de la succession forestière. Par ailleurs, l'effet des sphaignes sur le milieu, c.-à-d. la dégradation graduelle des conditions de croissance des arbres par l'accumulation progressive d'une épaisse couche fibrique, peut être à l'origine d'un déclin de la production de graines par les arbres (Van Bogaert et al., 2015). Ainsi, l'occurrence tardive d'un feu dans un site forestier en état de paludification avancée est susceptible de stabiliser l'état de tourbière à sphaignes sur le long-terme dans la mesure où le peuplement est alors peu apte à se régénérer par graines ou par marcottage (Van Bogaert et al., 2015). La transition peut également avoir lieu en cas de perturbation peu sévère ne réduisant pas suffisamment la couche organique au sol. L'absence de substrats adéquats pour la croissance de l'épinette noire (*Picea mariana* [Mill.] B.S.P.) ne permet pas le rétablissement d'arbres matures producteurs de graines, et favorise donc le maintien à long-terme d'une tourbière ouverte stable.

Les effets de la paludification successionnelle sont théoriquement réversibles à deux conditions : (i) la ou les perturbations sont suffisamment sévères pour réduire l'épaisseur de la couche organique de manière significative ; (ii) le peuplement comporte des arbres matures produisant des graines viables au moment de la (ou des) perturbation(s). En d'autres termes, la probabilité d'un rétablissement naturel d'une forêt productive fermée sur une station sujette à l'entourbement est inversement proportionnelle à l'épaisseur de la couche organique au sol, et donc au temps écoulé depuis le dernier feu de forte sévérité (Terrier et al., 2014).

1.2.3 Points communs entre les deux types de transition

Bien que les deux types de transition exposées précédemment reposent sur des schémas théoriques différents (transition induite par l'occurrence de perturbations dans le cas des clairières à lichens *versus* évolution naturelle de la succession forestière en l'absence de perturbation dans le cas des tourbières à sphaignes), elles présentent également plusieurs points communs : dans les deux cas, on observe (i) une modification de la composition de la strate muscinale/lichénique (remplacement des mousses hypnacées soit par les lichens dans des conditions de fort drainage, soit par les sphaignes dans des conditions de faible drainage), (ii) une modification des propriétés physico-chimiques et/ou biologiques du sol et (iii) un recul des arbres lié à un défaut de régénération et/ou de croissance ligneuse. Dans les deux cas, les modifications induites par l'ouverture du couvert forestier sur la composition de la strate des mousses et lichens semblent jouer un rôle clé à la fois en tant que moteur de la transition mais aussi en tant que facteur de stabilisation à long-terme des clairières ouvertes au sein de la matrice forestière fermée.

Les variations du degré d'ouverture du couvert forestier modulent entre autres la quantité et la qualité de la lumière transmise (Wagner et al., 2011), ainsi que les conditions microclimatiques du sous-bois en termes de température et d'humidité (Kovàcs et al., 2017). De cette façon, il influence la composition de la strate des mousses et lichens, qui affecte à son tour la croissance de la régénération ligneuse *via* son influence sur les conditions de surface du sol forestier (Figure 1.3). En cas d'ouverture de la canopée, les mousses hypnacées tendent à être remplacées soit par les lichens (Sulyma et Coxson, 2001), soit par les sphaignes (Fenton et Bergeron, 2006) suivant les conditions de drainage du site. Ce changement de composition, puisqu'il affecte les conditions physico-chimiques et biologiques du sol, peut contribuer à réduire la croissance des arbres et le succès de la régénération ligneuse. Le déficit de régénération ainsi provoqué, puisqu'il permet le maintien de l'ouverture du couvert forestier, aura pour effet de favoriser les lichens ou les sphaignes aux dépens des mousses hypnacées, et participera donc au maintien de conditions peu propices à la régénération et à la croissance ligneuse. Ces mécanismes de rétroaction positive liés à la strate des mousses et lichens sont susceptibles de jouer un rôle important dans l'établissement et le maintien de clairières ouvertes stables (Turetsky et al., 2012).

Le basculement de la forêt fermée vers un état de clairière ouverte, bien que pouvant résulter de processus strictement naturels, peut également être accentué par l'exploitation forestière. C'est dans cet écart à l'équilibre naturel que se dessine tout l'enjeu auquel doit répondre l'aménagement écosystémique en forêt boréale.

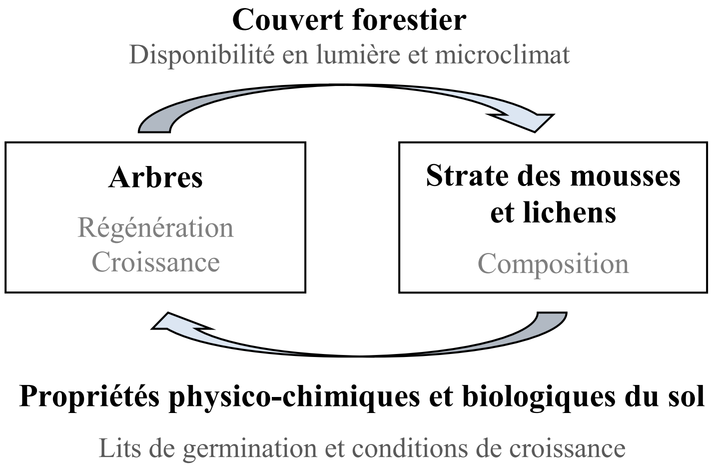

Figure 1.3 Relations réciproques entre les arbres et la strate des mousses et lichens. La productivité forestière module la composition de la strate des mousses et lichens *via* ses effets sur le degré d'ouverture du couvert forestier. La composition de la strate des mousses et lichens module la productivité forestière *via* ses effets sur les propriétés physico-chimiques et biologiques du sol.

1.3 Aménagement écosystémique en forêt boréale

Longtemps perçue comme une source quasi-inépuisable de matières ligneuses, c'est au vu de signes récents de sa vulnérabilité que l'on réalise aujourd'hui l'étendue des biens et services rendus par la forêt boréale. Source importante de bois dont dépend une grande partie de l'industrie forestière canadienne, elle abrite également une grande diversité de produits forestiers non ligneux et comporte un attrait touristique important notamment en termes d'usages récréatifs (MRNF, 2008 ; Brandt et al., 2013 ; Boulay, 2015). Au-delà de sa valeur économique, la forêt boréale est également au cœur de multiples enjeux sociaux, culturels et environnementaux. La mise en place d'un aménagement forestier durable vise à concilier l'ensemble de ces aspects de façon à maintenir une exploitation forestière performante sans nuire au maintien de l'intégrité de la ressource et de ses divers bénéfices. Pour parvenir à cet objectif, la loi québécoise préconise le recours à un aménagement écosystémique consistant à « assurer le maintien de la biodiversité et la viabilité des écosystèmes en diminuant les écarts entre la forêt aménagée et la forêt naturelle » (Loi sur l'Aménagement durable du territoire forestier, 2010).

1.3.1 Fondements de l'aménagement écosystémique

Depuis plusieurs milliers d'années, le feu est la principale perturbation qui régit la dynamique forestière à l'échelle régionale (Bergeron et al., 2004 ; Brandt et al., 2013). Cette perturbation naturelle récurrente peut donc être considérée comme faisant partie intégrante de l'équilibre dynamique de la forêt boréale actuelle. La récolte intensive au moyen d'outils mécaniques est quant à elle très récente en zone boréale, et nos connaissances en ce qui a trait à la réponse des écosystèmes forestiers à ces changements récents sont encore incomplètes étant donné qu'aucun site forestier aménagé de manière intensive (hors coupe sélective, Boucher et al., 2009) n'a encore atteint le stade de forêt mature (Brandt et al., 2013). Les effets à long-terme de cette perturbation sur la composition, la structure, ou encore l'âge des peuplements composant la mosaïque forestière ne sont qu'en phase d'être appréhendés par la recherche récente (Bergeron et al., 2002 ; Gauthier et al., 2008, 2015). L'ambition de l'aménagement écosystémique est d'intégrer la récolte de bois dans le système dynamique que constitue la forêt boréale sans perturber l'équilibre naturel établi depuis plusieurs milliers d'années. Il s'agit donc de s'inspirer des dynamiques naturelles telles que le feu pour établir un cadre opérationnel permettant de maintenir la forêt dans un état d'équilibre qui s'inscrit dans sa gamme de variabilité naturelle (Bergeron et al., 1999 ; Bergeron et al., 2002). A l'échelle du paysage, l'objectif est de faire en sorte que la mosaïque forestière aménagée s'écarte le moins possible de la variété d'âges, de compositions et de structures propre à la forêt naturelle.

1.3.2 L’expansion de milieux ouverts stables en forêt boréale, un enjeu écologique.

Les milieux forestiers ouverts jouent un rôle important au sein de la mosaïque forestière, notamment parce qu’ils sont associés à des flores et des faunes spécifiques et constituent des refuges et/ou habitats pour plusieurs espèces (Crittenden, 2000 ; Littlewood et al., 2010). Il ne s’agit donc pas de limiter la surface des milieux ouverts stables en deçà de leur occurrence naturelle, mais bien uniquement d’éviter que l’aménagement forestier ne favorise leur expansion aux dépens de la forêt fermée.

Bien qu’il soit souvent le fruit de processus naturels, l’établissement de milieux ouverts stables en forêt boréale tend à être accentué par certaines pratiques de l’aménagement forestier. Lorsqu’il n’est pas imposé par des contraintes topographiques ou édaphiques, l’établissement de tourbières à sphaignes résulte le plus souvent de la dynamique naturelle de la succession forestière (Foster, 1984 ; Simard et al., 2007). Cependant, le processus de paludification peut également être accéléré, voire stabilisé à long-terme, par des perturbations ponctuelles de faible sévérité telles que des feux de surface (Fenton et al., 2005 ; Lecomte et al., 2006), les coupes partielles (Fenton et Bergeron, 2007) ou les coupes avec protection de la régénération et des sols (Lafleur et al., 2010 ; Thiffault et al., 2013) qui brûlent ou exportent la matière ligneuse sans réduction suffisante de l’épaisseur de la couche organique au sol. De la même façon, l’établissement de landes à lichens stables peut être le résultat de processus strictement naturels tels que l’occurrence d’un feu très sévère (Pinno et al., 2013), de feux successifs (Girard et al., 2009 ; Deluca et al., 2013), ou bien l’occurrence d’un feu dans un peuplement forestier rendu vulnérable par une attaque d’insectes défoliateurs (Girard et al., 2009 ; Côté et al., 2013). Il peut également être en partie associé à des interventions anthropiques (Girard et al., 2008), notamment lorsqu’un feu subvient sur un site forestier récemment récolté, ou bien lorsqu’une attaque d’insectes s’immisce entre ces deux perturbations réduisant la vigueur de la régénération post-coupe (Payette et Delwaide, 2003). Ainsi, en venant s’ajouter aux perturbations et processus naturels, l’aménagement forestier conventionnel peut favoriser l’expansion des milieux ouverts stables dans la matrice forestière fermée (Girard et al., 2008 ; Fenton et al., 2009).

Cet écart à l’équilibre naturel recoupe plusieurs des enjeux écologiques rattachés à l’aménagement forestier boréal (Gauthier et al., 2008 ; Gauthier et al., 2015) : l’expansion des forêts ouvertes au détriment des forêts fermées a des répercussions sur la configuration spatiale de la forêt à l’échelle du paysage et peut constituer une perte nette d’habitat pour plusieurs espèces et un facteur de fragmentation des habitats forestiers ; le maintien de la productivité des sols forestiers est également remis en cause dans la mesure où les perturbations anthropiques sont susceptibles d’accélérer le processus de paludification dans les forêts subhydriques à hydriques, ou de favoriser le passage vers un état stable alternatif menant à un appauvrissement du sol à long-terme dans le cas des landes à lichens. Une meilleure compréhension des mécanismes à l’origine des accidents de régénération aidera non seulement à prévenir les pertes de productivité liées aux interventions anthropiques, mais aussi à restaurer la productivité des peuplements concernés. Par ailleurs, la perte de productivité forestière, si elle prend des proportions importantes, est d’autant plus préoccupante qu’elle est susceptible d’altérer la capacité de la forêt boréale à séquestrer le carbone dans la biomasse vivante. Ce compartiment peut cependant être supplanté par des compartiments permettant une séquestration plus stable du carbone, tels que le sol des tourbières à sphaignes riche en matière organique peu décomposée. Compte-tenu des effets du réchauffement climatique à venir sur la fréquence des feux en forêt boréale canadienne (Boulanger et al., 2014 ; Portier et al, 2016), les accidents de régénération risquent de se multiplier à l’échelle régionale (Pinno et al., 2013). Il est donc crucial de mieux comprendre les facteurs qui mènent à ces accidents de façon à pouvoir les inclure dans les modèles de dynamique de végétation et à mieux appréhender les effets du réchauffement climatique sur le devenir des stocks de carbone en forêt boréale.

1.4 Caractéristiques de la région d'étude

Délimitée par la taïga au nord et par la forêt tempérée nordique au sud, la forêt boréale canadienne est divisée en plusieurs domaines bioclimatiques caractérisés par différents types d'associations floristiques. Au Québec, la zone forestière boréale comprend la sapinière à bouleau blanc, au sud, et la pessière noire à mousses, au nord (Saucier et al., 1998 ; MRNQ, 2003). Ces deux domaines bioclimatiques sont eux-mêmes subdivisés en sous-domaines de l'est et de l'ouest du fait de leurs précipitations moyennes annuelles contrastées. La pessière noire à mousses de l'ouest du Québec est dominée par l'épinette noire (*Picea mariana* [Mill.] B.S.P.) et abrite également des proportions variables de sapins baumiers (*Abies balsamea* (L.) Mill.), de pins gris (*Pinus banksiana* Lamb.), de mélèzes (*Larix laricina* (Du Roi) K.Koch), de peupliers faux-tremble (*Populus tremuloides* Michx.) et de bouleaux blancs (*Betula papyrifera* Marshall.) selon les conditions de sol, le drainage et le stade de succession des peuplements considérés (MRNQ, 2003 ; Blouin et Berger, 2005). Le parterre de mousses et lichens est le plus souvent associé à une strate abondante d'Éricacées dominée par *Kalmia angustifolia* L., *Vaccinium angustifolium* Ait. et *Rhododendron groenlandicum* (Oeder) Kron & Judd.

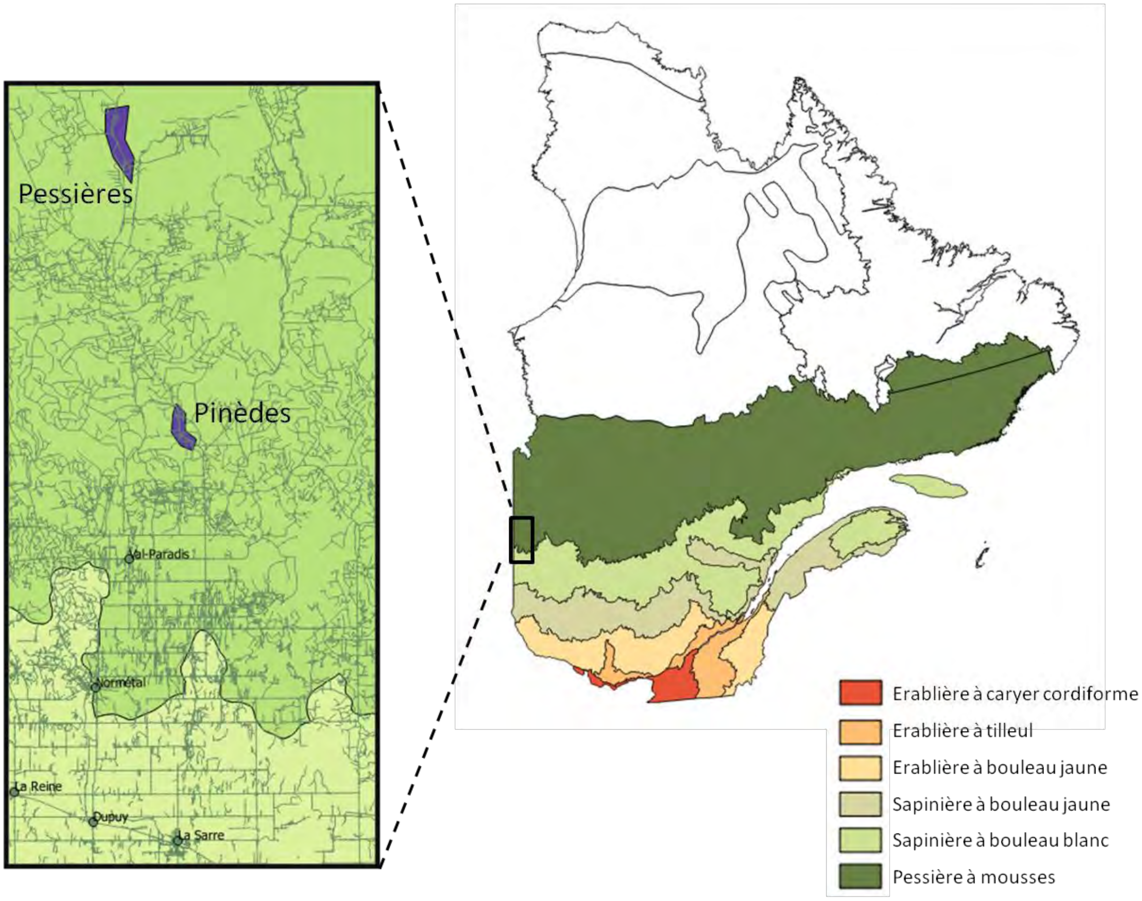

Figure 1.4 Délimitation des domaines bioclimatiques du Québec et localisation de la zone d'étude.

Dans le cadre de cette étude, nous nous sommes intéressés à des sites forestiers âgés de 25 à 38 ans caractérisés par une densité de régénération contrastée après perturbation. L'ensemble des sites considérés sont situés dans la pessière noire à mousses de l'ouest du Québec (Figure 1.4), sur la Ceinture d'argile (Allard, 1974) en région Nord-du-Québec (49°19' - 49°45' N, 79°11' - 79°18' W) et sont caractérisés par des conditions de faible relief. Deux types de peuplements ont été ciblés suivant leurs conditions de drainage : (i) des peuplements de pins gris situés sur des dépôts grossiers fluvio-glaciaires et (ii) des peuplements d'épinettes noires situés sur des dépôts argileux provenant de la sédimentation du lac pro-glaciaire Ojibway (Vincent et Hardy, 1977 ; Blouin et Berger, 2005). La zone d'étude est caractérisée par un climat subpolaire continental, la température moyenne (pour la période 1981-2010) étant de 0 ± 2.9°C et la moyenne des précipitations annuelles de 909.1 mm (Joutel, Québec ; Environnement Canada, 2017).

1.5 Problématique et objectifs de la thèse

Le rôle de la strate des mousses et lichens dans le déficit de régénération menant à la stabilisation de milieux ouverts en forêt boréale est souvent suggéré bien que peu démontré expérimentalement, et les facteurs à l'origine de ces effets restent à identifier. L'objectif principal de cette thèse est de déterminer le rôle de la strate des mousses et lichens dans l'établissement et/ou le maintien de milieux ouverts stables en forêt boréale. L'absence de couvert forestier tend à défavoriser les mousses hypnacées au profit des lichens sur les sites excessivement drainés (Sulyma et Coxson, 2001 ; Boudreault et al., 2013, 2015), et au profit des sphaignes sur les sites faiblement drainés (Bisbee et al., 2001 ; Fenton et Bergeron, 2006). Nous émettons l'hypothèse que ces changements de composition ont un impact négatif sur l'établissement et/ou la croissance de la régénération ligneuse (Figure 1.5), et participent de ce fait à la stabilisation de milieux ouverts *via* des mécanismes de rétrocontrôle positif. On suppose que la présence d'un couvert de mousses hypnacées a des effets bénéfiques sur la régénération et la croissance des résineux, favorisant le développement d'une forêt productive. A l'inverse, l'envahissement du sous-bois par les lichens ou les sphaignes tendrait à favoriser le basculement du système vers un état de forêt ouverte improductive. Plus spécifiquement, cette thèse vise (i) à déterminer les effets différentiels des mousses hypnacées, des lichens et des sphaignes sur la germination et la croissance du pin gris et de l'épinette noire, (ii) à identifier les mécanismes à l'origine de ces effets, et (iii) à évaluer les effets de l'ouverture du couvert forestier par éclaircie précommerciale sur la strate des mousses et lichens et les conséquences induites sur la productivité du peuplement.

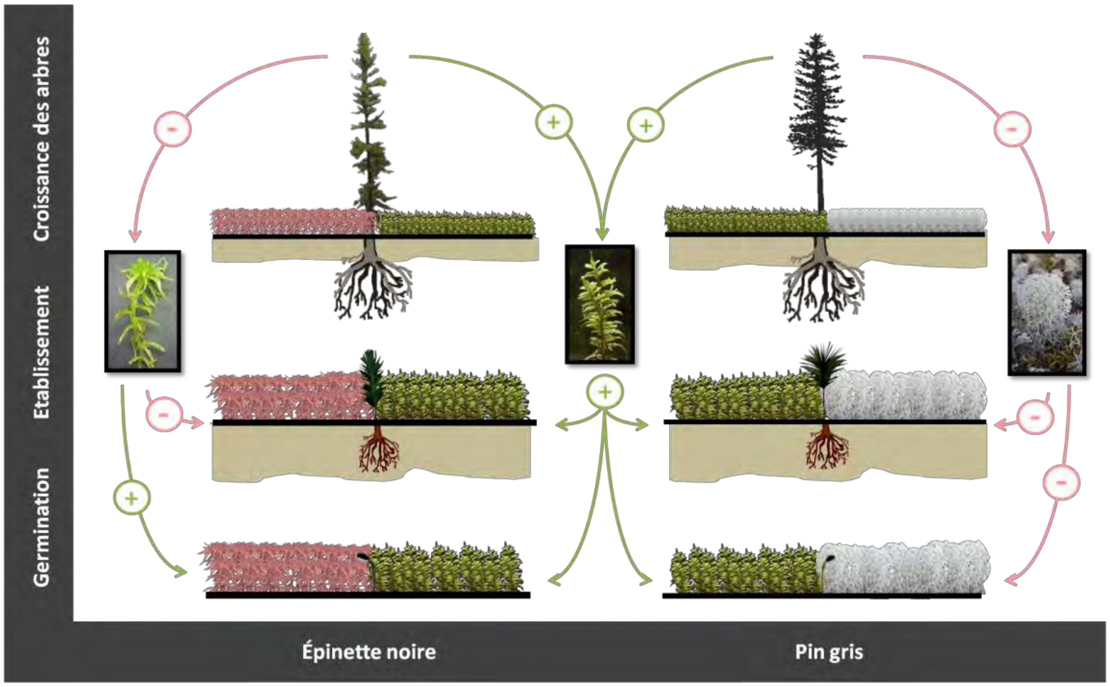

Figure 1.5 Schéma récapitulatif des hypothèses de travail quant aux effets des trois types de couvert au sol sur la régénération du pin gris et de l'épinette noire. Les flèches vertes et roses correspondent à des effets hypothétiques positifs et négatifs, respectivement.

La thèse s'articule autour de cinq chapitres regroupés dans quatre volets principaux :

- Dans le premier volet (chapitre 2), la biomasse de racines fines est utilisée comme indicateur de la qualité des conditions de croissance du pin gris et de l'épinette noire adulte (≈ 25 ans). Ce chapitre comporte une dimension à la fois descriptive et expérimentale. Dans un premier temps, il établit des patrons de corrélation généraux à l'échelle de la station forestière entre le degré d'ouverture du couvert forestier, la composition de la strate des mousses et lichens et la biomasse de racines fines. L'objectif est ensuite de prodiguer un support expérimental à ces patrons de corrélation en explorant les effets de la suppression du lichen et de la sphaigne sur la biomasse de racines fines des arbres et sur la disponibilité des nutriments dans le sol forestier. Dans le cadre de ce chapitre, nous faisons l'hypothèse que les sols couverts de lichens ou de sphaignes sont associés à des biomasses moindres de racines fines que les sols couverts de mousses hypnacées. Les effets des lichens et des sphaignes sur le développement des racines fines seraient liés à leur impact négatif sur la disponibilité des nutriments dans le sol forestier.
- L'objectif du second volet est de déterminer expérimentalement les effets de la composition de la strate des mousses et lichens sur la germination, la croissance des plantules (0 à 6 mois) et la croissance de jeunes plants (2 à 3 ans) de pin gris et d'épinette noire. Ce second volet est composé de deux chapitres distincts, l'un portant sur les effets des lichens et des mousses hypnacées sur le développement du pin gris (chapitre 3), l'autre sur les effets des sphaignes et des mousses hypnacées sur le développement de l'épinette noire (chapitre 4). En s'appuyant à la fois sur des manipulations *in situ* et *ex situ*, ce volet vise à explorer les mécanismes *via* lesquels les différents types de couvert au sol affectent la croissance de la régénération, en analysant notamment l'influence du type de couvert au sol sur la disponibilité des nutriments (chapitres 3 et 4) et les communautés fongiques ectomycorhiziennes (chapitre 3). Nous faisons l'hypothèse que les lichens et les sphaignes constituent de

moins bons substrats de germination et/ou de croissance que les mousses hypnacées, notamment parce qu'ils réduisent l'accès de l'arbre aux nutriments du sol.

- Le troisième volet (chapitre 5) se concentre sur les effets chimiques de la strate des mousses et lichens sur la croissance des arbres. A partir d'un dispositif expérimental *ex situ*, il s'agit de tester (i) l'effet des lessivats de mousses hypnacées et de lichens sur la croissance du pin gris, (ii) l'effet des lessivats de mousses hypnacées et de sphaignes sur la croissance de l'épinette noire. Les effets sont testés à deux stades du développement du pin gris et de l'épinette noire : la croissance de plantules (0 à 6 mois) et la croissance de jeunes plants (2 à 3 ans). Nous faisons l'hypothèse que les lichens, plus que les autres types de couvert au sol, affectent la croissance de l'arbre *via* l'émission de substances allélochimiques dans la solution du sol.
- Le quatrième volet (chapitre 6), de dimension plus appliquée, repose sur des données recueillies par le Ministère de la Forêt, de la Faune et des Parcs du Québec dans le cadre d'un suivi des effets de l'éclaircie pré-commerciale en forêt boréale. Les données utilisées dans ce volet concernent les régions Abitibi-Témiscamingue et Nord-du-Québec. L'objectif de ce chapitre est de déterminer la manière dont la composition de la strate des mousses et lichens est susceptible d'entraver les effets de l'éclaircie précommerciale sur la productivité future d'un peuplement. Le jeu de données correspond au suivi sur 15 ans d'un réseau de placettes ayant été mis en place entre 1995 et 1999. Ainsi, ce quatrième volet permet d'avoir un aperçu de la dynamique temporelle des effets de l'ouverture du couvert forestier sur les relations entre les arbres et la strate des mousses et lichens. Dans le cadre de ce volet, nous faisons l'hypothèse que l'ouverture du couvert forestier par éclaircie pré-commerciale favorise l'expansion du lichen dans des conditions de drainage excessif, de la sphaigne dans des conditions de drainage lent. Nous supposons que ces modifications de composition ont des effets négatifs sur la croissance ligneuse, limitant de ce fait les effets bénéfiques de l'éclaircie pré-commerciale sur la productivité du peuplement.

Ces cinq chapitres sont suivis d’une conclusion générale dans laquelle nous tentons d’élucider le rôle du lichen et de la sphaigne dans l’établissement et le maintien de milieux ouverts stables en forêt boréale. Cette dernière partie fait notamment le point sur les mécanismes potentiels *via* lesquels ces deux types de couvert au sol affectent la croissance du pin gris et de l’épinette noire. Nous utilisons ensuite ces informations pour formuler des recommandations visant à prévenir les accidents de régénération liés à l’aménagement forestier, en revenant notamment sur les effets indésirables de l’éclaircie pré-commerciale lorsqu’elle est appliquée sur des sites sujets à la sécheresse ou à l'entourbement. Nous discutons également de ce que ces résultats impliquent pour l’élaboration de techniques de restauration de la productivité des sites forestiers.

CHAPITRE II

GROUND LAYER COMPOSITION AFFECTS TREE FINE ROOT BIOMASS AND SOIL NUTRIENT AVAILABILITY IN JACK PINE AND BLACK SPRUCE FORESTS UNDER EXTREME DRAINAGE CONDITIONS

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2.1 Abstract

In the boreal forest, long-lasting canopy gaps are associated with lichens on dry sites and with *Sphagnum* spp. on wet sites. We hypothesize that ground layer composition plays a role in maintaining gaps through its effects on fine root biomass (Ø≤2mm) and soil nutrient availability. Along gradients of canopy openness in both jack pine-lichen and black spruce-moss forests, the relationships between canopy closure, ground layer composition, tree fine root biomass and soil nutrients were analyzed and decomposed using path analysis. The effects of lichen and *Sphagnum* spp. removal on tree fine root biomass and soil nutrients were tested *in situ*. Although variations in pine fine root biomass were mainly explained by stand aboveground biomass, lichen removal locally increased fine root biomass by more than 50%, resin extractable soil potassium by 580% and base cations by 180%. While *Sphagnum* cover was identified as a key driver of stand aboveground biomass reduction in paludified forest sites, its removal had no short-term effects on spruce fine root biomass and soil nutrients. Our results suggest that lichens, unlike *Sphagnum* spp., affect tree growth *via* direct effects on soil nutrients. These two different patterns call for different silvicultural solutions to maintain productive stands.

Key words: lichen, moss, *Sphagnum* spp., fine root, forest regeneration.

2.2 Résumé

En forêt boréale, l'ouverture prolongée du couvert forestier favorise un couvert de lichens sur les sites xériques et à un couvert de sphaignes sur les sites hydriques à subhydriques. Nous faisons l'hypothèse que la composition de la strate des mousses et lichens joue un rôle dans le maintien de clairières ouvertes en affectant la biomasse racinaire fine (Ø≤2mm) et la disponibilité des nutriments dans le sol. Le long de gradients d'ouverture du couvert en pinède à lichens et en pessière à mousses, les relations entre l'ouverture de la canopée, la composition de la strate des mousses et lichens, la biomasse de racines fines des arbres et les nutriments du sol ont été analysées et décomposées en suivant une analyse de pistes. Ces observations ont été complétées par une expérience *in situ* visant à mesurer les effets de la suppression du lichen et de la sphaigne sur la biomasse racinaire fine des arbres et sur le contenu en nutriments du sol. Bien que les variations de la biomasse de racines fines des pins soient principalement expliquées par les caractéristiques aériennes du peuplement, la suppression du lichen a localement augmenté la biomasse de racines fines de plus de 50 %, ainsi que la disponibilité en potassium et en cations basiques extraits de résine de 580 % et 180 % respectivement. Alors que le couvert en sphaignes est identifié comme un facteur clé de la réduction de biomasse aérienne des épinettes dans les sites paludifiés, la suppression de la sphaigne n'a pas directement affecté la biomasse des racines fines d'épinettes et le contenu en nutriments du sol. Ces résultats suggèrent que le lichen, à la différence de la sphaigne, affecte la croissance des arbres en modifiant les conditions nutritives du sol. Le maintien de peuplements forestiers productifs sur ces deux types de site nécessite des aménagements sylvicoles différents.

Mots-clés : lichen, mousse, sphaigne, racines fines, régénération forestière.

2.3 Introduction

The ground layer (i.e. bryophyte and lichen layer) is an important component of the boreal forest biome (Cornelissen et al. 2007), whose composition largely influences ecosystem processes, including the carbon cycle *via* differential rates of primary production (Turetsky 2003) and decomposition (Lang et al. 2009), and the nitrogen cycle *via* differential rates of atmospheric nitrogen fixation (DeLuca et al. 2002) or nitrogen immobilization (Augusto et al. 2015). It also influences soil processes through the modification of drivers such as pH, temperature, oxygenation and moisture regime (Fenton et al. 2006). Moss and lichen species affect microbial and fungal community composition (Ohtonen and Väre 1998; Sedia and Ehrenfeld 2003), either indirectly through their effects on soil conditions (Nilsson and Wardle 2005) or directly through allelochemical emission (Molnar and Farkas 2010; Chiapusio et al. 2013), although this second pathway remains highly controversial (Kytöviita et al. 2009).

The influence of the ground layer on ecosystem functions in the boreal forest may have visible consequences at the stand scale. Under some conditions, a forest can move from a productive state to an alternative state that is commercially unproductive (i.e., lichen woodland or forested peatland). These conditions of openness are maintained by deficits in tree regeneration and/or growth. They tend to occur on sites with extreme drainage conditions, i.e., either rapidly drained sites on coarse-grained deposits (Jasinski and Payette 2005) or poorly drained sites subject to paludification (Simard et al. 2007). In both cases, long-term forest stand opening is associated with a shift in the composition of the ground layer. Feather mosses are replaced by lichens on rapidly drained sites (Payette et al. 2000) and by *Sphagnum* spp. mosses on poorly drained sites (Bisbee et al. 2001) since the two are favoured by the increase in light availability. Since mosses and lichens have different effects on the physical, chemical and biological conditions of the forest soil, ground layer compositional changes may have consequences on tree regeneration and/or growth. For example, it has been demonstrated that seedling growth is greater in feather mosses than in *Sphagnum* spp. (Lafleur et al. 2011), and that some secondary metabolites produced by lichens (e.g., usnic acid) may have allelopathic effects on microorganisms, fungi, and trees (Sedia and Ehrenfeld 2003; Molnar and Farkas 2010). As the ground layer may affect tree growth through its effects on roots, we used fine root biomass as an indicator of the impact of the ground layer on tree physiology.

While aboveground forest processes have been relatively well studied, belowground processes remain poorly understood (Augusto et al. 2015). Trees adapt to belowground conditions and resource availability by changes in biomass allocation between above- and belowground organs (Brassard et al. 2009; Noguchi et al. 2012), root branching pattern and longevity (Persson and Ahlström 2002) and mycorrhizae colonization (Kalliokoski et al. 2010). Tree fine root biomass constitutes an easily measurable indicator of tree adaptation in contrasted environments. Indeed, fine roots are particularly important for nutrient and water uptake (Brassard et al. 2009) as they offer a maximized exchange area (Taskinen et al. 2003), in part through their association with symbiotic mycorrhizae (Hinsinger et al. 2009). Moreover, fine roots have a relatively short lifespan and adapt quickly to changes in soil conditions or water supply (Persson and Ahlström 2002).

In this study, we focus on the effects of ground layer composition on tree fine root biomass as an indicator of tree physiology adjustment, and the way these effects interact with the shading effect of forest cover. This approach is innovative for several reasons: firstly, we consider two types of sites that are very different *a priori*, but that are undergoing similar processes; secondly, we focus on the ground layer whose role in forest ecosystem processes is poorly appreciated; finally, we examine fine root biomass while previous research on long-term canopy opening has focused on aboveground tree growth (Gower et al. 1996; Fauria et al. 2008). We hypothesize that lichen and *Sphagnum* spp. covers, which are favored by the absence of shading effect from the forest cover, contribute to maintaining stand openness by inhibiting tree fine root development and maintaining a low soil nutrient availability. Based on both observational and experimental approaches, the objectives of this study are: (i) to determine the relationships between ground cover composition, tree fine root biomass, canopy closure and soil nutrient availability in forests that include the two stable states, i.e., open- and closed-crown stands; and (ii) to determine the effects of lichen and *Sphagnum* spp. removal on tree fine root biomass and soil nutrient availability as well as the way these effects are modified by shade and fertilization in open-crown forests. The first approach allows us establishing general correlation patterns of tree fine root biomass at the stand scale, while the second provides experimental support and a better understanding of the drivers responsible for the correlation patterns we observe.

2.4 Material and methods

2.4.1 Study area

The study area is located in the spruce-moss forest of western Quebec (Table 2.1). Forest composition is dominated by black spruce (*Picea mariana* [Mill.] B.S.P.) with variable abundance of jack pines (*Pinus banksiana* Lamb.) depending on soil conditions. The natural regeneration of these two tree species particularly depends on the occurrence of fires, which constitute the main natural disturbance in the study area (Bergeron et al. 2004). Average annual temperature is 0 ± 2.9°C and average annual precipitation is 909.1 mm (Joutel, QC; Environment Canada 2010). The territory is relatively flat and covered by organic or well-sorted mineral deposits. Two forest types were selected for this study: pure jack pine-lichen stands located on fluvioglacial coarse-grained deposits and essentially pure black spruce-moss stands situated on lacustrine clay deposited by the proglacial lake Ojibway (Blouin and Berger 2005). Common understory plant species are *Epigaea repens* L., *Kalmia angustifolia* L., *Linnaea borealis* L., and *Vaccinium angustifolium* Ait. in pine-lichen stands, and *Chamaedaphne calyculata* (L.) Moench, *Cornus canadensis* L., *Gaultheria hispidula*

(L.) Muhl. ex Bigelow (= Chiogenes hispidula (L.) T. & G.), *Rhododendron groenlandicum* (Oeder) Kron & Judd, and *Vaccinium angustifolium* Ait. in spruce-moss stands. *Pleurozium schreberi* (Brid.) Mitt., *Dicranum polysetum* Swartz*, D. undulatum* Schrad. ex Brid., *Polytrichum strictum* Brid., *Sphagnum capillifolium* (Ehrh.) Edw., *S. angustifolium* (C. Jens. ex Russ.) C. Jens., and *S. fuscum* (Schimp.) Klinggr. were the most frequent bryophyte species. Terricolous lichens were mainly represented by *Cladonia stellaris* (Opiz) Pouzar & Vĕzda, *C. rangiferina* (L.) F.H. Wigg., and *C. mitis* Sandst.

2.4.2 Sampling design

In 2014, we sampled 25- to 38- year-old stands of each forest type with variable post-fire or post-lodging density (Table 2.1). Each forest type was replicated four times using four geographically separate sites (2 to 12 km apart for the pine-lichen stands, and 1.5 to 6 km apart for the spruce-moss stands), each containing four to six randomly distributed circular 100 m^2 plots (located at least 200 m apart) with different degrees of forest canopy closure, for a total of 20 plots per forest type. Within each forest type, variations in canopy closure among plots were not related to variations in soil conditions (Table 2.2).

Table 2.1 Characteristics of the two sampled areas and experimental sites (mean and range).

Forest type	**Pine-lichen**	**Spruce-moss**
Sampled areas (20 plots nested in 4 sites for each forest type)		
Longitude		
Northern limit	49°25’ N	49°45’ N
Southern limit	49°19’ N	49°42’ N
Latitude		
Western limit	79°15’ W	79°18’ W
Eastern limit	79°11’ W	79°16’ W
Drainage	Rapid	Poor
Area covered by the study	2400 ha	1200 ha
Dominant tree species	*Pinus banksiana* Lamb.	*Picea mariana* [Mill.] B.S.P
Percentage of dominant species’ stems (%)	97 (77-100)	99 (92-100)
Last disturbance type	Clearcut	Fire
Year of the last disturbance	1980 and 1989	1976
Regeneration	Sowing or plantation	Natural
Dominant tree age estimated from tree rings (years)	26.8 (17-37)	22.3 (18-35)
Stand density ($trees.ha^{-1}$, all sizes)	3310 (1200-5500)	8800 (1600-17000)
Stand aboveground biomass ($t.ha^{-1}$)*	66.0 (27.2-104.0)	15.4 (1.2-45.9)
Stand canopy closure (%)	61.0 (37.0-72.7)	51.5 (11.0-86.2)
Micro-environmental conditions of the understory from June to September 2014		
Temperature (°C)	16.1 (-3.2-44.5)	16.0 (-3.2-43.6)
Air humidity (%)	87.1 (12.1-100)	86.8 (12.3-100.0)
Ericaceae aboveground biomass ($t.ha^{-1}$)	1.65 (0.56-3.55)	2.75 (0.44-6.72)
Ground cover composition (%)		
Feather mosses	45 (1-90)	45 (10-90)
Lichens	45 (1-90)	15 (0-25)
Sphagnum spp.	-	40 (0-90)
Ground living biomass ($t.ha^{-1}$)**	11.0 (4.4-18.1)	8.1 (0.5-28.4)
Tree fine root biomass ($kg.ha^{-1}$)	1380 (660-2060)	2810 (310-4440)
Experimental sites		
Longitude	49° 23’ N	49° 43’ N
Latitude	79° 14’ W	79° 17’ W
Drainage	Rapid	Poor
Area of the experimental site	2 ha	4 ha
Dominant tree species	*Pinus banksiana* Lamb.	*Picea mariana* [Mill.] B.S.P
Percentage of dominant species’ stems	99%	92%
Last disturbance type	Clearcut	Fire
Year of the last disturbance	1980	1976
Regeneration	Plantation	Natural
Dominant tree age estimated from tree rings (years)	26 (24-28)	27 (23-30)
Stand density ($trees.ha^{-1}$, all sizes)	2570	17000
Stand aboveground biomass ($t.ha^{-1}$)*	69.0	45.9
Stand canopy closure (%, one measure per plot)	60.2 (53.4-66.0)	80.54 (78.6-82.0)
Micro-environmental conditions of the understory from June to September 2014		
Temperature (°C)	16.3 (-1.0-40.6)	14.3 (-1.0-45.4)
Air humidity (%)	83.3 (11.0-100)	96.9 (34.4-100.0)
Initial tree fine root biomass ($kg.ha^{-1}$)	1070 (520-2110)	1010 (300-2760)

*Stand aboveground biomass was estimated from the sum of individual tree biomasses. Individual tree biomasses were estimated based on species-specific biomass equations developed for tree species of Canada (Ung et al. 2008). Model calibration is based on trees ranging from 1.6 to 38.4 cm in diameter at breast height (DBH) for black spruce, and from 2.5 to 48.9 cm in DBH for pine.

** Ground living biomass corresponds to the living biomass of the moss and/or lichen layer. The whole cryptogam part that did not present leaf/stem blackening or traces of decomposition was considered as living. In the case of *Sphagnum* spp., which can accumulate a thick layer of undecomposed fibric material, the white parts (unpigmented stems) that were more than 30 cm deep were not considered.

Table 2.2 Soil characteristics (mean and standard error) of the two sampled areas and links between these characteristics and the degree of canopy closure (Pearson correlation coefficient).

Soil characteristics	**Mean (± SE)**	**r***
Pine-lichen stands		
Mineral soil texture (20 cm deep)		
- Proportion of sand (%)	87 (± 5)	0.37
- Proportion of silt (%)	8 (± 6)	0.24
- Proportion of clay (%)	5 (± 2)	0.36
Organic layer depth (m)	0.12 (± 0.03)	0.14
Mineral soil		
- Dissolved inorganic nitrogen (mg.kg^{-1})	0.86 (± 0.20)	0.17
- Phosphorus (mg.kg^{-1})	0.67 (± 0.29)	0.20
Spruce-moss stands		
Organic layer depth (m)	0.72 (± 0.30)	0.10
Water table depth (m)	0.21 (± 0.06)	0.00
Deep organic matter (1 m deep)		
- Dissolved inorganic nitrogen (mg.kg^{-1})	11.66 (± 16.23)	0.00
- Phosphorus (mg.kg^{-1})	1.90 (± 1.91)	0.20

* None of the relationships were significant (*p*-value > 0.1).

Aboveground characteristics of the plots were sampled in August 2014. In each 100 m^2 plot, we surveyed species composition and cover of the ground layer in a central circular 5 m^2 subplot. Given the moderate speed of moss and lichen growth (Turetsky 2003; Kytöviita and Crittenden 2007), ground cover composition was supposed to be relatively constant through the growing season. Canopy closure was measured by means of fish-eye photos, taken at the centre of the subplot. The photos were analyzed in terms of percentage of pixels attributable to trees (including trunk, branches and foliage) using Adobe Photoshop Elements software (Adobe Systems, San José, CA). For six plots per forest type, temperature and air humidity close to the ground layer were recorded from June to September 2014 (Table 2.1) using HOBO® data loggers (HOBO® U23 PRO V2, Onset Data Loggers, Bourne, MA). All living trees were recorded within the 100 m^2 circular plots surrounding each subplot. Trees measuring less than 1.5 m were classified into three different height classes (less than 0.5 m, between 0.5 and 1 m, between 1 and 1.5 m). Diameter at breast height (DBH) was recorded on trees > 1.5 m tall. Stand age was estimated based on the time since the last disturbance determined from local archives (Bergeron, personal communication), and verified for each site by selecting 12 to 18 dominant trees and counting tree rings based on non-destructive cores (Table 2.1). Aboveground tree biomass was calculated from DBH using species-specific biomass equations (Ung et al. 2008).

Since tree fine roots are mainly located in the top 20 cm of soil (Kalliokoski et al. 2010), especially in jack pine and black spruce stands (Noguchi et al. 2012), tree fine root abundance was estimated by extracting three cores randomly located within the central circular 5 m^2 subplots of each plot. These cores, which were 5 cm in diameter and 20 cm deep from the bottom base of the living ground layer, were extracted using an auger in the beginning of September 2014. This date corresponds to the early end of the growing season, i.e. shortly before the seasonal peak of fine root decomposition (Brassard et al. 2009). We supposed that all the roots we found in the cores at this date have been produced under the influence of the ground layer sampled in august 2014.

Soil cores were transported to the laboratory in a cooler and kept frozen at -20°C until analysis. Each core was examined to discriminate tree roots from roots of other species (mainly Ericaceae), and to separate fine roots (≤ 2 mm diameter) from the larger roots (> 2 mm diameter) that were not considered in this study. We harvested one to three root samples of the most common species from the study sites, i.e., jack pine, black spruce, *Kalmia* spp., *Vaccinium* spp. and *Rhododendron* spp., and used them to develop recognition criteria based on morphological characteristics. Humidified pine fine roots were beige, slightly reddish and their root tips mostly presented a characteristic "Y" shape when mycorrhized. Spruce roots were reddish brown, darker in colour than pine. Ericaceae roots tended to be darker, thinner and less curved than the two tree species roots. Tree fine roots were rinsed with water, sorted (alive *vs* dead) following the criteria established (Brassard et al. 2011), dried at 65°C, and weighed. Fine root biomass was expressed in kilograms per unit area ($kg.ha^{-1}$).

Soil content in dissolved inorganic nitrogen (D.I.N.) was measured in each 5 m² subplot. The organic layer (O or FH) was sampled in both forest types. In spruce-moss stands, the organic layer was separated into surface and deep layers (1 m deep). Mineral soil was sampled only in the pine-lichen stands (top 20 cm). Mineral samples were air-dried and sieved at 2 mm. Organic samples were first sieved at 6 mm to remove large roots and debris, dried at 60°C, then grinded and sieved at 2 mm. NH_4-N and NO_3-N were extracted with a 2 *M* KCl solution and analyzed by spectrophotometry (QuikChem R8500 Series 2, Lachat Instruments, Milwaukee, WI).

2.4.3 Experimental design

One site per forest type-including a pine-lichen stand and a spruce-*Sphagnum* spp. stand-was selected in each study area for the experiment (Table 2.1). For each forest type, 38 1 m² circular plots were randomly distributed within the 2 to 4 ha sites so that they contained a homogeneous cover of lichen or *Sphagnum* spp. The aboveground portion of the Ericaceous plants was clipped off at the soil surface. Ericaceae roots were not removed to avoid ground cover disturbance. Initial tree fine root biomass (expressed in kg.ha^{-1}) was estimated by extracting two cores (5 cm diameter and 20 cm deep from the bottom base of the living ground layer) per plot at the beginning of the experiment (June 2014) using an auger. Lichens or *Sphagnum* spp. were then removed on 19 1 m^2 plots while the other 19 were used as controls. Among the 19 plots of each modality, seven were covered with a 50 % shade cloth (perforated net positioned 20 cm above the ground surface and covering the whole 1 m^2 plot) and 5 were fertilized with 5 g of controlled-release fertilizer (20% nitrogen, 7% phosphorus and 10% potassium, Plant-Prod Smartcote®, Master Plant-Prod Inc., Brampton, ON). Since trees can produce fine roots within a radius of 5 m around the trunk (Taskinen et al. 2003), all trees located within a radius of 5 m around the 1 m^2 plots were counted and their DBH was measured. Two other cores per plot were extracted at the end of the experiment (September 2014) to estimate final tree fine root biomass per unit area. June and September cores were stored and analyzed as previously described. For each plot, soil nutrient availability was measured for the duration of the experiment using ion exchange resins buried 10 cm deep in the soil from June to September 2014. Ion-exchange resin bags (see McCavour et al. 2014) were made using 20 g of mixed-bed ion-exchange resin (J.T. Baker ®, Avantor Performance Materials, Central Valley, PA) contained in beige nylon bags (made of standard stockings) and regenerated with 1*M* HCl. Resins were delicately removed from the soil, kept separately in sealed plastic bags, transported to the laboratory in a cooler, and stored at 4°C until analysis. NO_3-N and NH_4-N were extracted using a 2*M* KCl solution and analyzed by spectrophotometry (QuickChem R8500 Series 2, Lachat instruments) to estimate soil D.I.N. Phosphorus, potassium, magnesium, calcium and sodium were extracted using a 2*M* HCl solution and analyzed by inductively coupled plasma (ICP) using an optical emission spectrometer (OES) (Optima 7300 DV, Perkin Elmer, Waltham, MA). Soil base cations were estimated by summing the concentrations of the major base cations contained in the resins (K, Ca, Mg and Na).

2.4.4 Statistical analyses

We considered each forest type separately for statistical analyses. We first used a correlation analysis to examine the relationships between ground cover composition (lichen/*Sphagnum* spp. cover expressed in %), tree fine root biomass (kg.ha^{-1}), canopy closure (%), tree aboveground biomass (t.ha^{-1}) and D.I.N. (mg.kg^{-1}). A path analysis was then used to discriminate partial correlations between stand aboveground biomass, canopy closure, lichen/*Sphagnum* spp. cover and tree fine root biomass (Shipley 2002). The use of four variables in the path analysis allowed us to respect the recommendation by Hoagland and Boomstra (1998) advising a limit of eight free parameters for 20 observations for an acceptable performance of the general least squares χ^2 statistic (Shipley 2002). Path coefficients between these variables made possible the discrimination of direct, non-direct and non-causal correlations. Since our sample was small and may slightly deviate from normality, we used a Yuan Bentler scaled test statistic (Bentler and Yuan 1999) for the d-sep test (Shipley 2002) to determine the likelihood that an *a priori* structure was correct. Kurtoses were verified for the different variables used in the path analyses (Shipley 2002).

The relationships between initial tree fine root biomass and stand aboveground biomass in the two experimental sites were first tested to verify if this parameter should be included in the models. The effects of ground cover removal (lichen or *Sphagnum* spp., according to the forest type) and secondary treatments (shade and fertilization) were then tested on final tree fine root biomass (kg.ha^{-1}) and soil nutrient availability (measured from the ion exchange resins). Linear models were used to decompose the effects of the second factor (secondary treatments) i.e. to analyze the effects of fertilization *versus* control in a first phase and shade *versus* control in a second phase. When necessary, the dependent variables of the linear models were transformed to respect normality (*log*-transformations). When errors were heteroscedastic for one factor (especially for the secondary treatments since variance was higher in fertilized plots than in control and shaded plots), degrees of freedom were sacrificed to estimate the variance associated with each level of factor. All analyses were performed on R-3 software (R Core Team 2014).

2.5 Results

2.5.1 Relationships between stand aboveground biomass, canopy closure, ground cover composition, tree fine root biomass and soil nutrient availability in the sampled area

Pine-lichen stands

In the pine-lichen stands, variation in stand aboveground biomass was partly related to stand age (Fig. 2.1.a). Feather mosses and lichens varied with canopy closure as expected, with greater lichen cover under open canopies (Fig. 2.1a; Table 2.3). Pine fine root biomass, which was 1380 kg.ha^{-1} on average (range: 660 to 2060 kg.ha^{-1}, respectively), was positively associated with stand aboveground biomass and poorly related to lichen cover (Fig. 2.1a; Table 2.3). Interestingly, pine roots tended to be thinner under lichen than under feather moss (personal observation). Lichen cover tended to be slightly associated with low soil D.I.N. although the trend was not significant (R= -0.40, p = 0.0808). The structure determined by path analysis for the pine-lichen stands (Fig. 2.2.a) was not rejected by d-sep analysis (χ = 2.89, df = 2, *p*-value = 0.23), showing that the data were consistent with the proposed causal structure (Shipley 2002). It indicated that the direct effect of stand aboveground biomass on fine root biomass in the study area was much more important than its indirect effect *via* canopy closure and lichen cover, and that the slight correlation between lichens and fine root biomass fell more under a non-causal relationship between the two rather than under a direct effect (Fig. 2.2.a; Table 2.4).

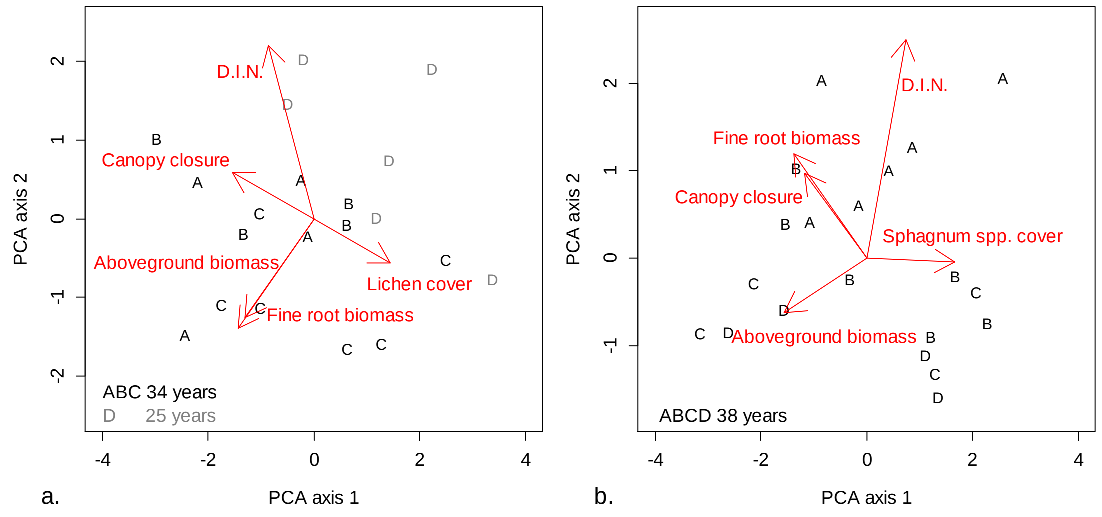

Figure 2.1 Scores of the 20 plots along axes 1 (explained variations = 56 %) and 2 (explained variations = 23 %) of the Principal Component Analysis based on six target variables. a) Pine-lichen stands; b) Spruce-moss stands. Each plot (20 per forest type) is represented by the letter of the matching site (A, B, C or D) in the colour corresponding to stand age (see figure for legend). For each variable, the direction of variation is indicated by an arrow.

Table 2.3 Pearson correlation coefficients between canopy closure, lichen/*Sphagnum* spp. cover, fine root biomass, stand aboveground biomass and D.I.N. for the two forest types.

	Lichen/*Sphagnum* spp. cover	**Fine root biomass**	**Stand above-ground biomass**	**D.I.N.**
Pine-lichen stands				
Canopy closure	**- 0.66***	0.47	0.55	0.49
Lichen cover	-	- 0.33	- 0.56	- 0.40
Fine root biomass	-	-	**0.69***	0.15
Stand aboveground biomass	-	-	-	0.01
Spruce-moss stands				
Canopy closure	**- 0.68***	0.39	**0.62 ***	0.00
Sphagnum spp. cover	-	**- 0.63***	**- 0.70****	0.32
Fine root biomass	-	-	0.32	- 0.04
Stand aboveground biomass	-	-	-	0.32

Significant relationships (after Bonferroni correction) are given in bold. * *p*-value < 0.005; ** *p*-value < 0.001.

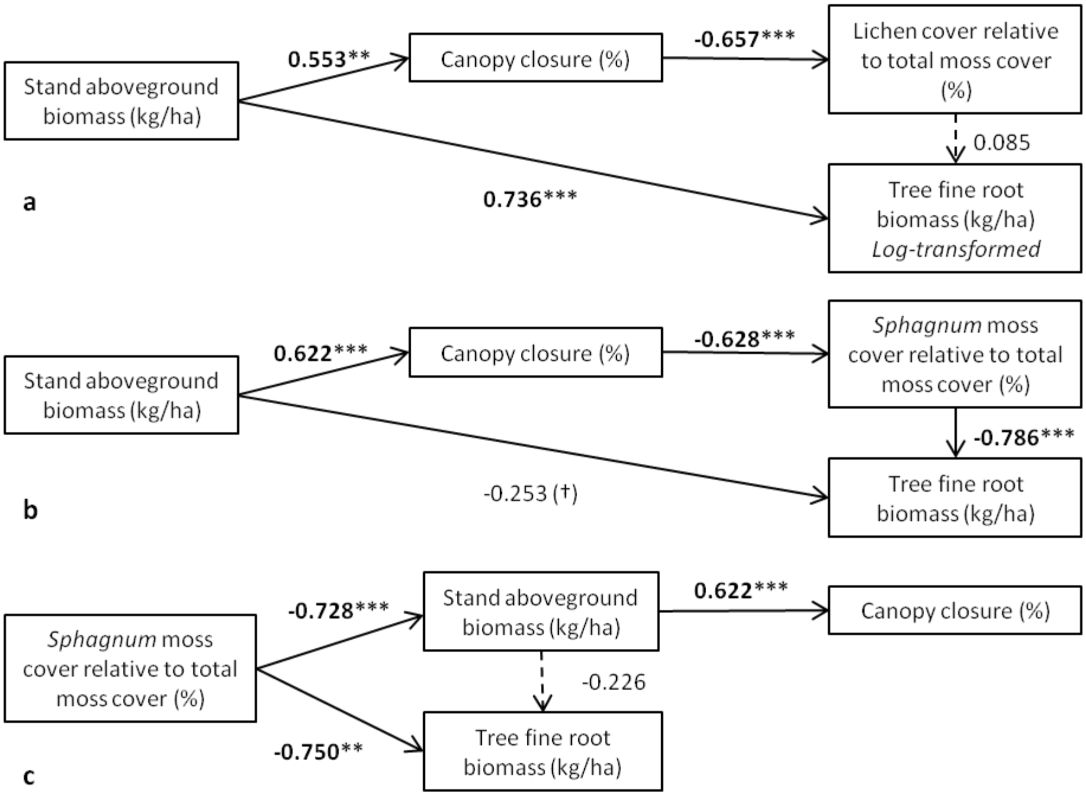

Figure 2.2 Schematic representation of three different hypothesized causal structures including stand aboveground biomass, canopy closure, ground cover composition and tree fine root biomass. a) Pine-lichen stands (χ = 2.91; df = 2; *p*-value = 0.23; scaling correction factor for the Yuan-Bentler correction = 0.801); b) Spruce-moss stands, model 1 (χ = 11.48; df = 2; *p*-value < 0.01; scaling correction factor for the Yuan-Bentler correction = 0.65); c) Spruce-moss stands, model 2 (χ = 2.59; df = 1; *p*-value = 0.11; scaling correction factor for the Yuan-Bentler correction = 0.87). Significant correlations are indicated in bold (** *p*-value < 0.01; *** *p*-value < 0.001). As recommended by Shipley (2002) for small size samples, possible edges characterized by a significant level lower than 0.2 (†) are also represented as solid lines.

Table 2.4 Direct effect, indirect effect, non-causal variation and total correlation for path analysis of tree fine root biomass per unit area based on the different hypothesized causal structures. Significant relationships are given in bold.

Variable	**Direct** Value (Error)	**Indirect**	**Non causal**	**Total** [1]
Pine-lichen forest				
Tree fine root biomass (log-transformed)				
Stand aboveground biomass	**0.736 (0.173) *****	-0.031	0	0.688
Lichen cover	0.085 (0.173)	0	-0.267	-0.327
Canopy closure	0	-0.056	0.407	0.469
Spruce-moss forest				
Tree fine root biomass (model 1)				
Stand aboveground biomass	- 0.253 (0.189)	0.307	0	0.319
Sphagnum spp. moss cover	**- 0.786 (0.189) *****	0	0.099	-0.602
Canopy closure	0	0.494	-0.157	0.390
Tree fine root biomass (model 2)				
Stand aboveground biomass	- 0.226 (0.254)	0	0.546	0.319
Sphagnum spp. moss cover	**- 0.750 (0.253) ****	0.165	0	-0.633
Canopy closure	0	0	0.258	0.390

[1] Total value represents the Pearson correlation coefficient (r).

** *p*-value < 0.01; *** *p*-value < 0.001.

Spruce-moss stands

The proportion of *Sphagnum* spp. in the ground layer significantly decreased with the degree of canopy closure in spruce-moss stands (Fig. 2.1.b; Table 2.3). Tree fine root biomass was higher in spruce-moss stands than in pine-lichen stands with an average of 2810 kg of spruce fine roots per hectare (range: 310 to 4440 kg.ha^{-1}). Spruce fine root biomass was negatively associated with *Sphagnum* spp. cover and poorly related to stand aboveground biomass (Fig. 2.1.b; Table 2.3). Moreover, ground cover composition was closely related to stand aboveground biomass, which decreased significantly with *Sphagnum* spp. cover (Table 2.3). *Sphagnum* spp. cover was not linked to soil D.I.N. Considering the close relationship between *Sphagnum* spp. cover and stand aboveground biomass, we proposed two causal structures for the path analysis in spruce-moss stands. The first (Fig. 2.2.b), which is the same as the one proposed for the pine-lichen stands, considers that the *Sphagnum* spp. cover results from stand aboveground biomass effect on canopy closure. The second considers that *Sphagnum* spp. cover does not depend on canopy closure, but directly influences stand aboveground biomass, which in turn affects canopy closure. Contrary to the first structure determined by path analysis (Fig. 2.2.b) that was rejected by d-sep analysis ($\chi = 11.48$, df = 2, *p*-value < 0.01), the second structure (Fig. 2.2.c) was plausible considering the data ($\chi = 2.77$, df = 2, *p*-value = 0.11). Hence, it suggests that the second causal structure we proposed was a better fit than the first, showing that *Sphagnum* spp. cover was less a consequence of canopy opening than the main factor explaining low stand aboveground biomass in the sampled area. The two path analyses indicate that tree fine root biomass was more closely related to *Sphagnum* spp. cover than to stand aboveground biomass (Table 2.4).

2.5.2 Effects of ground cover removal, fertilization and shade on tree fine root biomass and soil properties

Pine-lichen forest

Initially, there was on average 1070 kg of pine fine roots per hectare in the pine-lichen plots used for the experimental study (Table 2.1). Initial pine fine root biomass was poorly associated with stand aboveground biomass in the experimental site (Pearson's R = 0.14, t-test statistic = 0.87, *p*-value > 0.1); thus, we did not consider this covariable in the ensuing models. Three months after treatment application, lichen removal on the 1 m^2 plots locally increased pine fine root biomass by more than 50% (Table 2.5), rising from 1099 $kg.ha^{-1}$ on average for control plots to 1902 $kg.ha^{-1}$ for plots where ground cover had been removed (Fig. 2.3). Fertilization and shade did not significantly affect pine fine root biomass (Fig. 2.3; Table 2.5).

Lichen removal had no effect on D.I.N. and phosphorus, but it positively affected potassium and soil base cations (x 6.8 and x 2.8, respectively), including magnesium (x 2.3) and sodium (x 3.6). Phosphorus, potassium and D.I.N. tended to be higher after fertilization (x 3.1, x 8.8, and x 190, respectively; Fig. 2.4), although the trend was not significant for phosphorus (Table 2.5). Soil base cations were also significantly increased by fertilization (more than 3 times higher in fertilized plots compared with control plots). With the exception of phosphorus, the positive effects of fertilization on nutrient availability and base cations were lower in the case of lichen removal (significant negative effect of the interaction between the two treatments; Table 2.5). Shade reduced the positive effects of lichen removal on potassium and base cations, although it did tend to increase the positive effect of lichen removal on D.I.N. (marginal positive effect of the interaction).

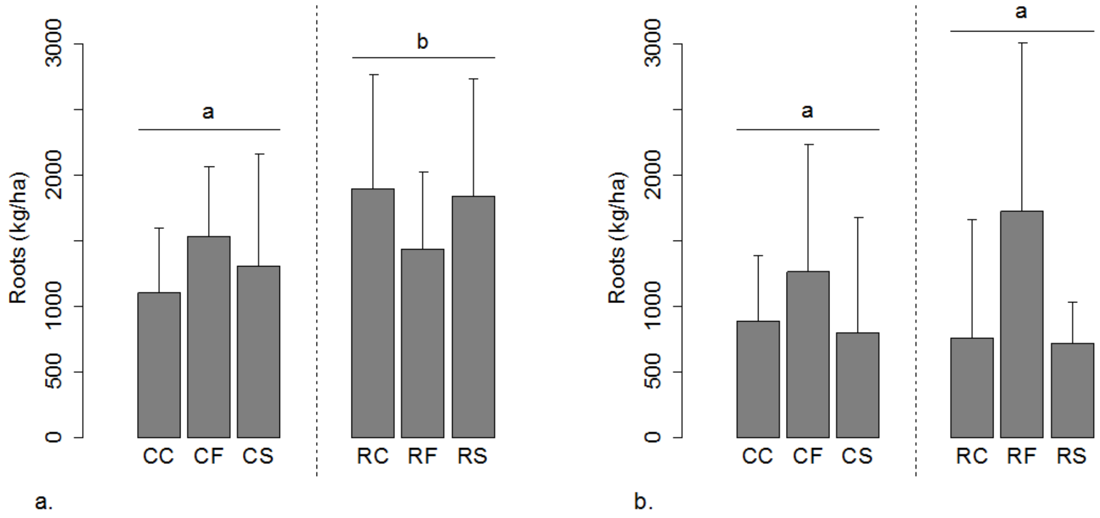

Figure 2.3 Treatment effect on tree fine root biomass for the two forest types. a) Pine-lichen stands; b) Spruce-moss stands. CC: Control x Control; CF: Control x Fertilization; CS: Control x Shade; RC: Removal x Control; RF: Removal x Fertilization; RS: Removal x Shade. Significant differences between ground cover treatments are represented by different letters. Vertical bars represent standard deviations.

Table 2.5 Treatment effect on tree fine root biomass and soil characteristics for the two forest types. Significant *p*-values are given in bold.

	Pine-lichen			Spruce-moss		
	t	*p*-value	R^2	t	*p*-value	R^2
Final tree fine root biomass (kg.ha^{-1})						
Lichen/*Sphagnum* spp. removal (1)	2.05	**0.0483**	0.04	0.15	0.8816	0.06
Fertilization (2)	1.29	0.2049		1.99	0.0550	
Shade (3)	0.35	0.7315		-0.21	0.8356	
Interaction (1) * (2)	-1.53	0.1368		-	-	
Interaction (1) * (3)	-0.41	0.6829		-	-	
Dissolved Inorganic Nitrogen (mg.kg^{-1})						
Lichen/*Sphagnum* spp. removal (1)	0.12	0.9065	0.58	-0.85	0.4044	0.66
Fertilization (2)	4.47	**0.0001**		3.57	**0.0011**	
Shade (3)	-1.26	0.2165		-0.77	0.4496	
Interaction (1) * (2)	-2.16	**0.0383**		2.49	**0.0183**	
Interaction (1) * (3)	1.75	0.0898		1.91	0.0651	
Phosphorus (mg.kg^{-1})						
Lichen/*Sphagnum* spp. removal	-1.09	0.2830	0.04	0.72	0.4746	0.30
Fertilization	1.26	0.2170		4.22	**0.0002**	
Shade	-0.50	0.6230		1.32	0.1972	
Potassium (cmol.kg^{-1})						
Lichen/*Sphagnum* spp. removal (1)	2.51	**0.0178**	0.26	-0.18	0.8560	0.19
Fertilization (2)	2.50	**0.0180**		2.87	**0.0071**	
Shade (3)	1.81	0.0803		-0.32	0.7486	
Interaction (1) * (2)	-3.65	**0.0010**		-	-	
Interaction (1) * (3)	-3.12	**0.0040**		-	-	
Sum of major base cations (cmol.kg^{-1})						
Lichen/*Sphagnum* spp. removal (1)	2.45	**0.0204**	0.24	-0.34	0.7335	0.13
Fertilization (2)	2.47	**0.0193**		-0.10	0.9204	
Shade (3)	1.07	0.2914		-0.77	0.4498	
Interaction (1) * (2)	-3.47	**0.0016**		1.41	0.1690	
Interaction (1) * (3)	-2.29	**0.0290**		2.03	0.0511	

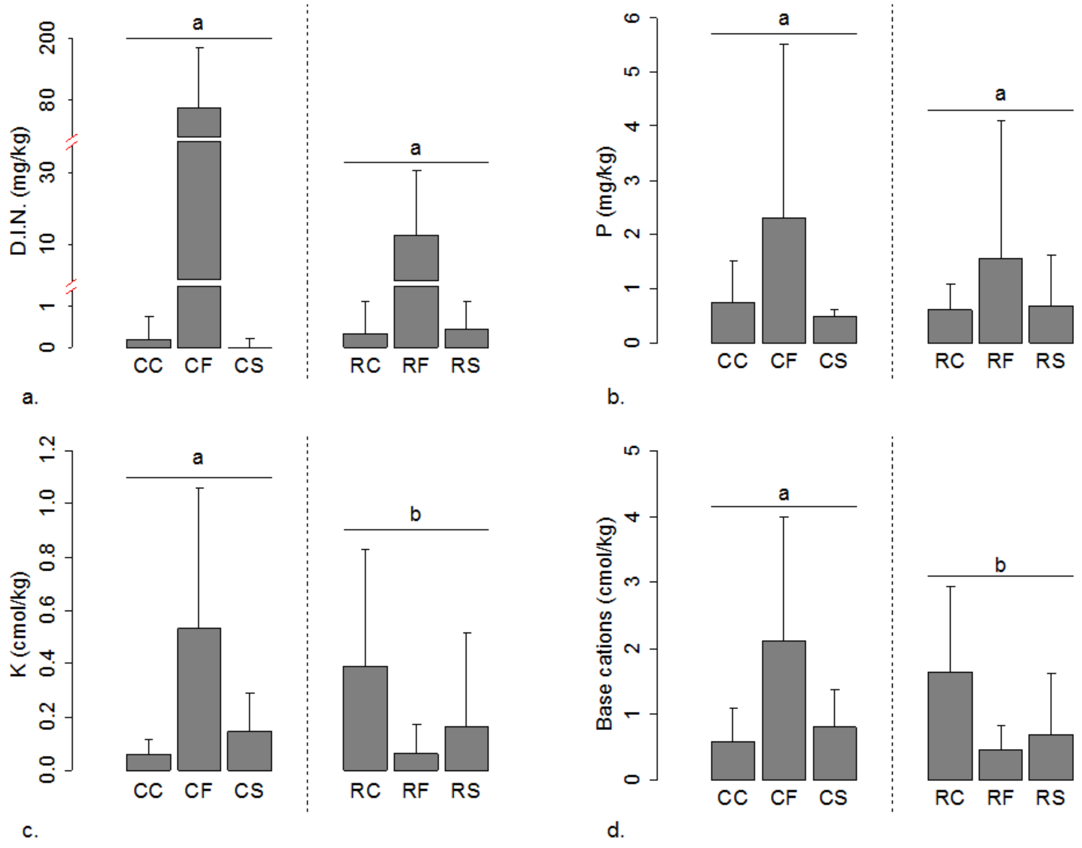

Figure 2.4 Treatment effect on soil characteristics in the pine-lichen forest. a) Dissolved Inorganic Nitrogen (D.I.N.); b) Phosphorus (P); c) Potassium (K); d) Base cations. CC: Control x Control; CF: Control x Fertilization; CS: Control x Shade; RC: Removal x Control; RF: Removal x Fertilization; RS: Removal x Shade. Significant differences between ground cover treatments are represented by different letters. Vertical bars represent standard deviations.

Spruce-moss forest

Average initial tree fine root biomass in the plots of the spruce-moss experimental site was 1010 kg of spruce fine roots per hectare (Table 2.1). As for the pine-lichen site, stand aboveground biomass was poorly associated with the initial spruce fine root biomass in the experimental site (Pearson R = 0.12, t-test statistic = 0.71, *p*-value > 0.1) and was not considered in the ensuing models. Spruce fine root biomass was not affected by *Sphagnum* spp. removal and shade after 3 months. However, it was marginally increased by fertilization (+ 42% on average) (Fig. 2.3; Table 2.5).

Sphagnum spp. removal and shade did not affect any of the measured soil nutrient concentrations (Fig. 2.5; Table 2.5). However, fertilization strongly affected soil D.I.N., phosphorus and potassium availability (x 58, x 9.4 and x 3.8, respectively), although it had no effect on base cations. *Sphagnum* spp. removal increased the positive effect of fertilization on soil D.I.N., but not on phosphorus and potassium.

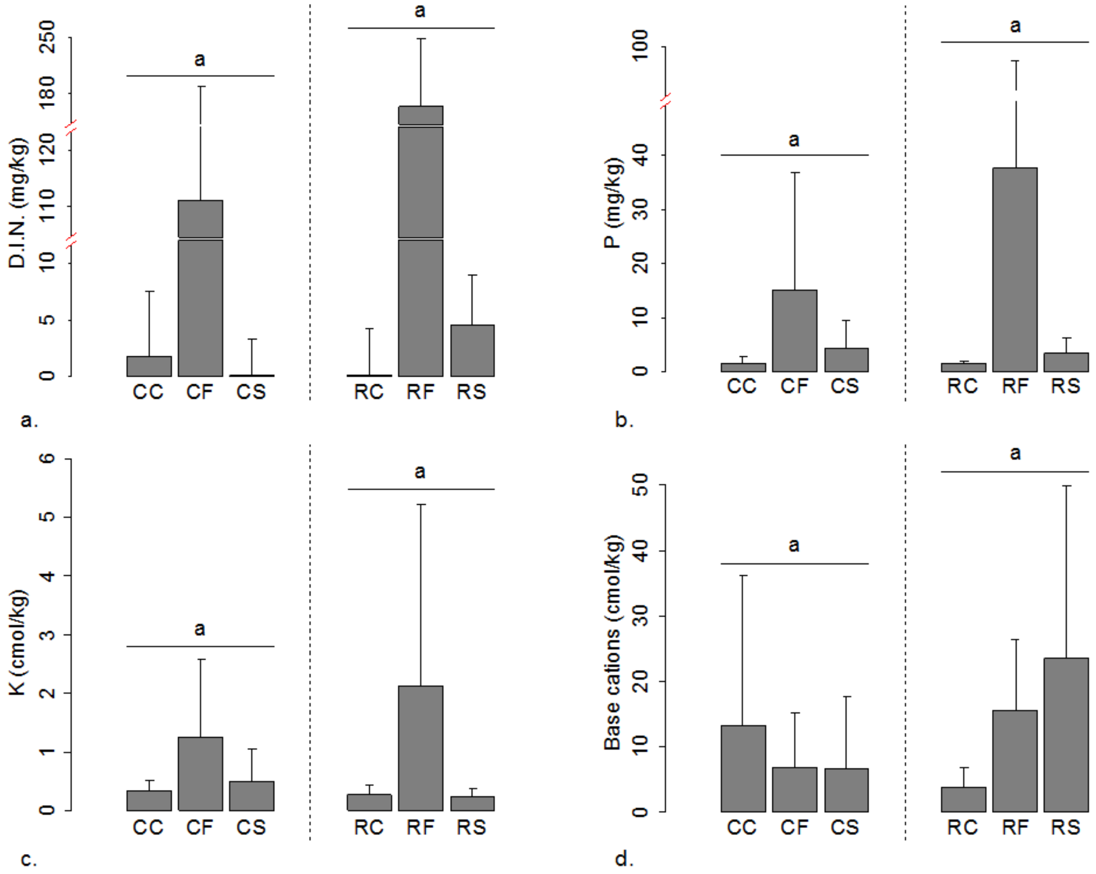

Figure 2.5 Treatment effect on soil characteristics in the spruce-moss forest. a) Dissolved Inorganic Nitrogen (D.I.N.); b) Phosphorus (P); c) Potassium (K); d) Base cations. CC: Control x Control; CF: Control x Fertilization; CS: Control x Shade; RC: Removal x Control; RF: Removal x Fertilization; RS: Removal x Shade. Significant differences between ground cover treatments are represented by different letters. Vertical bars represent standard deviations.

2.6 Discussion

Our results, along with those of previous studies (Fenton and Bergeron 2006; Boudreault et al. 2013; Haughian and Burton 2015), indicate that lichens and *Sphagnum* spp. are more abundant under open canopies than closed ones. The correlation and path analyses indicate that the patterns of variations in tree fine root biomass differ between the two forest types, suggesting that these two ground cover types differ in their influence on soil and tree growth conditions. Since lichens and *Sphagnum* spp. mosses are mainly associated with open canopies, the close relationship between tree aboveground and fine root biomasses observed in the pine-lichen stands makes the assessment of the direct effect of ground cover composition on fine roots difficult based only on observational data. The experimental manipulation of ground cover in the second part of this study alleviates this problem by neutralizing the confounding effect of tree aboveground characteristics on tree fine root biomass through randomisation of experimental plot location. Given the contrasting patterns observed in the two forest types, lichen and *Sphagnum* spp. effects on fine roots and soil properties are discussed separately.

2.6.1 Lichen effect on pine fine roots and soil properties

Our estimation of pine fine root biomass was lower than the average values reported by Finér et al. (2007) for Scots pine in the European boreal forest (2290 ± 1020 kg.ha^{-1}) and by Yuan and Chen (2010) for pine in the North American and Eurasian boreal forests (2520 ± 130 kg.ha^{-1}). By comparing plots with various degrees of canopy closure, we showed that pine fine root biomass per hectare was more closely linked to stand aboveground biomass than it was to lichen cover (Figs. 2.1 and 2.2; Tables 2.3 and 2.4). The positive relationship between fine root biomass and stand aboveground biomass in pine-lichen stands of the sampled area suggests that more abundant and/or bigger pines produce more fine roots in the surface soil. This result seems logical as higher aboveground productivity means greater resource needs and, consequently, a larger fine root network to maximize tree resource acquisition. The absence of correlation between initial tree fine root biomass and stand aboveground biomass in the experimental even-aged stand probably results from the higher homogeneity of age and aboveground biomass of the 2 ha experimental site compared with the much larger sampled area.

Although the path analysis suggests that there was no direct relationship between lichen cover and pine fine root biomass in the sampled area, this link may have been concealed by the close relationship between tree fine root biomass and stand aboveground characteristics. If we refer to the experimental part of this study, we showed that lichen removal locally increases pine fine root biomass as observed by Fauria et al. (2008) who asserted that lichen grazing positively affects Scots pine growth. This result suggests a negative effect of lichens on tree fine root development as it indicates that pine fine root production may have been stimulated in the short-term by a reduced influence of lichens. We also observed that jack pine roots tend to be thinner under lichens, thus indicating that either pines adapt to the local environment by modifying their fine root structure (Zadworny et al. 2016) or that lichens reduce the quantity of enlarged pine root tips through their negative effects on mycorrhization (Sedia and Ehrenfeld 2003).

It has been proposed that lichens modify soil hydric conditions (Bonan and Shugart 1989), as their hydrophobic properties (Shirtcliffe et al. 2006) might contribute to favour dry soils, surface run-off, and heterogeneous horizontal infiltration. Fine root growth can be largely affected by soil moisture (Yuan and Chen 2010) and dry conditions may favour denser tree root networks that optimize prospection and water absorption. Water deficit may also affect soil nutrient transport and diffusion from the soil to root absorbing surfaces and in this way affect tree access to nutritional resources (Barber et al. 1963). Because it was limited to 1 m^2 in our experiment, ground layer removal might have favoured water infiltration and locally stimulated root densification. Therefore, the higher nutrient absorption by the resins when lichens were removed may have been favoured by a greater water flow, while shade cover may have partially mimicked the effects of a lichen mat that limits rain water supply at the surface and thus reduces nutrient transport to the resins.

Lichens have been shown to be associated with lower soil nitrogen availability than feather mosses (Ohtonen and Väre 1998). Haughian and Burton (2015) also found a strong negative correlation between lichen cover and phosphorus availability in the forest soil. Lichen removal did not affect D.I.N. and phosphorus concentration in our experimental plots. One possible explanation is that lichen effects on soil nitrogen and phosphorus content are long-lasting and persisted for 3 months after ground layer removal. However, we can point out that lichen removal significantly increased soil potassium and base cations (including calcium, sodium and magnesium), which confirms that lichens also had short-term effects on soil chemical properties. Nutrient availability may be influenced by lichens not only by their low rate of litter accumulation (Sedia and Ehrenfeld 2005), but also through their impact on soil temperature and decomposer activity as they are highly reflective and have low thermal conductivity (Bonan and Shugart 1989). Lichens might also produce antimicrobial and antifungal substances that have negative effects on the activity of soil microbial communities (Sedia and Ehrenfeld 2005) and fungi, including mycorrhizae (Sedia and Ehrenfeld 2003; Molnar and Farkas 2010). Nitrogen mineralization, which should have been stimulated by the positive effect of lichen removal, probably was limited in our experiment by the low availability of decomposable litter in the bare soil plots.

The direction of the correlation between fine root biomass and nutrient availability has been shown to be species-specific (Finér et al. 2007), and relationships in both directions have been found (Persson and Ahlström 2002; Kalliokoski et al. 2010). In the present study, although pine fine root biomass response to fertilization was highly variable and not significant, lichen removal stimulated pine fine root biomass at the same time as it increased soil potassium and base cations. These observations suggest that pines locally produce more fine roots in nutrient-rich spots in a globally low-nutrient forest site. Hence, pines are able to adapt quickly to heterogeneous environments *via* local stimulation of fine root production in places that are more favourable.

2.6.2 *Sphagnum* spp. effect on spruce fine roots and soil properties

Spruce fine root biomass was lower in our study sites than the average values reported by Finér et al. (2007) for Norway spruce in the European boreal forest (3300 ± 1570 $kg.ha^{-1}$) and very close to the average value reported by Yuan and Chen (2010) for spruce in the North American and Eurasian boreal forest (2780 ± 130 $kg.ha^{-1}$).

The key biological drivers of forest ecosystem processes can vary with time (forest succession) and space (disturbance history; Nilsson and Wardle 2005). The first structure we proposed for the spruce-moss stands corresponds to a middle-aged forest in which canopy closure is the main biological ecosystem driver. In this theoretical model, stand aboveground biomass affects understorey vegetation through variation in canopy closure. The second considers *Sphagnum* spp. as the cause instead of the consequence of the variation in stand aboveground biomass. This pattern is more suited to paludified forests where *Sphagnum* spp. cover and ground layer thickness constitute the most influent ecosystem drivers, more so than forest cover and stand aboveground biomass. Since this second structure best fitted our data, we can deduce that our sites were already quite advanced in the paludification process. The spruce-moss stands we selected for the first part of this study were relatively young and originated from the same fire (1976). Hence, the paludification we observe today on these sites has probably been favoured by a surface fire that burnt aboveground tree parts without completely removing the organic layer.

Spruce fine root growth was not stimulated by *Sphagnum* spp. removal, but it was stimulated by local fertilization. Hence, we can deduce that the absence of a *Sphagnum* spp. removal effect on spruce fine root biomass did not result from the lack of spruce reactivity to local environmental changes. Instead, it seems more likely that *Sphagnum* spp. removal did not sufficiently improve local root growth conditions to have visible consequences on spruce fine root biomass: either *Sphagnum* spp. effect on soil is long-lasting and continues long after removal, or *Sphagnum* spp. cover has limited effect on soil properties, at least in the case of a moderately thick moss layer. Another possibility is that the treated surfaces were too small to have significant effect on root growing conditions, given that *Sphagnum* spp. cover disruption at the stand level has been shown to positively influence soil properties and tree growth (Lafleur et al. 2010). *Sphagnum* spp. cover was not related to soil D.I.N. and its removal had no effect on soil nutrients. However, *Sphagnum* spp. removal seemed to increase the positive effect of fertilization on spruce fine root biomass, and significantly increased the fertilization effect on the accumulation of D.I.N. in the forest soil. This suggests that *Sphagnum* spp. may have immobilized part of the D.I.N. released from fertilizers or that the presence of a ground cover limited nutrient liberation from fertilizer pellets.

2.6.3 Management implications

Open pine-lichen and spruce-*Sphagnum* spp. woodlands occur naturally in the boreal forest. Hence, the restoration of forest productivity should not to be systematic and should only be encouraged in managed forests, especially on sites that have been modified by human interventions such as partial or total harvest. Three months of ground layer shading were not sufficient to significantly modify tree fine root biomass and soil properties in both lichen and *Sphagnum* spp. covers, which confirms that the shading effect of forest cover mainly consists in an indirect long-term influence on soil through change in ground layer composition. The contrasting effects of lichen and *Sphagnum* spp. cover on soil properties and tree fine root development indicate that the restoration of forest productivity in pine-lichen and spruce-moss woodlands may require different silvicultural approaches.

Lichen cover affects both pine fine root growth and soil nutrients, suggesting that nutrient management may be critical to restore forest productivity in excessively drained sites. Even if lichen removal locally stimulated pine fine root production in our experiment, the effect of lichen disturbance on tree regeneration at a larger scale may differ according to site conditions. Indeed, while Hébert et al. (2006) showed a positive effect of lichen disruption on jack pine growth on sites with good to moderate drainage, other studies suggested that lichen cover favours moisture retention in the surface soil in dry open woodlands and offers more appropriate conditions for jack pine germination and growth than bare soil or feather mosses (Bonan and Shugart 1989; Steijlen et al. 1995). Hence, favouring rapid reforestation that promotes rapid colonization of the understory by feather mosses would be more adapted than ground cover disruption in open dry forests to restore forest productivity in excessively drained sites.

Under poor drainage conditions, partial or total harvesting, similarly to low-intensity wildfires and contrary to severe fire disturbances, opens the forest canopy without seriously disturbing the ground layer. In this way, harvesting may favour *Sphagnum* spp. at the expense of feather mosses. According to our results, *Sphagnum* spp. removal did not modify fine root development and soil properties. However, path analysis showed that *Sphagnum* spp. can be the main driver of stand aboveground biomass reduction in paludified forest, indicating that *Sphagnum* spp. cover becomes very influential late in the paludification process. Indeed, low temperature, low oxygenation and excessive moisture, which are associated with *Sphagnum* spp. litter accumulation and may not induce particular root adaptations but rather a proportional reduction in both above- and belowground biomass, may be the most important factors limiting forest productivity (Gower et al. 1996; Fenton et al. 2006). Hence, controlling *Sphagnum* spp. moss development may be the only key to a successful management of these ecosystems (Thiffault et al. 2013).

2.7 Conclusion

In this study, we showed that lichen and *Sphagnum* spp. covers, which are favoured by conditions of canopy openness, contribute to maintaining stand openness by affecting tree growth conditions in different ways. Lichens affect pine growth conditions by reducing fine root biomass and modifying soil nutrients and major base cations. *Sphagnum* spp. cover, which was found to be a key driver of spruce biomass reduction on paludified sites, affects black spruce growth through the long-term impact of the accumulation of a thick organic layer on soil physical conditions. The application of a shading cover, as a simulation of forest cover recovery, had no short-term influence on the effects of lichen and *Sphagnum* spp. on tree fine root growth. In both cases, it appears that managing forest regeneration to accelerate canopy closure and favour feather mosses instead of lichens or *Sphagnum* spp. mosses may be crucial to restore forest productivity in sites characterized by extreme conditions of drainage.

2.8 Acknowledgements

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CHAPITRE III

LICHENS CONTRIBUTE TO OPEN WOODLAND STABILITY IN THE BOREAL FOREST THROUGH DETRIMENTAL EFFECTS ON PINE GROWTH AND ROOT ECTOMYCORRHIZAL STATUS

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En préparation pour soumission à *Journal of Vegetation Science*

3.1 Abstract

Questions: In the boreal forest, open lichen woodlands have been described as an alternative stable state to the feather moss closed-crown forest. Composition of the ground layer is known to influence many ecosystem functions in boreal forest stands. Do lichens contribute to open woodland stability in the closed-crown boreal forest by reducing jack pine regeneration and/or growth? If so, what are the drivers generating these effects?

Location: Pure *Pinus banksiana* Lamb. stands located on fluvioglacial coarse-grain deposits, spruce-moss bioclimatic domain, western Québec, Canada (49° 19’ N; 79° 11’ W).

Methods: Based on field and greenhouse experiments, we compared germination and growth of jack pine (*Pinus banksiana* Lamb.) seedlings and saplings on two types of ground cover, namely feather mosses (primarily *Pleurozium schreberi* (Brid.) Mitt.) and lichens (primarily *Cladonia stellaris* (Opiz) Pouzar & Vĕzda), using bare mineral soil as a control. We explored the drivers of ground cover effects by manipulating nutrient supply (N, P, K) and applying different levels of light availability to the ground layer, with the assumption that simulating the shade impact of a closed forest canopy would mitigate lichen effect on pine growth. Pine root ectomycorrhizal colonisation and diversity were examined as indicators of the ability of pine to uptake nutrients.

Results: For greenhouse-grown seedlings and for both greenhouse- and field-grown saplings, pine growth was significantly greater in feather moss than in lichen while germination was not affected by ground cover type. In the field, phosphorus and base cation availability was greater in feather mosses than in lichens. However, fertilisation did not entirely remove the negative effects of lichens on sapling growth in the greenhouse, suggesting that nutrient limitation in lichens was not the only factor accounting for the difference in pine growth between substrates. Lichen cover was also associated with reduced abundance and modified composition of the root ectomycorrhizal community, thus potentially contributing to reduced pine growth by limiting pine ability to uptake soil nutrients. Ground cover shading did not improve pine sapling growth.

Conclusions: Together, these results suggest that lichens are a less favourable substrate than feather mosses for jack pine seedling and sapling growth, at least in conditions of moderate dryness. Lichens are likely to limit pine regeneration, thus favouring the self-perpetuation of open lichen woodlands in the closed-crown boreal forest.

Keywords: *Cladonia* spp.; ecosystem bistability; ectomycorrhizae; feather moss; ground cover; jack pine; lichen woodland; pine regeneration; stable alternative state; terricolous lichen

3.2 Résumé

Questions : En forêt boréale, l'état de lande à lichens ouverte a été décrit comme un état stable alternatif de la forêt fermée à mousses hypnacées. La composition de la strate au sol est connue pour avoir des effets importants sur le fonctionnement de l'écosystème dans les peuplements forestiers boréaux. Les lichens contribuent-ils à stabiliser les clairières ouvertes au sein de la mosaïque forestière fermée en réduisant la régénération et/ou la croissance du pin gris ? Si oui, quels sont les facteurs à l'origine de ces effets ?

Localisation : Peuplements purs de *Pinus banksiana* Lamb. sur dépôts grossiers d'origine fluvioglaciaire, domaine bioclimatique de la pessière noire à mousses, ouest du Québec, Canada (49° 19' N ; 79° 11' W).

Méthodes : Basés sur des expériences menées en serre et sur le terrain, nous avons comparé la germination et la croissance de plantules et de jeunes plants de pin gris (*Pinus banksiana* Lamb.) sur deux types de couvert au sol, les mousses hypnacées (principalement *Pleurozium schreberi* (Brid.) Mitt.) et les lichens (principalement *Cladonia stellaris* (Opiz) Pouzar & Vĕzda), en utilisant un sol nu minéral comme contrôle. Nous avons exploré les facteurs responsables des effets de la strate des mousses et lichens en manipulant la disponibilité des nutriments (N, P, K) dans le sol forestier et en soumettant la végétation au sol à différents niveaux d'intensité lumineuse. Cette seconde manipulation est basée sur l'hypothèse selon laquelle la simulation d'un ombrage similaire à celui produit par la présence d'un couvert forestier est susceptible d'atténuer les effets du lichen sur la croissance du pin. La mycorhization des racines de pin gris et la diversité des ectomycorhizes associées ont été examinées dans la mesure où elles constituent des indicateurs de la capacité du pin à prélever les nutriments dans le sol.

Résultats : La croissance des plantules et des jeunes plants ayant poussé en serre ou sur le terrain a été significativement plus importante dans les mousses hypnacées que dans les lichens. La germination n’a pas été affectée par le type de couvert au sol. Sur le terrain, la disponibilité du phosphore et des cations basiques était plus grande dans les mousses hypnacées que dans les lichens. Cependant, dans la mesure où la fertilisation n’a pas entièrement supprimé les effets négatifs du lichen sur la croissance des jeunes plants en serre, nos résultats suggèrent que la limitation par les nutriments dans les lichens n’est pas le seul facteur responsable de la réduction de croissance du pin dans ce type de substrat. Le couvert de lichens était associé à un degré de mycorhization moindre et à une composition différente de la communauté des ectomycorhizes associées aux racines de pin gris. Ces deux facteurs ont potentiellement contribué à réduire la croissance du pin dans les lichens en limitant la capacité du pin à prélever les nutriments du sol. L’application d’un ombrage sur la strate au sol n’a pas amélioré la croissance des jeunes plants de pin gris.

Conclusions : L’ensemble de ces résultats suggère que les lichens constituent un substrat moins favorable que les mousses hypnacées pour la croissance des plantules et des jeunes plants de pin gris, du moins en conditions de sécheresse modérée. Il est donc vraisemblable que les lichens limitent la régénération du pin, favorisant de ce fait le maintien de landes à lichens ouvertes dans la matrice forestière boréale fermée.

Mots-clés : bistabilité de l’écosystème, *Cladonia* spp., ectomycorhize, état stable alternatif, lande à lichens, lichen terricole, mousse hypnacée, pin gris, régénération, végétation du sous-bois

3.3 Introduction

In the boreal forest, open lichen (*Cladonia* spp.) woodlands have been described as an alternative stable state to the feather moss (*Pleurozium schreberii* (Brid.) Mitt.) closed-crown forest (Jasinski & Payette 2005). Switching states, i.e. the conversion of closed-canopy forests into lichen woodlands, may result from repeated and/or combined disturbances such as fire, logging or insect outbreaks (Girard et al. 2008; DeLuca et al. 2013). Open lichen woodlands have been rapidly expanding in the closed-crown boreal forest in eastern Canada over the last 50 years (Girard et al. 2008). A better understanding of the factors contributing to switching and stabilizing the two alternative states of the ecosystem is needed to prevent forest management from accentuating forest opening and lichen woodland expansion in the landscape.

Jack pine (*Pinus banksiana* Lamb.) is a serotinous species, producing cones that remain closed until exposed to high temperatures such as those caused by fires (Gauthier et al. 1996). Post-fire jack pine regeneration depends on two key factors: seed availability and seedbed quality. While seed availability may be deficient in some stands as it relies on disturbance history (Girard et al. 2008; DeLuca et al. 2013), fire intensity (Sirois 1993) and post-fire salvage logging (Greene et al. 2013), seedbed quality is also crucial in xeric sites where seed germination and seedling growth are limited by dry conditions. Bare soil has been shown to constitute the most suitable seedbed for pine germination and establishment in the field (Greene et al. 2007). However, this result was not specific to the xeric sites.

High light intensity and associated microclimatic conditions encourage the formation of a thick layer of lichens in open woodlands (Sedia & Ehrenfeld 2003; Boudreault et al. 2013) while shaded conditions in closed-crown forests tend to favour understory colonisation by feather mosses (Sulyma & Coxson 2001). After fire, these two ground cover types offer contrasting seedbeds and growth conditions for conifer regeneration (Steijlen et al. 1995; Wheeler et al. 2011) by providing the seedlings with different levels of light, water and nutrient availability. Ground cover type influences soil carbon and nutrients through primary productivity (Bond-Lamberty & Gower 2007), organic matter decomposition (Lang et al. 2009), atmospheric nitrogen fixation (DeLuca et al. 2007), mineral nitrogen immobilisation (Startsev & Lieffers 2006) and drivers such as pH, temperature and moisture regimes (Cornelissen et al. 2007; Fauria et al. 2008). Cover also affects the structure of soil microbial communities (Ohtonen & Väre 1998; Sedia & Ehrenfeld 2003) either indirectly through effects on soil (e.g. decomposition and nutrient flow, Nilsson & Wardle 2005), or directly through allelopathy (Molnár & Farkas 2010).

Among soil microbial communities, fungi represent a significant amount of the microbial biomass in boreal forest (Högberg & Högberg 2002). They play important roles in ecosystems (Christensen 1989) and soil biogeochemical processes (Wardle et al. 2004). Ectomycorrhizae, symbiotic associations between select fungi and tree roots, favor tree nutrient uptake (Hinsinger et al. 2009; Peterson et al. 2004). In nutrient-poor conditions, tree growth is stimulated by the degree of ectomycorrhizal colonisation and has been correlated with the diversity of root-associated ectomycorrhizal fungi (Wardle et al. 2004).

It has been suggested that tree seed bank reduction could be one of the main factors responsible for tree establishment deficit and, therefore, for lichen woodland self-perpetuation in the boreal forest (Payette et al. 2000). Here, we investigate a second driver, seedbed quality in xeric sites, with the assumption that the formation of a thick lichen layer in open woodlands exacerbates tree regeneration and growth deficit, thereby stabilising an alternative open woodland state. The main objectives of this study were (1) to determine the differential effects of lichen and feather moss ground cover on jack pine germination, survival and growth, and (2) to identify the potential drivers that may be involved in those effects by manipulating nutrient supply and light availability to the ground cover, and by analyzing the effects of the ground cover type on soil nutrient availability, ectomycorrhizal colonisation and diversity.

3.4 Material and methods

3.4.1 Ground cover effect on jack pine: sowing and plantation experiments

Germination and seedling growth

Sixty square pots (size: 12 x 12 x 14 cm) were used to test the effects of three different ground cover types on pine germination in a greenhouse experiment: (1) 20 pots were filled with sand from the field, referred to as controls; (2) 20 were filled with sand and then covered by feather moss (mainly *Pleurozium schreberi* (Brid.) Mitt., 6-8 cm including living and dead organic matter); (3) 20 were filled with sand and covered by lichen (mainly *Cladonia stellaris* (Opiz) Pouzar & Vězda, 6-8 cm including living and dead organic matter). In May 2015, five seeds were sown on the surface of each pot (see Appendix A for details). Pots were watered twice a day with 10 mL of demineralised water and checked for germination every day for four weeks. On Day 28, three seedlings were selected per pot. Extra seedlings were removed and redeployed to pots with low germination rate of the same ground cover type. Pine seedlings were harvested in November 2015. The root system of one seedling per pot was randomly selected among the three individuals of each pot and frozen (-80 °C) for the analysis of the ectomycorrhizal colonisation and diversity. Below- and aboveground parts of the two other seedlings were dried (60 °C) and weighed separately. The small size of the square pots used in the seedling growth experiment made them susceptible to moisture regime modification due to ground cover type. Thus, soil water content at the end of the experiment was measured by weighing soil samples before and after air-drying (one week at 22 °C).

Greenhouse sapling growth

The three ground cover treatments described above were applied to 60 two-year-old jack pine saplings (see Appendix A for details) in May 2015 using 3 x 20 round pots

(23 cm in diameter, 24 cm deep). Pine roots were washed with demineralised water to remove nursery soil. Each tree was measured and weighed before planting. Ten pines were randomly chosen to calculate fresh to dry weight conversion factors. In November 2015, pine saplings were harvested and roots were washed with water to remove soil particles. Below- and aboveground parts were dried (60 °C) and weighed separately.

Field sapling growth

The field experiment took place in the boreal forest of western Quebec, in a pure jack pine stand located on fluvioglacial coarse-grain deposits (49°22' N, 79°13'W). Average annual temperature (1981-2010) was 0.0 +/- 2.9 °C (Joutel, QC, Environment Canada 2010). The ground cover was composed of alternating lichen and feather moss patches (1-5 m wide). Seventy two-year-old jack pine saplings (see appendix for details) were weighed and planted with intact root plugs in May 2014 (30 in feather mosses, 30 in lichens and 10 in bare soil, i.e. areas where feather mosses had been removed). Contrary to the greenhouse experiment, pine roots were not washed before field planting to favour their survival in harsh field conditions. Five additional pine saplings were used to calculate the fresh to dry conversion factor. Each type of ground cover was homogeneous within a radius of at least 50 cm around each planted pine. Pines were harvested in October 2015 and roots were washed with water. Below- and aboveground parts were dried at 60 °C and weighed separately.

3.4.2 Assessment of drivers associated with ground cover effects on pine growth

Manipulation of environmental variables

A fertilisation treatment was applied in two of the greenhouse experiments to test the influence of nutrient availability in each ground cover type. In July 2015, 0.05 g of water-diluted fertiliser (20 % Nitrogen, 7 % Phosphorus and 10 % Potassium, Plant-prod Smartcote®, Brampton, ON, Canada) was applied to 10 pots containing two-month-old seedlings per ground cover treatment. In addition, 2 g of controlled-release fertiliser (same concentrations, granulated form) were administered to 10 greenhouse saplings per ground cover type at the beginning of the sapling growth experiment (May 2015).

Given that lichen metabolism is affected by light and humidity availability in the understory (Boudreault et al. 2013), we manipulated those conditions using a shade cover in the field sapling growth experiment. The shade cover was used to simulate the impact of a closed forest canopy on the moss and lichen layer only. A 50 % shade cover (perforated net) was positioned 15 cm above the ground cover (below the sapling foliage) in a third of the lichen and feather moss plots (10 per ground cover type) and half of the bare soil plots (5 plots).

Soil nutrient analysis

Soil nutrient availability with respect to ground cover type was measured for both greenhouse and field sapling growth experiments. Substrates used in the greenhouse trials were subsampled before the experiment (May 2015), and soil samples from 10 pots per ground cover type (five fertilised and five non-fertilised) were harvested at the end of the experiment (November 2015). Soil properties of the plantation site used for the field sapling growth experiment were determined based on two mineral and eight organic samples per ground cover type (one mineral and four organic samples each per shade treatment) at the end of the experiment (October 2015). Mineral samples were air-dried and sieved at 2 mm. Organic samples were first sieved at 6 mm to remove large roots and debris, dried at 60 °C, then ground and sieved at 2 mm. NH4-N and NO3-N were extracted with a 2 M KCl solution and analysed by spectrophotometry (QuikChem R8500 Series 2, Lachat Instruments, Milwaukee, WI, USA). Phosphorus, potassium, calcium, magnesium and sodium were separated with a Mehlich extraction and analysed by inductively coupled plasma (ICP) using an optical emission spectrometer (OES) (Optima 7300 DV, Perkin Elmer, Waltham, MA, USA). Soil concentration in base cations was estimated by summing potassium, calcium, magnesium and sodium concentrations.

Ectomycorrhizal colonisation and identification

Ground cover effects on root ectomycorrhizal colonisation and diversity were examined to determine whether cover affects the ability of pines to uptake nutrients by impacting pine mycorrhization. Root tips from the six-month-old seedlings originating from seed sown in May 2015 were analysed. The whole root system of one seedling per pot was assessed. For each seedling, ectomycorrhizal colonisation rate was calculated as the number of colonised root tips divided by the total number of root tips. Colonised root tips were further categorised as different morphotypes using standard macroscopic and microscopic characters as previously described (Robertson et al. 2006), including reference to published descriptions (Agerer 1987-2008; Ingleby et al. 1990). Molecular identification of each ectomycorrhizal morphotype was performed. Total genomic DNA was isolated from a unique root tip using the QIAamp® genomic DNA extraction kit (Qiagen, Hilden, Germany), eluted with 40 µL of Buffer AE and stored at -30 °C until used. Using primers ITS1-F (Gardes & Bruns 1993) and ITS4 (White et al. 1990), 1 µL of DNA extract was used to amplify ectomycorrhizal/fungal ITS regions in a 25 µL reaction containing reaction buffer, 0.5 µM of each primer, 0.4 µM dNTPs (Invitrogen, Carlsbad, CA, USA) and 5 units Taq polymerase (New England Biolabs, Ipswich, MA, US). An MJ PCR was performed on a research PTC-200 Thermocycler (MJ-Research, St-Bruno, QC, Canada) with the following cycling conditions: initial denaturation at 94 ˚C for 1 min, followed by 35 cycles of 94 ˚C for 10 s, 53 ˚C for 30 s and 72 ˚C for 30 s, and a final elongation step at 72 ˚C for 10 min. Amplicon purification and sequencing (ABI3730xl, Applied Biosystems, Foster City, CA, US) were performed at the Genomic Sequencing and Genotyping Platform (Centre de Recherche du Centre Hospitalier de l'Université Laval, Québec, QC, Canada). Sequences were edited and cleaned in SeqMan Pro (DNASTAR Inc., Madison, WI, US). ITS sequences were clustered at 97 % of similarity and the NCBI GenBank database was queried using BLASTn (Altschul et al. 1990) to match the consensus sequences of each operational taxonomic unit (OTU) with their closest relatives present in the database. Nucleotide consensus sequences of each OTU were deposited in the NCBI GenBank database and are registered under accession numbers: KY353999–KY354009.

3.4.3 Statistical analysis

The effects of ground cover type on pine germination were tested using a generalised linear model based on a binomial distribution of the dependant variable (germination rate per pot 28 days after sowing). Residual dispersion was estimated at 1.65 and considered in the model analysis. Seedling growth was estimated summing the biomasses of the three individual seedlings per pot, while sapling relative growth for the greenhouse and the field experiments was calculated as the difference in sapling biomass between the beginning and the end of the experiment divided by the initial sapling biomass. The effects of ground cover type and fertilisation treatment on greenhouse seedling and sapling relative growth, as well as the effects of ground cover type and shade on field sapling relative growth were tested using linear models. The model for the field plantation did not consider the bare soil treatment because of an insufficient number of healthy trees at the end of the experiment (related to hare herbivory in the experimental site). For each experiment, treatment effects were tested on below- and aboveground growth separately, total growth, and root allocation, i.e., the difference between final and initial belowground biomass divided by the difference between final and initial total biomass. The effects of ground cover type and fertilisation on soil nutrient content, ectomycorrhizal colonisation and OTU number per seedling in the greenhouse, as well as the effects of ground cover type and shade on nutrient availability at the end of the field experiment were analysed using linear models. The effects of ground cover type and fertilisation on the composition of the ectomycorrhizal community (OTU) associated with the seedling roots were investigated using a redundancy analysis (RDA) after a Hellinger transformation of the presence-absence data (Borcard et al. 2011). A permutation test was used to check for RDA significance.

When necessary, the dependent variables were transformed to respect linear model conditions (square root or log-transformation). When homoscedasticity was not verified for one factor, supplementary parameters were used to estimate the variance associated with each level of a factor and models were analysed based on the maximum likelihood method. When data did not accurately fit into a specific distribution, we resorted to a bootstrap procedure in which treatment effect significance was deduced from the probability that the associated individual coefficient of the linear or generalised linear model was equal to zero considering the bootstrap confidence intervals (Fox & Weisberg 2012). We used contrasts to analyse the effects of ground cover *versus* bare soil in a first phase and to compare the effect of feather mosses and lichens in a second phase. All analyses were performed on R-3 software (R Foundation for Statistical Computing, Vienna, Austria), using the packages 'nlme' (Pinheiro et al. 2014), 'lme4' (Bates et al. 2015), 'car' (Fox & Weisberg 2011) and 'MASS' (Venables & Ripley 2002). See Appendix A for additional information on material and methods.

3.5 Results

3.5.1 Ground cover type effect on pine germination and growth

Greenhouse germination and seedling growth

The presence of a ground cover had a marginally significant positive effect on pine germination success after three weeks in the greenhouse (77 ± 5 % against 64 ± 6 % on bare soil, z = 1.91, *p*-value = 0.0557). Germination success was not significantly different between feather mosses and lichens (83 ± 6 % and 71 ± 5 %, respectively; z

= 1.55, *p*-value > 0.1). Six months after germination, 93.7 % of the seedlings had survived. Belowground, aboveground and total dry seedling biomass per pot was affected by ground cover type (Table 3.1), and the difference was substantial as the total biomass of feather moss-grown seedlings was more than twice that of seedlings grown on the other substrates (Fig. 3.1a). Root allocation was not different between ground cover and bare soil or between lichens and feather mosses (Table 3.1). Pots with lichens contained more water at the end of the seedling growth experiment than the feather moss pots (26.4 ± 0.8 % *vs* 21.4 ± 0.3 %, bootstrap coefficient = -1.78; $p < 0.001$).

Greenhouse sapling growth

Relative belowground growth was higher in feather mosses and bare soil than in lichens (Fig. 3.1b), while relative aboveground and total growth were not affected by ground cover type (Table 3.1). Pines allocated more biomass to roots in bare soil than in the presence of a ground cover, and more in feather mosses than in lichens (85 ± 4 %, 80 ± 3 % and 74 ± 5 %, respectively).

Field sapling growth

Forty-eight percent of the trees died in the field because of hare herbivory; we only considered healthy trees for the statistical analyses (N = 30). Relative aboveground and total growth was higher in feather mosses than in lichens, while belowground growth and root allocation was not affected by ground cover type (Table 3.1 and Fig. 3.1b).

Table 3.1 Treatment effects on seedling and sapling growth in greenhouse and field experiments. Significant *p*-values (95 % confidence interval) are given in bold. Transformation of the response variable is indicated in brackets (Sqrt or Log)

	Belowground			**Aboveground**			**Total**			**Root allocation**		
	β	t	*p*-value	β	t	*p*-value	β	t	*p*-value	β	t	*p*-value
Greenhouse seedlings	(Sqrt)			(Sqrt)			(Sqrt)			(Sqrt)		
Ground cover *vs* bare soil (1)	1.04	3.26	**0.0019**	1.04	6.43	**< .0001**	1.46	3.82	**0.0003**	-0.05	-1.28	0.2043
Lichens *vs* feather mosses (2)	4.00	5.18	**< .0001**	3.06	7.01	**< .0001**	5.03	5.15	**< .0001**	0.08	1.48	0.1437
Fertilisation (3)	1.33	1.71	0.0922	1.32	2.16	**0.0352**	1.88	1.95	0.0568	-0.11	-1.43	0.1585
Interaction (1) x (3)	-0.13	-0.28	0.7794	-0.01	-0.02	0.9879	-0.10	-0.19	0.8531	-0.05	-0.91	0.3644
Interaction (2) x (3)	2.72	2.49	**0.0159**	1.74	1.99	0.0517	3.20	2.31	**0.0245**	0.19	2.38	**0.0209**
Greenhouse saplings	(Log)						(Sqrt)			(Sqrt)		
Ground cover *vs* bare soil	0.01	0.18	0.8339	0.49	1.63	0.1096	0.14	0.45	0.6526	-0.15	-2.64	**0.0107**
Lichens *vs* feather mosses	0.15	2.79	**0.0073**	-0.09	-0.24	0.8077	0.60	1.71	0.0916	0.24	2.45	**0.0175**
Fertilisation	0.88	8.67	**< .0001**	7.41	10.97	**< .0001**	7.54	10.68	**< .0001**	-0.95	-6.01	**< .0001**
Field saplings*				(Sqrt)			(Sqrt)					
Lichens *vs* feather mosses	-32.5	-1.67	0.1070	-2.53	-2.09	**0.0462**	-2.32	-2.29	**0.0299**	6.28	0.87	0.3910
Shade	-29.2	-1.47	0.1520	-0.64	-0.52	0.6089	-1.00	-0.97	0.3421	-2.17	-0.30	0.7690

* The model used for the field sapling plantation does not consider bare soil because of an insufficient number of healthy trees at the end of the experiment. Dead or unhealthy trees were not considered in this model (N = 30).

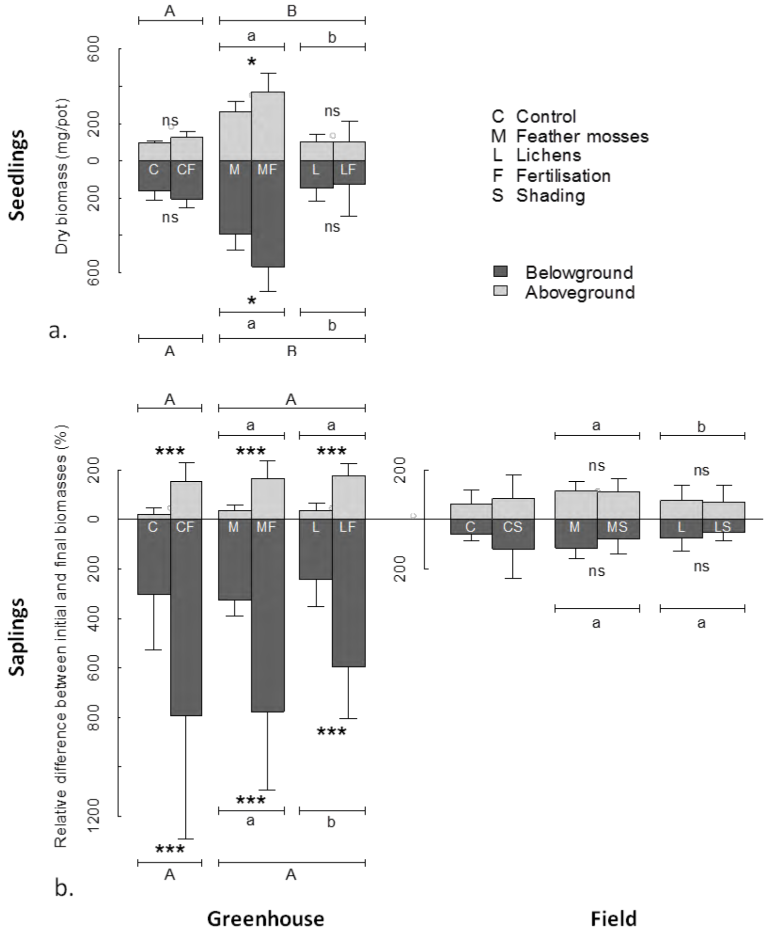

Figure 3.1 Treatment effects on (a) greenhouse seedling growth and (b) greenhouse and field sapling growth. Vertical lines represent the standard deviations of the above- and belowground biomass. Horizontal lines and letters indicate differences between ground cover types. Contrasts were used for the statistical analyses. The differences between ground cover and bare soil treatments are indicated by capital letters (A-B), while the differences between lichen and feather moss treatments are indicated by lower case letters (a-b). The differences between ground cover and bare soil were not analysed in the field sapling experiment because of an insufficient number of healthy trees on bare soil. The significance of fertilisation and shading effects are indicated for each ground cover type by asterisks (*** significant at 0.1 %, * significant at 5 %, ns non-significant)

3.5.2 Effects of fertilisation and ground cover shading on pine growth

Belowground, aboveground and total seedling growth was significantly enhanced by fertilisation in feather mosses only (Table 3.1 and Fig. 3.1a). Nutrient supply increased the total biomass of the seedlings that grew in feather mosses by 284 mg (+ 43.6 %) without significantly affecting seedling root allocation (Table 3.1). In contrast, sapling growth was positively affected by fertilisation in all ground cover types, and the intensity of this effect did not differ among the three ground cover types (Table 3.1 and Fig. 3.1b). Root allocation in saplings was significantly reduced in the case of fertilisation (regardless of the ground cover type, 64 ± 2 % for fertilised saplings compared to 80 ± 2 % for non-fertilised saplings) and this effect was similar for all ground cover types (Table 3.1). In the field, ground cover shading had no positive influence on the growth of pine saplings regardless of the ground cover type (Table 3.1 and Fig. 3.1b).

3.5.3 Treatment effects on soil nutrients

Pot nitrogen content at the end of the experiment was slightly affected by the presence of a ground cover when compared to bare soil (Table 3.2, NH_4^+: bootstrap coefficient = 0.05, p-value < 0.1; NO_3^-: bootstrap coefficient = -0.02, p-value < 0.05), with no difference between lichens and feather mosses (NH_4^+: bootstrap coefficient = -0.06, p-value > 0.1; NO_3^-: bootstrap coefficient = -0.01, p-value > 0.1). The phosphorus content of the pots was not affected by ground cover type (ground cover *vs* bare soil: bootstrap coefficient = -0.39, p-value > 0.1; lichens *vs* feather mosses: bootstrap coefficient = -0.65, p-value > 0.1). In the field, there were significantly more ammonium, phosphorus and base cations under ground cover than under bare soil, and significantly more phosphorus and base cations in feather mosses than in lichens (Tables 3.2 and 3.3). There was no detectable nitrate in the field organic soil samples.

Fertilisation had no effect on the soil nutrient content of the sapling pots at the end of the greenhouse experiment (data not shown). Ground cover shading negatively affected the ammonium content of the organic layer (-27.8 mg.kg^{-1} on average), especially in lichens (-73.4 mg.kg^{-1}) and, to a lesser extent, in bare soil (-27.1 mg.kg^{-1}), but not in feather mosses. Shade did not affect the phosphorus content of the organic layer and tended to increase the positive effect of feather mosses on base cations (Table 3.3).

Table 3.2 Available nutrient concentrations in the substrate at the end of two sapling experiments by ground cover type (mean ± SE, additional treatments are not considered here but are available in Appendix B). Bare soil values in bold indicate a significant effect of ground cover on soil nutrients (ground cover *vs* bare soil), while feather moss values in bold indicate a significant difference between lichens and feather mosses (confidence interval = 95 %)

Experiment	**Soil**	**Ground cover**	**NH$_4^+$** (mg.kg^{-1})	**NO$_3^-$** (mg.kg^{-1})	**P** (cmol.kg^{-1})	**Major base cations** (cmol.kg^{-1})
Greenhouse	Mineral	Bare soil	0.77 ± 0.05	**0.50 ± 0.10**	57.43 ± 1.03	0.13 ± 0.01
		Feather mosses	0.90 ± 0.04	0.41 ± 0.05	58.85 ± 2.47	0.16 ± 0.01
		Lichens	0.96 ± 0.08	0.38 ± 0.01	58.95 ± 1.25	0.16 ± 0.01
Field	Mineral*	Bare soil	1.35 ± 0.01	0	2.85 ± 0.57	0.19 ± 0.00
		Feather mosses	1.52 ± 0.09	0	4.29 ± 0.81	0.26 ± 0.01
		Lichens	1.39 ± 0.02	0.08 ± 0.06	0.52 ± 0.37	0.13 ± 0.06
	Organic	Bare soil	**75.3 ± 7.9**	0	**87.6 ± 8.4**	**6.63 ± 0.42**
		Feather mosses	120.4 ± 16.0	0	**146.9 ± 18.0**	**9.3 ± 0.32**
		Lichens	156.4 ± 6.0	0	45.8 ± 8.3	5.91 ± 0.76

*Differences between ground cover types were not tested for the field mineral soil samples since average values are based on two samples only.

Table 3.3 Treatment effects on nutrient contents of the organic layer for the field sapling experiment. Significant *p*-values are given in bold (* $p < 0.05$, ** $p < 0.01$)

	NH_4^+			**P**			**Base cations**		
	Estimate	*t*-value	*p*-value	Estimate	*t*-value	*p*-value	Estimate	*t*-value	*p*-value
Ground cover *vs* bare soil (1)	21.02	4.04	**0.0016 ****	11.90	2.32	**0.0361***	0.51	2.64	**0.0215***
Lichens *vs* feather mosses (2)	17.99	2.00	0.0688	-25.27	-2.84	**0.0130***	-1.14	-3.41	**0.0052****
Shade (3)	-27.75	-2.67	**0.0204***	1.70	0.12	0.9082	-0.04	-0.10	0.9253
Interaction (1) x (3)	-0.32	-0.04	0.9660	-	-	-	0.19	0.70	0.4962
Interaction (1) x (2)	-45.31	-3.56	**0.0039****	**-**	**-**	**-**	-1.78	-3.77	**0.0027****

3.5.4 Ectomycorrhizal colonisation and diversity

Only the root tips of healthy roots were analysed; therefore, the effect of lichens was estimated on a smaller seedling sample size (15 root systems for lichens instead of 20 each for bare soil and feather mosses). When considered together against the control, feather moss and lichen covers did not increase the ectomycorrhizal colonisation rate (ground cover *vs* bare soil: t = 1.31, *p*-value > 0.1). However, this rate was higher for seedlings growing in feather mosses than the ones growing in lichens (Table 3.4, lichens *vs* feather mosses: t = 2.29, *p*-value = 0.0268). Mycorrhizal root tips were categorised into seven morphotypes, from which eleven different OTUs were recorded (see Appendix B for details). Number of OTUs per seedling root system was higher under ground cover than under bare soil (bootstrap coefficient = 0.14, *p*-value < 0.01), and higher under feather mosses than under lichens (bootstrap coefficient = 0.31; *p*-value < 0.05, Table 3.4). OTU composition was significantly affected by ground cover type (Fig. 3.2). RDA explained 35 % of the total variance (F = 10.68; p-value < 0.001). Only the first axis was significant (F = 29.95, p-value < 0.001), explaining about 21 % of the total variance. The OTUs associated with the seedlings that grew in feather mosses were different from those associated with the seedlings that grew in control, and the OTU assemblage associated with the seedlings that grew in lichens was intermediate (Fig. 3.2). Fertilisation did not affect ectomycorrhizal colonisation (t-value = -1.28, *p*-value > 0.1) nor diversity (bootstrap coefficient = 0.02, *p*-value > 0.1), nor OTU composition (Fig. 3.2).

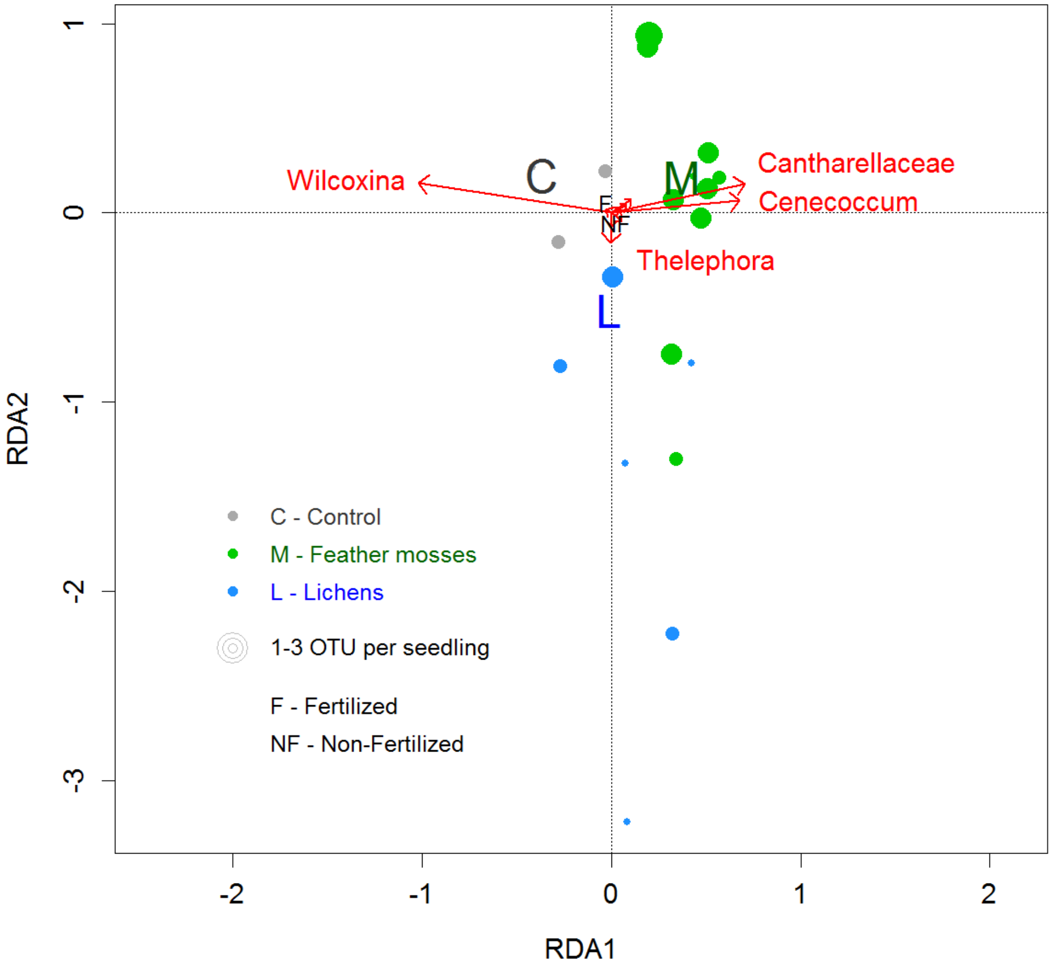

Figure 3.2 Effects of ground cover type and fertilisation on the composition of the ectomycorrhizal community associated with each greenhouse seedling (OTU composition). Only the four most abundant OTUs are represented for readability. Site scores (each corresponding to one seedling) are given as weight average. RDA is constrained by ground cover type and fertilisation treatment: Adjust $R^2 = 35$ %; $F = 10.68$; p-value < 0.001. Axis RDA 1: $R^2 = 0.21$; $F = 29.95$, p-value < 0.001. Axis RDA 2: $R^2 = 0.01$; $F = 1.37$, p-value $= 0.22$.

Table 3.4 Ectomycorrhizal colonisation and diversity per greenhouse seedling (mean and range) and total number of OTUs by ground cover type. All greenhouse seedlings are considered regardless of fertilisation treatment. Different letters indicate significant differences between ground cover types (confidence interval of 95 %)

	Seedling					**Total number of OTUs**
	Number of root tips	**Colonisation rate**		**Number of OTUs**		
Bare soil	351 (190-520)	0.57 (0.21-0.72)	**A**	1.25 (1 – 2)	**A**	3
Feather mosses	778 (390-1600)	0.71 (0.45-0.89) **a**	**A**	2.60 (1 - 4) **a**	**B**	9
Lichens	134 (20-1010)	0.45 (0.14-0.82) **b**		1.36 (1 – 3) **b**		7

3.6 Discussion

3.6.1 Influence of ground cover type on pine germination and growth

Our greenhouse experiment shows no differential effect of lichens and feather mosses on jack pine germination. However, despite differences in the magnitude of the effects and in above- and belowground responses, all three growth experiments (seedlings, greenhouse and field saplings) indicated that jack pine grew better in feather mosses than in lichens. These results are especially consistent as field and greenhouse experiments were used as complementary approaches. Field plantation did not allow for a complete randomisation of sapling placement and possibly introduced a slight bias, given that ground composition may be linked to localised microenvironmental conditions such as light, temperature, moisture or soil characteristics (Boudreault et al. 2013; Haughian & Burton 2015). In contrast, greenhouse watering and light levels were the same for all ground cover types, enabling us to isolate the effect of ground cover.

Root growth for pine saplings of equivalent aboveground biomass was substantially greater under greenhouse conditions compared to the field, resulting in a much higher total biomass. Although the greenhouse experiment was shorter in duration than the field experiment, the treatment effect may have been amplified by the favourable temperature, moisture and light conditions that enhanced sapling belowground growth in the greenhouse. Inversely, higher variation in aboveground biomass increment in the field may have been related to the longer duration of this experiment compared to the greenhouse one (two growing seasons against only one in the greenhouse). Transplant shock (Struve, 2009) must have been stronger in the harsh field conditions than in the greenhouse and may explain the lower response of field saplings to experimental treatments. Difference in magnitude of the effects between the two experiments may also be related to root washing of all soil residues prior to planting in the greenhouse experiment, perhaps making these saplings more receptive to their new growth environment. In contrast, field saplings were planted with intact root plugs, within which roots are often constrained and may be slower to colonise their new soil environment. Root plugs may have also offered nutrient-rich environments compared to the surrounding soil.

3.6.2 Lichen effect on pine growth: identification of potential drivers

Our results, along with those of previous studies (Ohtonen & Väre 1998; Sedia & Ehrenfeld 2005; Wheeler et al. 2011; DeLuca et al. 2013), indicate that, under field conditions, lichen cover is associated with lower availability of soil nutrients, including P and base cations, compared to feather mosses. High lichen albedo reduces soil temperature (Kershaw et Rouse 1971; Bernier et al. 2011). Thereby, lichens decrease microbial activity and organic matter decomposition rates (Sedia & Ehrenfeld 2006), and lead to a reduction in soil nutrient availability (Ohtonen & Väre 1998; DeLuca et al. 2013; Pacé et al. 2017). In contrast, feather mosses may increase soil nutrient availability through atmospheric nitrogen fixation (DeLuca et al. 2007). Despite this, the effect of fertilisation on greenhouse sapling growth was the same regardless of ground cover type, although one might expect a more positive effect in lichens compared to feather mosses.

Fertilised seedlings and saplings remained smaller in lichens than in feather mosses, suggesting that low nutrient availability was not the only factor reducing pine growth in lichens. In another greenhouse experiment conducted in similar conditions, we observed that lichen leachates reduced jack pine sapling growth (Pacé et al. in preparation), indicating the existence of chemical interference *via* the soil solution between the two organisms as already suggested in the literature (Crittenden 2000; Sedia & Erhenfeld 2003, Molnár & Farkas 2010).

The increased seedling and sapling growth found in feather mosses may have been promoted by higher levels of mycorrhizal colonisation and diversity that possibly improved soil nutrient uptake under this ground cover type. Fungal/bacterial biomass ratio has been positively correlated with soil organic matter content (Frostegård & Bååth 1996). Thus, we can suppose that higher ectomycorrhizal colonization and higher OTU diversity under feather mosses compared to bare soil were linked to the presence of soil organic matter. Mycorrhizal colonization and OTU richness were lower under lichens than under feather mosses. This suggests possible facilitative or inhibitory relationships between ground cover types and specific ectomycorrhizal associations, or differences in growth stages and soil exploration between the two ground cover types. Lichens have been suspected to inhibit root colonization by ectomycorrhizae, either through direct effects such allelopathy (Brown & Mikola 1974) or indirect effects *via* their impact on soil physical conditions (Ohtonen & Väre 1998; Sedia & Ehrenfeld 2003).

Simulating the shading effect of a closed forest cover did not limit the negative impact of lichens on pine growth. The application of a shade cover above the ground layer might have reduced secondary metabolism in lichens, but the effect was not strong or long enough to modify lichen influence on field sapling growth. However, it reduced ammonium availability under lichens, suggesting a negative shade effect on nitrogen mineralisation through a reduction in temperature.

3.6.3 Lichen contribution to open woodland stability

The transition between alternative stable states, i.e. from a closed forest to an open lichen woodland, is presumably first initiated by successive disturbances that reduce the seed bank of the stand (Payette et al. 2000; Pinno et al. 2013). Canopy opening favors lichens at the expense of feather mosses (Sulyma & Coxson 2001, Pacé et al. in press), and our results suggest that this change in ground layer composition is likely to degrade pine growth conditions through different mechanisms including long-term reduction of soil nutrient availability and chemical interferences. The negative effects of lichen cover on root mycorrhization also suggest that the presence of this ground cover type may contribute to reduce jack pine ability to uptake nutrients (Wardle et al. 2004). Feather moss replacement by lichens in open woodlands is thus likely to constitute an important factor of stabilisation of the open woodland state by aggravating the tree growth deficit initiated by seed rarefaction.

Our results, along with those of Wheeler et al. (2011), indicate that feather moss cover constitutes a better substrate than lichens for jack pine early development. However, our experiments were conducted under favourable moisture conditions (greenhouse and ~ 60 % forest cover) while post-fire pine regeneration mainly occurs in open sites that can be subject to drier conditions. While we showed a positive influence of feather mosses on pine growth through effects on nutrient availability and ectomycorrhizal colonisation, water availability may also constitute a crucial limiting factor in post-fire sites with no canopy (Girard et al. 2011). As suggested by the higher soil moisture found under lichens than under feather mosses, lichens may help maintain a higher moisture level in full-light dry conditions by favoring water retention in the surface soil (Kershaw & Rouse 1971; Bonan & Shugart 1989) through a lower evapotranspiration rate than feather mosses (Lafleur & Schreader 1994). Therefore, dry field conditions might change the positive effect of feather mosses to a negative one, resulting in a reduced global success of conifer recruitment in feather mosses compared with lichen seedbeds (e.g. only 3 % for Scot pines in Steijlen et al. 1995). Despite the fact that germination and tree growth were lower in lichens, high-density seed sowing and tree plantation in lichen woodlands may be an efficient way to re-establish a forest cover in these sites, as suggested by other studies (Sirois 1993; Tremblay et al. 2013).

In conclusion, our study shows that lichens constitute a less favourable substrate compared to feather mosses and bare soil for early jack pine development. Although lichens did not reduce germination success compared to feather mosses, they reduced the growth of seedlings and 2-year-old saplings through their influence on soil nutrients and ectomycorrhizal communities. Our results support the hypothesis that lichens constitute an exacerbating factor of the tree growth deficit that would prevent pine stand re-closure and stabilise an alternative open woodland state in the closed-crown boreal forest of eastern Canada.

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CHAPITRE IV

DIFFERENTIAL EFFECTS OF FEATHER MOSSES AND *SPHAGNUM* SPP. ON BLACK SPRUCE GERMINATION AND GROWTH

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En préparation pour soumission à *Forest Ecology and Management*

4.1 Abstract

The composition of the bryophyte layer influences forest growth, and this effect is likely to be mediated by its effects on soil conditions. We use an experimental approach to examine the differential effects of *Sphagnum* spp. and feather mosses on black spruce germination and growth, specifically the role of nutrient limitation in generating these effects. We also simulated the shade impact of a closed forest canopy on the ground layer with the assumption that it would influence bryophyte effect on tree growth. *Sphagnum* spp. mosses did not affect spruce germination and seedling growth (0-6 months) in the greenhouse. However, fertilization removed the negative effect of *Sphagnum* spp. on greenhouse sapling growth (2 year-old), suggesting that saplings grew less in *Sphagnum* spp. mosses than in feather mosses because of lower soil nutrient availability. These effects were not visible in the field plantation where sapling growth was also limited by harsh environmental conditions. Ground cover shading did not have any short-term positive impact on spruce growth. These results suggest that *Sphagnum* spp. mosses not only affect spruce sapling growth through the build-up of an organic layer often associated to low soil temperature and excess water, but also through more direct effects on nutrient availability. Therefore, silvicultural treatments that would favor *Sphagnum* spp. expansion, such as partial or total harvesting with protection of regeneration and soils, may result in subsequent tree growth problems even in sites with moderate organic layer accumulation.

4.2 Résumé

La composition de la strate des bryophytes influence la croissance forestière *via* ses effets sur les conditions du sol. Notre approche expérimentale vise à examiner les effets différentiels de la sphaigne et des mousses hypnacées sur la germination et la croissance de l'épinette noire, en s'intéressant plus spécifiquement au rôle de la limitation par les nutriments. Nous avons également simulé l'effet d'ombrage lié à la présence d'un couvert forestier fermé au-dessus de la strate des bryophytes en vue d'en mesurer l'impact sur la croissance des arbres. Les sphaignes n'ont pas affecté la germination de l'épinette et la croissance des plantules en serre (0-6 mois). Cependant, la fertilisation a supprimé l'effet négatif des sphaignes sur la croissance des jeunes plants en serre (2 ans), suggérant que les sphaignes offrent des conditions de croissance moins favorables que les mousses hypnacées dans la mesure où elles sont associées à une disponibilité moindre des nutriments dans le sol. Ces effets n'étaient pas visibles sur les arbres plantés *in situ* sans doute parce que la croissance des plants y était également limitée par des conditions environnementales plus rudes. L'application d'un ombrage sur la strate muscinale n'a pas eu d'effet positif à court-terme sur la croissance des jeunes plants. Ces résultats suggèrent que les sphaignes n'affectent pas seulement la croissance des épinettes *via* leurs effets à long-terme sur l'accumulation de la couche organique et l'humidité accrue du sol, mais aussi *via* des effets plus directs sur la disponibilité des nutriments dans le sol forestier. Ainsi, les traitements sylvicoles qui affectent peu le sol et qui sont susceptibles de maintenir ou de favoriser l'expansion de la sphaigne dans le parterre forestier, tels que la coupe partielle ou la coupe avec protection de la régénération et des sols, peuvent mener à des problèmes subséquents de régénération ligneuse, et cela même dans les sites forestiers non fortement entourbés.

4.3 Introduction

There is an increasing awareness of the influence the bryophyte layer has on ecosystem function in different ecosystems, including boreal forests (Cornelissen et al., 2007; Turetsky et al., 2012). The composition of this layer can affect, among others, soil carbon as well as nutrient accumulation and cycling (Bond-Lamberty and Gower, 2007; Lang et al., 2009; Lindo and Gonzalez, 2010) with visible consequences on ecosystem processes and states (Pacé et al. 2017). An example is the long-term decline in forest productivity associated with paludification that is directly driven by ground layer composition changes (Lavoie et al., 2005; Simard et al., 2007). The functional traits of *Sphagnum* spp. mosses, which have a higher net primary productivity (Bisbee et al., 2001; Swanson and Flanagan, 2001; O'Connell et al., 2003) and a lower decomposition rate (Lang et al., 2009; Fenton et al., 2010) than feather mosses, favor long-term organic matter accumulation and water table rise (Fenton et al., 2005; Fenton et al., 2006). This results in a decrease in soil oxygenation and temperature, which in turn reduces microbial activity and nutrient availability in the organic layer (Gower et al., 1996; Elliott-Fisk, 2000). Although these long-term effects of feather moss replacement by *Sphagnum* spp. mosses are relatively well-known, there is still sparse information on the short-term effects of this change on tree growth conditions i.e. before *Sphagnum* spp. cover is associated with the accumulation of a thick organic layer.

Black spruce (*Picea mariana* [Mill.] B.S.P.) is one of the most widespread and important commercial tree species in the North American boreal forest (Gagnon and Morin, 2001). Because it is tolerant to nutrient-poor conditions, this tree species is able to colonize a wide range of environments from wet peatlands to highly-drained sandy soils. Several studies have reported deficits of black spruce growth after low severity fires (Fenton et al., 2005; Lecomte et al., 2006; Simard et al., 2007) and careful logging

(Fenton and Bergeron, 2007; Lafleur et al., 2010a, 2010b). These regeneration problems have been attributed to the bryophyte layer and its effect on soil conditions.

The effects of *Sphagnum* spp. mosses on black spruce germination and growth have mainly been investigated in paludified sites (Ohlson and Zackrisson, 1992; Groot and Adams, 1994; Hörnberg et al., 1997; Lavoie et al., 2005; Lafleur et al., 2011), and thus the direct effects of living *Sphagnum* spp. mosses on black spruce have rarely been separated from their long-term effects *via* the gradual accumulation of fibric material on the forest soil. Moreover, few studies have tested the differential effects of intact living layers of *Sphagnum* spp. and feather mosses on tree growth in conditions of complete randomisation of sapling location (Stuiver et al., 2014 for *Pinus sylvestris*) - i.e. independently of the micro-environmental conditions that are closely related to ground cover composition in the field such as light, temperature, moisture or soil characteristics (Bisbee et al., 2001; Fenton and Bergeron, 2006) - and little is known about the main drivers behind these effects. We propose to (1) determine the differential effects of living *Sphagnum* spp. and feather mosses on black spruce germination, survival and growth in both paludified field and greenhouse fully-randomized conditions, and (2) explore the drivers associated with these effects by investigating the role of nutrients and analyzing how these effects are impacted by ground cover shading. We hypothesize that a ground layer of living *Sphagnum* spp. facilitates germination but constitutes a less suitable substrate for spruce seedling and sapling growth than feather mosses as it is associated with a lower soil nutrient availability. We also suppose that the shade provided by a closed forest cover reduces the effect of *Sphagnum* spp. on tree growth by affecting moss metabolism.

4.4 Material and methods

4.4.1 Living material and substrate

Picea mariana [Mill.] B.S.P. seeds and saplings originated from provincial nurseries of the Natural Resource Minister of Québec. Seeds (germination success = 99 %; germinative value = 46) were produced in the forest seed center of Berthier (Sainte-Geneviève de Berthier, Québec, Canada). Saplings came from the provincial nurseries of Guyenne and Trécesson (Abitibi, Québec, Canada) where they grew in greenhouses for two years. Spruce sapling growth in nurseries was stimulated by the application of fertilizers. Living material (feather and *Sphagnum* spp. mosses) and substrate (1 m deep humic peat, decomposition stage was 6-7 on the von Post scale, Stanek and Silc, 1977) were harvested in May 2015 in the boreal forest of western Québec (spruce-moss bioclimatic domain, Bergeron et al., 1999). Substrate was harvested in a highly paludified black spruce-moss stand (organic layer > 1 m; 49° 44' N, 79° 17' W). Moss layers (living moss and dead material) were harvested in a non-paludified forest characterized by alternating feather and *Sphagnum* spp. moss patches (49° 44' N; 79° 17' W). Dead material origin did not systematically correspond to the moss type above, e.g. a *Sphagnum* moss layer could include feather moss dead material. The two sampling sites were located on lacustrine clay deposited by the proglacial lake Ojibway (Blouin and Berger, 2005). Common understory plant species were *Rhododendron groenlandicum* (Oeder) Kron & Judd, *Kalmia angustifolia* L., and *Vaccinium angustifolium* Ait. Ground covers were harvested with their associated poorly to well-decomposed dead organic matter and Ericaceae (above and belowground parts) were entirely removed from the moss and lichen layer. Harvested *Sphagnum* spp. mosses were mainly *Sphagnum capillifolium* (Ehrh.) Edw., *S. angustifolium* (C. Jens. ex Russ.) C. Jens., *S. fuscum* (Schimp.) Klinggr., and *S. magellanicum* Brid. Feather moss covers were dominated by *Pleurozium schreberii* (Brid.) Mitt. with few occurrences of

Polytrichum strictum Brid., *Dicranum polysetum* Swartz, and *Ptilidium ciliare* (L.) Hampe.

4.4.2 Ground cover effect on black spruce: sowing and plantation experiments

Germination

60 square pots (size: 12 x 12 x 14 cm) were used to test the effects of three different ground cover types on spruce germination in a greenhouse experiment: (1) 20 pots were filled with the peat harvested in the field, referred to as controls; (2) 20 were filled with the peat from the field (6 to 8 cm) and then covered by feather moss (6 to 8 cm including living mosses and organic matter); (3) 20 pots were filled with peat and covered by *Sphagnum* spp. (including living *Sphagnum* spp. and organic matter). Spatial distribution of the pots assigned to these three treatments was randomly determined. In May 2015, five seeds were sown on the surface of each pot. Pots were watered twice a day with 10 mL of demineralized water and checked for germination every day for three weeks.

Seedling establishment and growth

Three weeks after spruce seed germination, three seedlings originating from the germination experiment were selected per pot. Extra germinated seeds were removed and attributed to low germination success pots characterized by the same ground cover type. Spatial distribution of the seedling pots was randomized once a month for the duration of the seedling experiment *i.e.* five times from June to November 2015. Pots were watered with demineralized water twice a day (10 mL per pot) throughout the summer 2015 to spare seedlings from water stress. Watering was progressively reduced to 10 mL once a day in September 2015 and to 10 mL three times a week in October and November 2015. Spruce seedlings were harvested in November 2015. Below and aboveground parts of the seedlings were dried (60°C) and weighed separately.

Greenhouse sapling growth

The three same ground cover treatments as previously described were applied to 60 two year-old spruce saplings in a greenhouse: (1) 20 round pots (23 cm in diameter, 24 cm deep) were filled with peat from the field (control pots) while the 40 others were filled with peat (16-18 cm) and covered with (2) a living layer of feather mosses or (3) a living layer of *Sphagnum* spp. mosses (6 to 8 cm including living and dead organic matter). Spruce sapling roots were washed with demineralized water to remove nursery soil. Each tree was measured and weighed before planting. 10 spruces were used to calculate fresh to dry weight conversion factors. Spruce placement in the greenhouse was randomized once a month from May to November 2015. Pots were watered twice a day with demineralized water at a rate of 60 mL per pot and per day from May to August 2015 to spare saplings from water stress. Watering was reduced to 30 mL per day in September 2015 and to 30 mL three times a week in October and November 2015. In November 2015, the spruce saplings were harvested and roots were washed with water to remove soil particles. Below and aboveground parts were dried (60°C) and weighed separately. For each greenhouse experiment, temperature and air humidity were recorded each hour from May to November 2015 (Table 4.1) using HOBO® data loggers (HOBO® U23 PRO V2, Onset Data Loggers, Bourne, MA).

Field sapling growth

The field experiment took place in the boreal forest of western Québec, in a pure *Picea mariana* [Mill.] B.S.P. stand located on lacustrine clay deposits (49°44’N; 79°17’W) and originating from a fire that occurred in 1976. The average annual temperature (1981-2010) is 0 +/- 2.9°C and the average annual precipitation is 909.1 millimeters (Joutel (QC), Environment Canada, 2016). Understory plant species, including mosses and Ericaceae, were the same as mentioned above. The ground layer was composed of alternating feather and *Sphagnum* spp. moss patches (1-5 meters wide). The field plantation site (about 1 ha) originated from a fire that occurred in 1976 and presented evident signs of paludification including low stand aboveground biomass (15.4 $Mg.ha^{-1}$) and a thick organic layer (70 cm in average).

Seventy spruce saplings were weighed and planted with their root plug in May 2014. Thirty spruces were planted in feather mosses, 30 in *Sphagnum* spp. mosses and 10 in bare organic soil where feather mosses had been removed. There were no more than two planted saplings per patch of one ground cover type. Patches of the two moss types were well-dispersed in the site and saplings were considered as randomly distributed (no clumping by moss type). Five additional spruce saplings were used to calculate a fresh to dry conversion factor. Contrary to the greenhouse experiment, spruce roots were not washed before field planting to favor their survival in harsh field conditions. Each type of ground cover was homogeneous within a radius of at least 50 cm around the spruce sapling. Before planting, the aboveground parts of the Ericaceae were removed by cutting the stems at the soil surface. Ericaceae roots were not removed to avoid ground cover disturbance. To account for a possible bias in light availability due to the higher abundance of *Sphagnum* spp. mosses in forest openings (Fenton and Bergeron, 2006), canopy closure was measured in July 2014 using fish-eye photos at each sapling location. Photos were analyzed in terms of percent of pixels attributable to trees using Adobe Photoshop Elements software. This analysis revealed an average canopy closure of 75 % with no significant differences between ground cover types (F-value = 0.08, p-value > 0.1). Air temperature and humidity 10 cm above ground were recorded hourly from July 2014 to October 2015 using HOBO® data loggers (Table 4.1). Spruce saplings were harvested in October 2015 and roots were washed with water. Below and aboveground parts were dried at 60°C and weighed separately.

Table 4.1 General characteristics and environmental conditions associated with the four experiments

	Location	Duration	Additional treatment	Period	Temperature			Air humidity		
					Mean	Range	SD	Mean	Range	SD
Germination	Greenhouse	3 weeks	-	May 2015	21.2 ˚C	11.9-33.6 ˚C	3.7 ˚C	60.8 %	13.3-100.0 %	23.7 %
Seedling growth	Greenhouse	6 months	Fertilization (2 levels)	June 2015 to Nov. 2015	21.2 ˚C	11.9-33.6 ˚C	3.7 ˚C	60.8 %	13.3-100.0 %	23.7 %
Sapling growth	Greenhouse	7 months	Fertilization (2 levels)	May 2015 to Nov. 2015	21.5 ˚C	12.6-39.6 ˚C	4.1 ˚C	60.2 %	10.8-100.0 %	24.4 %
	Field	18 months	Shading (2 levels) Fertilization (2 levels)	July 2014 to Oct. 2014	10.8 ˚C	-10.5-41.8 ˚C	9.4 ˚C	90.8 %	19.3-100 %	17.2 %
				Nov. 2014 to May 2015	-0.7 ˚C	-12.9-32.5 ˚C	6.5 ˚C	81.3 %	1-100 %	14.4 %
				May 2015 to Oct. 2015	15.0 ˚C	-9.1-46.5 ˚C	9.6 ˚C	88.6 %	15.1-100 %	17.8 %

4.4.3 Exploring the drivers associated with ground cover effect on spruce growth

Manipulation of environmental variables: fertilization and ground cover shading

A fertilization treatment was applied in the field and two of the greenhouse experiments to test the influence of nutrient availability in each ground cover type. Water-diluted fertilizer (0.05 g, 20% Nitrogen, 7% Phosphorus and 10% Potassium, Plant-prod Smartcote®) was applied to 10 two months-old seedlings per ground cover type in July 2015. In addition, 2 g of controlled release fertilizer (same nutrient concentrations in granulated form, Plant-prod Smartcote®) were administered to 10 saplings per ground cover type in the greenhouse experiment and 10 saplings per ground cover type except bare soil in the field experiment in May 2015.

As forest cover affects light availability, temperature and humidity in the understory, it may have an impact on moss metabolism (Swanson and Flanagan, 2001; Gundale et al., 2012; Stuiver et al., 2015) and thus modify the effects of ground layer composition on spruce sapling growth. A 50% shade cloth (standard perforated net used in horticulture) was used to simulate the impact of a closed forest canopy on the moss layer only. The shade cover was positioned 15 cm above the ground cover (below the sapling foliage) in a third of the *Sphagnum* spp. and feather moss plots (10 plots per ground cover type) and half of the bare soil plots (5 plots) in the field sapling growth experiment.

Soil nutrient analysis

The effect of ground cover type on soil nutrient availability was estimated for both greenhouse and field sapling growth experiments. Samples of the substrate used to fill the pots of the greenhouse plantation were harvested before the experiment in May 2015 for soil analyses. Potting soil samples (randomly sampled from the whole pot content) of 10 pots per ground cover type (five fertilized and five non-fertilized) were harvested at the end of the experiment in November 2015. In the field sapling growth experiment, three organic samples per treatment type (top 20 cm of the organic layer) were harvested in October 2015 to analyze the effects of the different treatments on nutrient availability. Organic samples were first sieved at 6 mm to remove large roots and debris, dried at 60°C, then ground and sieved at 2 mm. NH4-N and NO3-N were extracted with a 2 M KCl solution and analyzed by spectrophotometry (QuikChem R8500 Series 2, Lachat Instruments, Milwaukee, WI). Phosphorus, potassium, calcium, magnesium and sodium were separated with a Mehlich extraction and analyzed by inductively coupled plasma (ICP) using an optical emission spectrometer (OES) (Optima 7300 DV, Perkin Elmer, Waltham, MA). Soil concentration in base cations was estimated by summing potassium, calcium, magnesium and sodium concentrations.

4.4.4 Statistical analysis

We first tested the effects of ground cover type on spruce germination using a generalized linear model based on a binomial distribution of the dependant variable (germination rate per pot 28 days after sowing). Residual dispersion was estimated at 2.87 and considered in the model analysis. Seedling growth was estimated by summing the biomasses of the three individual seedlings per pot while sapling relative growth for the greenhouse and the field experiments was calculated as the difference of sapling biomass between the beginning and the end of the experiment divided by the initial sapling biomass. The effects of ground cover type and fertilization treatment on greenhouse seedling and sapling relative growth, as well as the effects of ground cover type, fertilization and shade on field sapling relative growth were tested using linear models. For each experiment, treatment effects were tested on below and aboveground growth separately, total growth, and root allocation, i.e., the difference between final and initial belowground biomass divided by the difference between final and initial total biomass. The effects of ground cover type and fertilization on final potting soil nutrients, as well as the effects of ground cover type, fertilization and shade on nutrient availability at the end of the field experiment were analyzed using linear models.

When necessary, the dependent variables were transformed to respect linear model conditions (square root or log-transformation). When homoscedasticity was not verified for one factor, supplementary parameters were used to estimate the variance associated with each level of a factor and models were analyzed based on the maximum likelihood method. Finally, when data did not accurately fit into a specific distribution, we resorted to a bootstrap procedure in which treatment effect significance was deduced from the probability that the associated individual coefficient of the linear or generalized linear model was equal to zero considering the bootstrap confidence intervals (Fox and Weisberg, 2012). We used contrasts to analyze the effects of ground cover *versus* bare soil in a first phase and to compare the effect of feather and *Sphagnum* spp. mosses in a second phase. All analyses were performed on R. 3. Software (R development core team, 2014), using the packages 'nlme' (Pinheiro et al., 2014), 'lme4' (Bates et al., 2014), 'car' (Fox et al., 2016) and 'MASS' (Ripley et al., 2013).

4.5 Results

4.5.1 Effect of ground cover type on spruce germination, survival and growth

Greenhouse germination

A high percentage of the seeds (≈ 85 %) germinated in the greenhouse. While the presence of a ground cover had no effect on spruce germination success after three weeks in the greenhouse (84 ± 4 % vs 82 ± 5 % on bare soil, $z = 0.49$, *p*-value > 0.1), germination success tended to be higher in *Sphagnum* spp. than in feather mosses (92 ± 6 % against 76 ± 7 %, respectively, $z = 1.74$, *p*-value = 0.0813).

Greenhouse seedling survival and growth

Mortality was low as only 5.3 % of the seedlings died in the six months following germination. Belowground, aboveground and total dry seedling biomass per pot was positively affected by the presence of a ground cover but did not differ between feather and *Sphagnum* spp. mosses (Table 4.2, Fig. 4.1). Root allocation was higher in bare soil than in *Sphagnum* spp. and feather mosses (Table 4.2).

Greenhouse sapling growth

Relative belowground and total growth of the greenhouse saplings was reduced in the presence of a ground cover, while relative aboveground growth was not affected (Table 4.2 and Fig. 4.2). Contrary to belowground growth that was little affected by the composition of the ground cover, relative aboveground and total growth were higher in feather than in *Sphagnum* spp. mosses (Table 4.2 and Fig. 4.2). Spruce allocated more biomass to roots in *Sphagnum* spp. than in feather mosses (62 ± 3 % and 52 ± 2 %, respectively, Table 4.2).

Field sapling growth

We only considered healthy trees for the statistical analyses (N = 64) and discarded saplings that died in the field (9 % of the total). Total biomass increase after two growing seasons in the field was slightly lower than the biomass increase after one growing season in the greenhouse (Fig. 2). Relative belowground growth and root allocation were lower in bare soil than in the presence of a ground cover (root allocation: 56 ± 6 % and 61 ± 2 %, respectively). Spruce growth and root allocation were not affected by the composition of the ground cover (no difference between feather and *Sphagnum* spp. mosses, Table 4.2 and Fig. 4.2).

Table 4.2 Treatment effects on spruce seedling and sapling growth for the greenhouse and field experiments. Significant *p*-values (95% confidence interval) are given in bold († p-value < 0.1). Transformation of the response variable is indicated in italics for each model. Interaction effects that were not at least marginally significant were not considered in the models.

	Belowground			**Aboveground**			**Total**			**Root allocation**		
	β	t	*p*-value	β	t	*p*-value	β	t	*p*-value	β	t	*p*-value
Greenhouse seedlings	*(log)*			*(log)*			*(log)*					
Ground cover *vs* bare soil	0.36	11.25	**< .0001**	0.44	12.22	**< .0001**	0.41	12.10	**< .0001**	-1.68	-5.28	**< .0001**
Sphagnum spp. *vs* feather mosses	0.05	0.91	0.3660	0.06	0.94	0.3490	0.06	0.95	0.3470	-0.17	-0.31	0.7560
Fertilization	0.46	5.04	**< .0001**	0.51	5.01	**< .0001**	0.49	5.11	**< .0001**	-1.05	-1.16	0.2510
Greenhouse saplings	*(log)*			*(log)*			*(log)*					
Ground cover *vs* bare soil (1)	-0.08	-2.09	**0.0415**	-0.10	-1.86	0.0690†	-0.08	-2.12	**0.0386**	0.05	0.04	0.9677
Sphagnum spp. *vs* feather mosses (2)	-0.09	-1.04	0.3048	-0.45	-3.69	**0.0005**	-0.21	-2.38	**0.0208**	7.58	3.60	**0.0007**
Fertilization (3)	0.37	4.09	**0.0001**	0.96	7.75	**< .0001**	0.61	6.81	**< .0001**	-13.30	-5.47	**< .0001**
Interaction (1) x (3)	0.05	0.86	0.3916	-0.07	-1.01	0.3187	-0.02	-0.47	0.6393	3.25	1.89	0.0637†
Interaction (2) x (3)	0.23	1.82	0.0738†	0.46	2.65	**0.0106**	0.29	2.25	**0.0283**	-4.45	-1.49	0.1409
Field saplings										*(log)*		
Ground cover *vs* bare soil (1)	42.43	2.25	**0.0286**	-1.09	-0.18	0.8550	8.31	0.89	0.3785	0.09	2.38	**0.0208**
Sphagnum spp. *vs* feather mosses (2)	-23.33	-0.97	0.3385	0.21	0.04	0.9720	-10.81	-0.90	0.3706	-0.01	-0.23	0.8204
Fertilization (3)	56.66	1.65	0.1039	21.49	1.45	0.1530	33.21	1.95	0.0557†	-0.03	-0.43	0.6670
Shade (4)	53.75	1.64	0.1070	-16.31	-1.21	0.2300	0.88	0.05	0.9570	0.15	2.27	**0.0271**
Interaction (2) x (3)	67.00	1.96	0.0556†	-	-	-	24.23	1.43	0.1594	0.04	0.62	0.5351
Interaction (1) x (4)	-52.51	1.98	0.0532†	-	-	-	-8.93	-0.68	0.5007	-0.10	-1.78	0.0811†
Interaction (2) x (4)	70.53	2.12	**0.0386**	-	-	-	27.72	1.68	0.0988†	0.04	0.64	0.5271

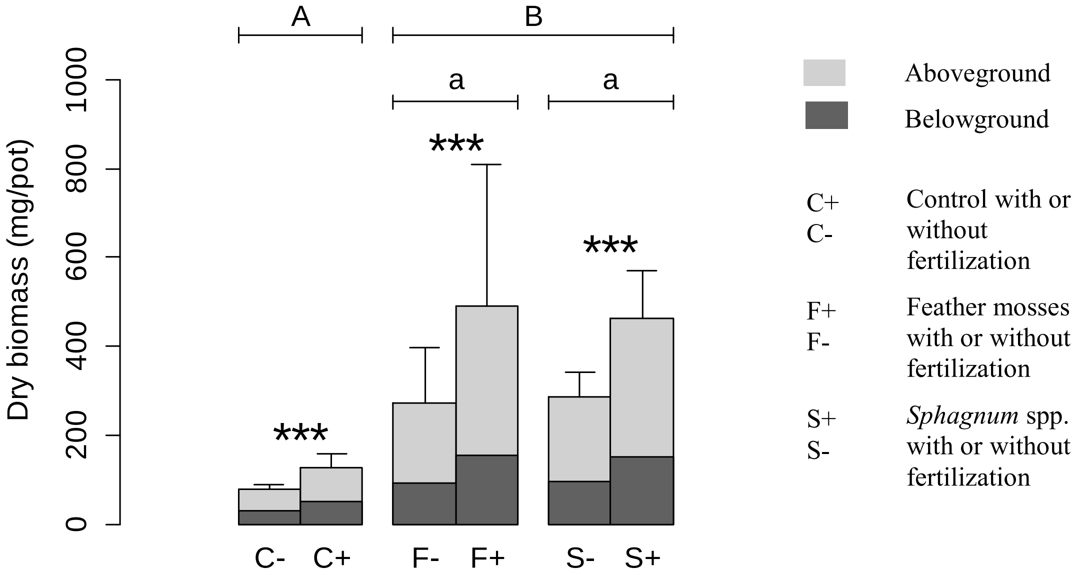

Figure 4.1 Ground cover type and fertilization effects on greenhouse spruce seedling final biomass. Vertical lines correspond to standard deviations of the total biomass. Horizontal lines and letters indicate differences between ground cover types. Contrasts were used for the statistical analyses. The differences between ground cover and bare soil treatments are indicated by capital letters (A-B), while the differences between lichen and feather moss treatments are indicated by lower case letters (a-b). Difference between fertilization treatments are indicated for each ground cover type by asterisks (*** significant at 0.01 %).

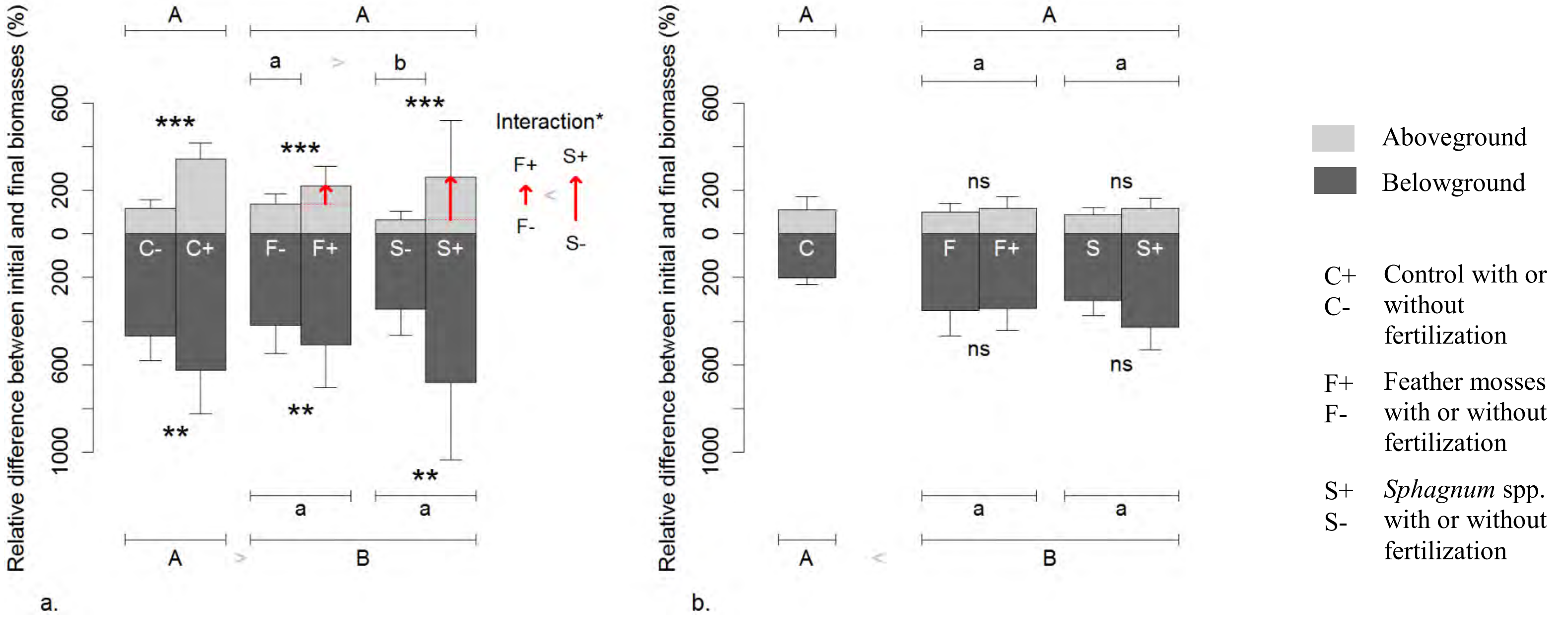

Figure 4.2 Effects of ground cover type and fertilization on (a) greenhouse and (b) field sapling relative growth. Vertical lines correspond to standard deviations of the above and belowground biomasses. Horizontal lines and letters indicate differences between ground cover types. Contrasts were used for the statistical analyses. The differences between ground cover and bare soil treatments are indicated by capital letters (A-B), while the differences between lichen and feather moss treatments are indicated by lower case letters (a-b). In case of significant interaction between ground cover types and fertilization treatment, letters indicate difference for non-fertilized treatment only and interaction effect is indicated on the right side of the figure. Difference between fertilization treatments are indicated for each ground cover type by asterisks (*** significant at 0.1 %, ** significant at 1 %, * significant at 5 %, ns non-significant).

4.5.2 Fertilization and shade effects on spruce growth

Belowground, aboveground and total seedling growth was significantly enhanced by fertilization and this effect did not differ among the three ground cover types (Table 4.2 and Fig.4.1). Nutrient supply increased the total biomass of the seedlings by 149 mg on average (+ 70 %) without significantly affecting seedling root allocation (Table 4.2).

Greenhouse sapling growth was positively affected by fertilization in all the ground cover types, especially in *Sphagnum* spp. mosses where the positive effect of nutrient supply was higher than in feather mosses (Table 4.2 and Fig. 4.2). Fertilization effect was less visible in the field where sapling total growth was only marginally increased by nutrient supply (Table 2). Although it was less clear than for the greenhouse saplings, field belowground growth tended also to be more stimulated by fertilization in *Sphagnum* spp. than in feather mosses (Table 2). Root allocation in greenhouse saplings was significantly reduced in the case of fertilization (regardless of the ground cover type, 49 ± 2 % for fertilized saplings against 62 ± 2 % for non-fertilized saplings) and this effect was similar for all ground cover types (Table 2). In contrast, as for the greenhouse seedlings, root allocation in field saplings was not affected by nutrient supply.

In the field, shade increased sapling root allocation, especially in bare soil and *Sphagnum* spp. mosses (+ 19 % and + 7 %, respectively), but did not affect spruce growth (Table 4.2 and Fig. 4.3).

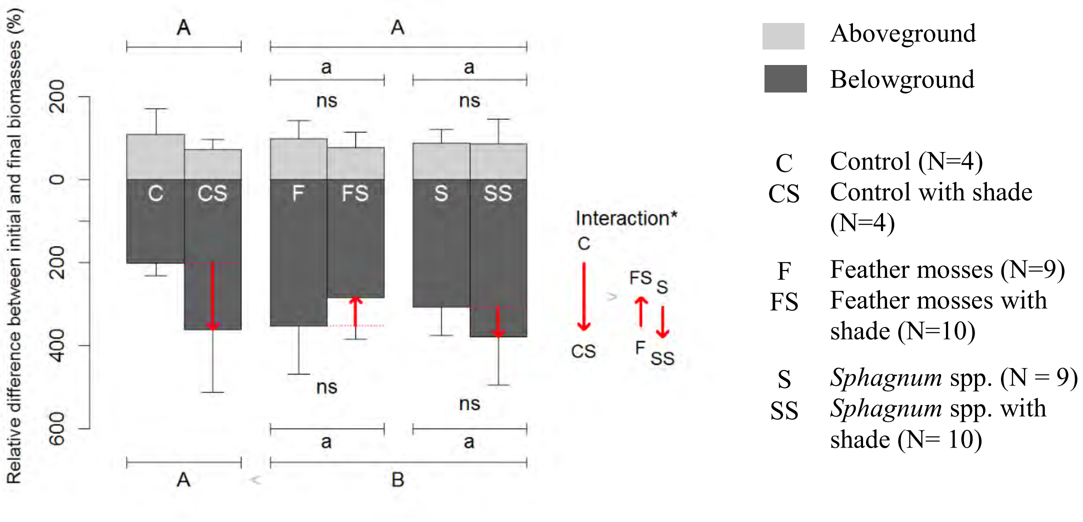

Figure 4.3 Effects of ground cover type and shade on field sapling relative growth. Vertical lines correspond to standard deviations of the above and belowground biomasses. Horizontal lines and letters indicate differences between ground cover types. Contrasts were used for the statistical analyses. The differences between ground cover and bare soil treatments are indicated by capital letters (A-B), while the differences between lichen and feather moss treatments are indicated by lower case letters (a-b). In case of significant interaction between ground cover types and fertilization treatment, letters indicate difference for non-fertilized treatment only and interaction effect is indicated on the right side of the figure. Difference between shading treatments are indicated for each ground cover type (ns non-significant).

4.5.3 Nutrient analysis

The initial chemical composition of the peat used to fill the greenhouse sapling pots (NH_4^+: 138.3 ± 27.7 mg.kg^{-1}; NO_3^-: 0.00 ± 0.01 mg.kg^{-1}, P: 28.3 ± 3.3 cmol.kg^{-1}; base cations: 11.9 ± 1.9 cmol.kg^{-1}) slightly differed from the final nutrient concentrations of the unfertilized bare soil pots (Table 4.3). While nitrogen content (NH_4^+ and NO_3^-) was not affected by ground cover type, phosphorus and base cation content of the greenhouse sapling pots were lower under *Sphagnum* spp. than under feather mosses (Tables 4.3 and 4.4). Fertilization of the greenhouse saplings only increased pot NO_3^- content. In the field, none of the nutrients were affected by ground cover type, and fertilization tended to reduce soil concentration in phosphorus and base cations at the end of the experiment (Table 4.4). There was no detectable nitrate in the field organic soil samples. Shade did not modify any of the field nutrient concentrations we measured (Table 4.4).

4.6 Discussion

4.6.1 Influence of ground cover type on spruce germination and growth

The growth of the few month-old seedlings was more influenced by the presence of a ground cover than it was by ground cover type. Compared to bare soil conditions, the presence of a ground layer may have maintained favorable micro-environmental conditions that protected seedlings from high daily or seasonal variations in temperature and/or moisture (Wheeler et al., 2011; Soudzilovskaia et al., 2013). Germination and early seedling development in feather mosses may have been favored by good moisture conditions in our greenhouse experiment, as the lower water-holding capacity of this ground cover type has been identified as an important limiting factor of seedling growth in several previous studies, whether it be in controlled conditions (Lavoie et al., 2007a) or in the field (Lavoie et al., 2007b; Groot and Adams, 1994).

Table 4.3 Substrate available nutrient concentrations at the end of the two sapling experiments according to treatment and ground cover type (mean ± se). Feather moss values in bold indicate a significant difference between feather and *Sphagnum* spp. mosses (confidence interval = 95%). Significant differences are indicated for ground cover types only, regardless of the secondary treatment (fertilization or shade).

Experiment	**Treatment**	**Ground cover**	**NH_4^+** (mg.kg^{-1})	**NO_3^-** (mg.kg^{-1})	**P** (cmol.kg^{-1})	**Major base cations** (cmol.kg^{-1})
Greenhouse	Control	Bare soil	77.5 ± 8.1	0	39.0 ± 2.8	12.5 ± 1.3
		Feather mosses	109.3 ± 19.9	1.5 ± 1.1	**43.0 ± 2.9**	**13.8 ± 0.8**
		Sphagnum spp.	80.3 ± 4.3	0.2 ± 0.1	29.8 ± 1.3	12.2 ± 0.7
	Fertilization	Bare soil	182.6 ± 61.0	27.1 ± 18.9	126.6 ± 59.6	11.9 ± 1.5
		Feather mosses	100.2 ± 21.8	5.0 ± 4.6	54.4 ± 8.0	14.4 ± 0.6
		Sphagnum spp.	99.4 ± 25.4	6.3 ± 3.5	32.9 ± 1.6	11.1 ± 2.0
Field	Control	Bare soil	65.8 ± 12.5	0	109.4 ± 22.3	10.0 ± 1.7
		Feather mosses	151.7 ± 22.8	0	126.0 ± 10.8	11.1 ± 2.6
		Sphagnum spp.	111.7 ± 50.1	0	107.6 ± 21.0	14.2 ± 0.5
	Fertilization	Feather mosses	60.8 ± 47.3	0	62.3 ± 30.6	6.0 ± 2.7
		Sphagnum spp.	105.1 ± 37.9	0	97.1 ± 5.5	9.7 ± 0.6
	Shading	Bare soil	103.6 ± 32.7	0	130.7 ± 42.3	10.1 ± 2.5
		Feather mosses	92.9 ± 32.7	0	112.0 ± 17.7	12.4 ± 2.9
		Sphagnum spp.	127.4 ± 6.1	0	105.2 ± 16.1	10.4 ± 0.4

Table 4.4 Treatment effects on soil nutrient content for the greenhouse and field sapling experiments. Coefficient estimates that are significantly different from zero are given in bold.

	NH_4^+			**NO_3^-**			**P**			**Base cations**		
	β	t-value	*p*-value	β	t-value	*p*-value	β	t-value	*p*-value	β	t-value	*p*-value
Greenhouse	*(log)*			*(sqrt)*			*(log)**					
Ground cover *vs* bare soil	-0.06	-0.96	0.3460	0.14	1.20	0.2397	-0.05	-	> 0.1	0.24	0.69	0.4965
Sphagnum spp. *vs* feather mosses	-0.06	-0.59	0.5600	-0.21	-1.06	0.3004	-0.20	-	**< .0001**	-1.23	-2.10	**0.0451**
Fertilization	0.20	1.18	0.2480	1.75	2.20	**0.0363**	0.16	-	> 0.1	-0.32	-0.33	0.7443
Field							*(log)*					
Ground cover *vs* bare soil	12.09	1.25	0.2270	-	-	-	-0.01	-0.10	0.9230	0.65	1.13	0.2719
Sphagnum spp. *vs* feather mosses	6.47	0.47	0.6420	-	-	-	0.07	0.71	0.4900	0.79	0.97	0.3458
Fertilization	-38.85	-1.21	0.2410	-	-	-	-0.47	-1.95	0.0660	-4.62	-2.42	**0.0259**
Shade	-1.76	-0.06	0.9490	-	-	-	-0.01	0.03	0.9800	-0.82	-0.51	0.6193

* A bootstrap procedure was used because of the non-normal distribution of the residuals.

As already observed in previous field studies (Chrosciewicz, 1976; Ohlson and Zackrisson, 1992; Groot and Adams, 1994; Hörnberg et al., 1997), the high germination success, survival rate and early growth of the seedlings we obtained in *Sphagnum* spp. mosses indicate that this type of ground cover constitutes a high-quality substrate for black spruce germination and early development. Relationship to ground cover type was different for the two-year-old saplings that grew more in feather mosses than in *Sphagnum* spp. in the greenhouse experiment. Furthermore, *Sphagnum* spp. mosses have been shown to constitute a lower quality substrate than feather mosses for sapling growth in paludified site plantations (Lavoie et al., 2007a; Lafleur et al., 2011), although the difference was not significant in our field experiment that may have been too short in duration to allow sapling acclimation to harsh field conditions. These results indicate that *Sphagnum* spp. mosses do not reduce black spruce recruitment but have a negative effect on the growth of the established trees, as already suggested in previous studies (Saint-Denis et al. 2010, Pacé et al. in press).

Among others, the contrasts between treatments may have been amplified in the greenhouse because sapling roots were washed from all soil residues prior to planting, which made them more sensitive to their new growth environment. Furthermore, transplant shock (Struve, 2009) must have been stronger in the harsh field conditions than in the greenhouse and may explain the low response of field saplings to experimental treatments. Field and greenhouse experiments were used as complementary approaches. Field plantation did not allow a complete randomisation of sapling placement while greenhouse design did not reproduce the harsh environmental conditions of the field. The two also differed in that moss layer thickness was lower in the greenhouse where *Sphagnum* spp. mosses were shown to affect black spruce growth independently from their long-term effect on site paludification.

4.6.2 *Sphagnum* spp. effect on spruce growth: identification of potential drivers

Long-term effects of *Sphagnum* spp. colonization on organic layer accumulation and hydric regime in paludified forests has been largely described in the literature (Lavoie et al., 2005; Fenton et al., 2005, 2006; Fenton and Bergeron, 2006; Simard et al., 2007). However, what we showed in this study is that even a thin transplanted layer of *Sphagnum* spp. has negative effects on spruce growth conditions, suggesting the existence of more direct inhibiting mechanisms such as short-term effect of *Sphagnum* spp. on soil nutrient availability.

Several pieces of evidence indicate that greenhouse sapling growth was more limited by nutrient availability in *Sphagnum* spp. mosses than it was in feather mosses, as already suggested in previous studies (Lavoie et al., 2007a, 2007b; Camill et al., 2010; Lafleur et al., 2011). Firstly, the positive effect of fertilization on greenhouse sapling growth was higher in *Sphagnum* spp. than in feather mosses. Secondly, greenhouse saplings allocated more biomass to roots when they grew in *Sphagnum* spp. compared to those that grew in feather mosses, suggesting a greater limitation in soil resources. Finally, although there was no difference in final soil NH_4^+ and NO_3^- concentrations, *Sphagnum* spp. pots contained significantly less phosphorus and base cations at the end of the greenhouse experiment than the feather moss pots. *Sphagnum* mosses have been shown to have a higher ion exchange capacity than feather mosses and vascular plants (Clymo, 1963; Chapin et al., 1987). Therefore, the low nutrient availability in the *Sphagnum* spp. pots may have been related to nutrient absorption and retention in the moss tissues. These results are coherent with those of Lavoie et al. (2007b) who measured lower foliar nitrogen and phosphorus concentrations in seedlings that grew in *Sphagnum* spp. than in seedlings that grew in feather mosses.

Fertilization had a positive impact on greenhouse seedling and sapling growth in all ground cover types, indicating that spruce growth was limited by nutrients regardless of the ground cover treatment. However, the high positive effect of the presence of a ground cover on early seedling growth suggests that micro-environmental conditions were as crucial factors as nutrient availability at this stage of spruce development. Vertical growth of the moss layer in the greenhouse seedling experience had no significant impact on tree seedling access to light. Interestingly, it seems that greenhouse fertilization inversed the effects of feather moss and *Sphagnum* spp. on spruce sapling growth, i.e. the fertilized trees tended to be smaller in feather mosses than in *Sphagnum* spp. mosses and control pots. This may indicate that the positive effect of feather mosses on non-fertilized black spruce growth compared to *Sphagnum* spp. was mainly related to their positive effect on soil nutrient availability. When nutrient limitation was removed, feather mosses turned out to be a less suitable substrate for black spruce growth than bare soil or *Sphagnum* spp., suggesting that feather mosses, more than *Sphagnum* spp., are susceptible to affect tree growth through other potential drivers such as chemical interference (Steijlen et al., 1995; Michel et al., 2011).

The effect of fertilization on spruce sapling growth was not as important in the field as it was in the greenhouse experiment. Soil nitrogen and phosphorus concentrations at the end of the field experiment were not increased by fertilization, and soil phosphorus even tended to be lower in fertilized plots. Nutrient loss in the field may have resulted from absorption by the neighbouring vegetation or microbial communities. The low fertilization effect on field sapling growth, especially in feather mosses, may have also resulted from the existence of other more limiting factors in the field, such as unfavorable moisture or temperature conditions, which did not exist in the greenhouse.

The application of a shading cloth, as a simulation of the shading effect of forest cover, did not have any short-term positive impact on total sapling growth through potential modification of moss metabolism. However, it had a positive effect on sapling root allocation, especially in bare soil and *Sphagnum* spp. This result suggests that ground cover shading may have reduced soil resource availability for spruce saplings, probably by reducing surface soil temperature and microbial activity. It may also have reduced atmospheric nitrogen fixation by mosses as this process has been shown to be light-dependent in some bryophyte species (Stuiver et al., 2015).

4.6.3 Implications for forest management

One of the objectives of forest management is to promote the establishment of productive post-harvest stands (Fenton et al., 2009). Our results suggest that the dominance of *Sphagnum* spp. (including *Sphagnum capillifolium*, *S. angustifolium*, *S. fuscum*, and *S. magellanicum*) in a particular site can be used as an indicator of poor growth conditions, even in the absence of organic layer accumulation. Therefore, total or partial harvesting in forest sites with high *Sphagnum* spp. cover may result in subsequent tree growth problems, regardless of the organic layer thickness. *Sphagnum* spp. cover can be reduced in these sites by prescribed burning or soil preparation (Lavoie et al., 2005; Fenton et al., 2009; Thiffault et al., 2013; Lafleur et al., 2016), followed by high density seeding or plantation to favor rapid reforestation that would promote a rapid colonization of the understory by feather mosses. These interventions will also reduce the cover of competing vegetation, such as Ericaceae, which is likely to interfere with trees for nutrient uptake (Thiffault et al., 2006, 2012). Furthermore, stands with high *Sphagnum* spp. cover should not be targeted for silvicultural interventions such as precommercial and commercial thinning, which are likely to favor *Sphagnum* spp. expansion at the expanse of feather mosses by opening the canopy (Bisbee et al., 2001; Pacé et al., in press) and thus accentuate the transition to low-productivity stands.

4.7 Conclusion

In this study, we showed that *Sphagnum* spp. mosses (including *Sphagnum capillifolium*, *S. angustifolium*, *S. fuscum*, and *S. magellanicum*) affect tree growth conditions by offering lower nutrient availability than feather mosses. Further, our results indicate that this nutritional effect exists independently of the long-term effects of *Sphagnum* spp. mosses on excess water and consequences on soil physical, chemical and biological conditions in the paludified forest. Based on these results, we suggest that the dominance of *Sphagnum* spp. in a particular site can be used as an indicator of poor growth conditions, even in the absence of thick organic layer accumulation and waterlogged conditions, and considered as a warning in regards of post-logging productivity. Unless it is followed by soil preparation, harvesting is likely to aggravate tree growth conditions in these sites by favoring *Sphagnum* spp. growth and accentuating paludification.

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CHAPITRE V

DIFFERENTIAL EFFECTS OF LICHEN, *SPHAGNUM* SPP. AND FEATHER MOSS LEACHATES ON JACK PINE AND BLACK SPRUCE GROWTH

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En préparation pour soumission à *Plant and Soil*

5.1 Abstract

In the boreal forest, ground layer composition is known to strongly modify the soil microclimatic conditions. However, its impact on the composition of the soil solution and tree growth are poorly documented. In this study, we use an experimental set-up allowing us to investigate (i) the effects of lichen and feather moss leachates on jack pine growth, and (ii) the effects of feather moss and *Sphagnum* spp. leachates on black spruce growth. Tests were performed on seedling (0-6 month-old) and sapling (2 year-old) growth. Despite greater concentrations in dissolved inorganic nitrogen (D.I.N.) than the control leachates, pine seedling growth was negatively affected by both feather moss and lichen leachates while pine sapling growth was only reduced by lichen leachates. A substance having the same migration time as usnic acid was detected in the lichen leachates by high-performance liquid chromatography, suggesting that this phenolic compound is likely to be released by lichens in the soil solution. No effects of *Sphagnum* spp. and feather moss leachates were found for black spruce seedling and saplings despite a higher nutrient supply through the moss leachates compared to controls. D.I.N. of the feather moss leachates tended to be higher than D.I.N. concentration of the *Sphagnum* spp. leachates, and phosphorus availability was higher in pots submitted to feather moss leachates than to *Sphagnum* spp. leachates. This confirms that feather mosses are associated with higher nutrient availability than *Sphagnum* spp. These results suggest that lichens and feather mosses, more than *Sphagnum* spp. mosses, are likely to have chemically-mediated detrimental effects on seedlings and saplings, either directly or indirectly through effects on the composition and activity of the soil microbial communities.

5.2 Résumé

En forêt boréale, la composition de la strate au sol est connue pour affecter les conditions microclimatiques du sol. Cependant, son impact sur la composition de la solution du sol et sur la croissance des arbres est peu documenté. Dans cette étude, on utilise un dispositif expérimental nous permettant de déterminer (i) les effets des lessivats de mousses hypnacées et de lichens sur la croissance du pin gris, et (ii) les effets des lessivats de mousses hypnacées et de sphaignes sur la croissance de l'épinette noire. Les tests ont été effectués sur la croissance de plantules (0-6 mois) et de jeunes plants (2 ans). Malgré une plus grande concentration en azote inorganique dissous (A.I.D.) par rapport aux lessivats témoins, la croissance des plantules de pin gris a été négativement affectée par les lessivats de mousses hypnacées et de lichens. La croissance des jeunes plants a quant à elle été seulement réduite par les lessivats de lichens. Une substance ayant le même temps de migration que l'acide usnique a été détectée par chromatographie en phase liquide à haute performance (HPLC) dans les lessivats de lichens. Ce résultat suggère que ce composé phénolique a possiblement été émis par les lichens dans la solution du sol. Les lessivats de mousses hypnacées et de sphaignes n'ont pas eu d'effet visible sur les plantules et les jeunes plants d'épinette noire malgré un plus grand apport de nutriments dans les lessivats de mousses que dans les lessivats contrôle. La concentration en A.I.D. était plus grande dans les lessivats de mousses hypnacées que dans les lessivats de sphaignes, et la disponibilité du phosphore était plus grande dans les pots soumis aux lessivats de mousses hypnacées que dans les pots soumis aux lessivats de sphaignes. Ceci confirme que les nutriments sont plus disponibles sous les mousses hypnacées qu'ils ne le sont sous les sphaignes. Nos résultats suggèrent que les lichens et les mousses hypnacées, plus que les sphaignes, sont susceptibles d'avoir des effets chimiques inhibiteurs *via* la solution du sol, en affectant la croissance des arbres soit directement, soit indirectement *via* des effets sur la composition et l'activité des communautés microbiennes du sol.

5.3 Introduction

In the boreal forest, cryptogam composition of the ground cover varies with canopy closure and associated microclimatic conditions (Bisbee et al. 2001; Sulyma and Coxson 2001; Boudreault et al. 2013). While feather mosses (e.g. *Pleurozium schreberi* (Brid.) Mitt.) are dominant in the shady conditions of the closed-crown forest (Bisbee et al. 2001; Sulyma and Coxson 2001; Sedia and Ehrenfeld 2003), the ground covers of open canopy woodlands (i.e., lichen woodlands or forested peatlands) tend to be dominated by terricolous lichens (mainly *Cladonia* spp.) in rapidly drained sites (Sedia and Ehrenfeld 2003) and *Sphagnum* spp. mosses in poorly drained sites (Bisbee et al. 2001). These three groups of cryptogams influence ecosystem processes through differential effects on soil physical, chemical and biological properties (Sedia and Ehrenfeld 2003; Fenton et al. 2006; Cornelissen et al. 2007; Pacé et al. 2017), and thus constitute different quality substrates for tree regeneration and/or growth (Sedia and Ehrenfeld 2003; Lafleur et al. 2011; Pacé et al. in preparation (a) and (b)). When compared to bare soil and feather mosses, lichens have been shown to reduce pine growth through effects on root mycorrhization and soil nutrient availability (Sedia and Ehrenfeld 2003; Pacé et al. in preparation (a)), thus contributing to open lichen woodland stability in the closed-crown forest. *Sphagnum* spp. cover has also been shown to constitute a less favourable growth substrate for black spruce than feather mosses by offering nutrient-poorer conditions (Lavoie et al. 2007a, 2007b; Pacé et al. in preparation (b)), especially in paludified sites where its effect on organic layer accumulation greatly reduces soil oxygenation and temperature (Fenton et al. 2006; Simard et al. 2007; Lafleur et al. 2011).

In a previous study, we showed that fertilization did not entirely remove the detrimental effect of lichens on pine sapling growth, suggesting that lichen effect on nutrient availability is not the only limiting factor of pine growth (Pacé et al. in preparation (a)). Lichens and mosses produce a diverse range of phenolic compounds whose ecological roles are poorly understood (Crittenden 1999; Molnar and Farkas 2010; Chiapusio et al. 2013). Some secondary metabolites produced by lichens (e.g., usnic acid) and mosses (e.g. Basile et al. 2003) have been shown to negatively affect trees (Sedia and Ehrenfeld 2003; Molnar and Farkas 2010; Michel et al. 2011; Chiapusio et al. 2013) and soil microorganisms including fungi (Brown and Mikola 1974; Cardarelli 1997). However, whether these substances are released in the soil solution in a concentration sufficient to have detrimental effects on other organisms remains to be verified.

In this study, we propose an experimental design to investigate the allelopathic potential of living *Cladonia* lichens, *Sphagnum* spp. and feather mosses. Considering that allelochemicals are released in the soil solution by living or decomposing organisms (Inderjit and Callaway 2003), we investigated the effects of ground cover leachates on tree growth in two *ex situ* experiments, by testing (i) the difference in effect of lichen and feather moss leachates on jack pine growth, and (ii) the difference in effect of *Sphagnum* spp. and feather moss leachates on black spruce growth. Donor (lichens, *Sphagnum* spp. and feather mosses) and target (jack pine and black spruce) species were contained in separated pots to eliminate resource effects and to focus on chemical effects alone (Inderjit and Callaway 2003). The objectives were (i) to determine and compare the differential effects of ground cover leachates on 0 to 6 month-old seedlings and two year-old saplings, (ii) to identify the potential drivers of any leachate effect by measuring leachate contents in nitrogen, polyphenols and usnic acid and by determining leachate effects on soil chemical characteristics.

5.4 Material and methods

5.4.1 Living material

Seeds and saplings of *Picea mariana* [Mill.] B.S.P. and *Pinus banksiana* Lamb. originated from provincial nurseries of the Natural Resource Ministry of Québec. Seeds were produced in the forest seed center of Berthier (Sainte-Geneviève de Berthier, Québec, Canada). Saplings originated from the provincial nurseries of Guyenne and Trécesson (Abitibi, Québec, Canada) where they grew in greenhouses for two years. Spruce or pine sapling growth in nurseries was stimulated by the application of fertilizers.

Ground covers were harvested in May 2015 in the boreal forest of western Québec (spruce-moss bioclimatic domain, Bergeron et al. 1999). Lichens originated from a pure jack pine-lichen stand located on fluvioglacial coarse-grain deposits (49° 19' N; 79° 11' W), while *Sphagnum* spp. were harvested in a pure black spruce-moss stand located on lacustrine clays (49° 44' N, 79° 17' W). Feather mosses were harvested in the two stand types. Common understory plant species were *Epigaea repens* L., *Kalmia angustifolia* L., *Linnaea borealis* L. and *Vaccinium angustifolium* Ait. in the jack pine-lichen stand, and *Rhododendron groenlandicum* (Oeder) Kron & Judd, and *Vaccinium angustifolium* Ait. in the black spruce-moss stand. Ground covers were harvested with their associate poorly to well-decomposed dead organic layer and Ericaceae (above and belowground parts) were entirely removed from the harvested mosses and lichens. Harvested lichens were mainly *Cladonia stellaris* (Opiz) Pouzar & Vĕzda with some inclusions of *C. rangiferina* (L.) F.H. Wigg. and *C. mitis* Sandst., while harvested *Sphagnum* spp. mosses were mainly *Sphagnum capillifolium* (Ehrh.) Edw., *S. angustifolium* (C. Jens. ex Russ.) C. Jens., *S. fuscum* (Schimp.) Klinggr., and *S. magellanicum* Brid. Other mosses were mainly represented by *Pleurozium schreberii* (Brid.) Mitt. with some *Dicranum polysetum* Swartz, *D. undulatum* Schrad. ex Brid., *Ptilidium ciliare* (L.) Hampe., and *Polytrichum strictum* Brid.

5.4.2 Experimental design

The effects of ground cover composition on jack pine and black spruce growth were investigated separately in two greenhouse experiments. The experimental design that was adapted from Dommanget et al. (2014) and Viard-Crétat at al. (2009) implied pairs of donor and target pots organized in such a way that each donor pot leachate was applied to an associated target pot (Fig. 5.1). All the donor pots (Ø 22 cm, 30 cm deep) were filled with Silica gravel (n°10, Ø 4 mm), a neutral mineral substrate, in order to prevent leachate contamination by organic material. The potting soil used to fill the target pots (Ø 23 cm, 24 cm deep) was constituted of ⅓ dry peat soil, ⅓ vermiculite and ⅓ Silica in the pine experiment, ½ dry peat soil and ½ vermiculite in the spruce experiment. The bottom part of each donor pot was removed and replaced by a poly-ethylene funnel (15 cm in diameter, Bel-Art™, Thermo Fisher Scientific, Waltham, MA). The funnel was connected to a poly-ethylene pipe (Orbit irrigation, North Salt Lake, UT) whose extremity was placed above the target pot. The position of each pair of pots was randomized every month to limit spatial effects of light, temperature and humidity in the greenhouse. Temperature and air humidity were recorded using HOBO® data loggers (HOBO® U23 PRO V2, Onset Data Loggers, Bourne, MA). From May to November 2015, average temperature and air humidity in the greenhouse were 21.5 ˚C (range: 12.6-39.6 ˚C) and 60.2 % (range: 10.8-100.0 %), respectively.

Three ground cover treatments were tested in each experiment. (1) 11 donor pots were filled with silica gravel only, referred to as controls in both experiment. (2) 11 were filled with silica and covered by feather moss. The feather moss cover used in the pine experiment originated from the pine-lichen stand while the one used in the spruce experiment was harvested in the spruce-moss stand considering that the two types of feather moss cover may differ slightly in terms of composition and phenotypic characteristics. (3) 11 donor pots were filled with silica and covered by lichen in the pine experiment, and by *Sphagnum* spp. moss in the spruce experiment. Each ground layer was transplanted with its associate living and dead organic matter.

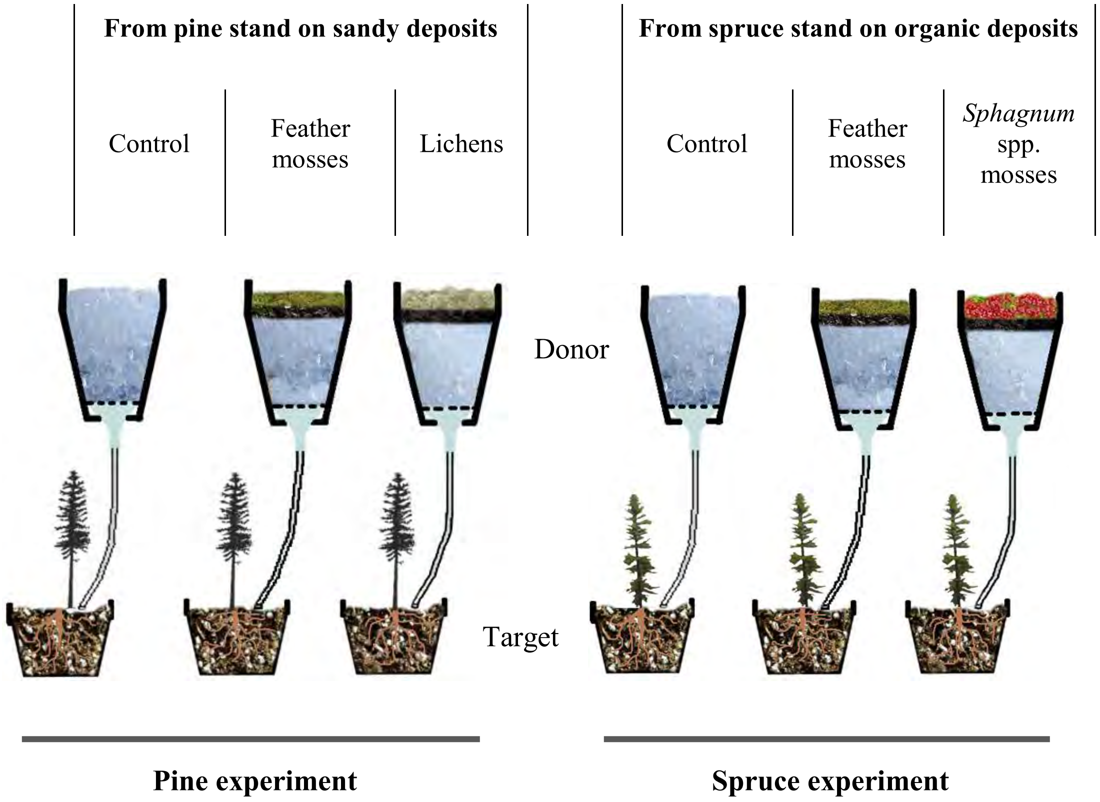

Figure 5.1 Schematic representation of the experimental design.

The effects of ground cover leachates were tested on both sapling and seedling growth of jack pine and black spruce. Sapling roots were washed with demineralized water to remove nursery soil. Each tree was measured and weighed before planting. 10 spruces and 10 pines were used to calculate species-specific factors of fresh to dry weight conversion. Among the 33 donor pots per experiment, 30 were associated with a target pot containing one sapling. The three remaining donor pots (one per ground cover type) were associated with a target pot containing no sapling that was used to analyze the effects of ground cover type on potting soil chemistry at the end of the experiment. Pot pairing (one donor and one target pot containing a sapling or not) was maintained throughout the experiment. Donor pots were watered five times a week from May to November 2015 (250 to 500 mL per pot depending on substrate dryness). From June to November 2015, 70 seedlings of each tree species originating from seeds that germinated in the greenhouse in May 2015 were also submitted to the different ground cover leachate treatments. Three times a week, the leachates (originating from 500 mL waterings) of four control donor pots and five donor pots per ground cover type (feather moss and lichen or *Sphagnum* spp.) in each experiment were applied to 14 additional target pots containing five seedlings each. In November 2015, saplings and seedlings were harvested and roots were washed with water to remove soil particles. Below and aboveground parts were dried (60°C) and weighed separately.

5.4.3 Chemical analysis of the leachates

Donor pot leachates of each ground cover type originating from 500 mL waterings were collected monthly in poly-ethylene bottles and filtered at 0.45 µm before chemical analyses. Mineral N content (NH4-N and NO3-N) of the leachates was measured by spectrophotometry (QuikChem R8500 Series 2, Lachat Instruments, Milwaukee, WI). Total polyphenol content of the leachates, as an indicator of secondary metabolite production by the ground cover, was measured in September and October 2015 based on the Folin-Ciocalteu method (Folin and Ciocalteu's phenol reagent, MP Biomedicals Inc., Santa Ana, CA) using gallic acid (Gallic acid 98%, ACROS Organics, Fisher Scientific Acros, Hampton, NH) as a standard (Dommanget et al. 2014).

Finally, leachates from the pine experiment were analyzed to detect the presence of usnic acid, which has been described as a potential allelochemical compound of lichen (Cardarelli et al. 1997). 25 mL leachates from the 11 donor pots containing lichens as well as leachates from 3 donor pots containing feather mosses and 3 control donor pots were collected in October 2015. They were freeze-dried, and the solid content was dissolved in 1 mL of acetone and filtered at 0.45 µm before analysis. We also prepared six lichen and three feather moss extracts from 0.3 g of dry material (directly sampled from 3 donor pots of each ground cover type and dried at 60 °C). Dry lichen and feather moss material was ground, diluted in 10 mL of acetone, filtered at 0.45 µm and rinsed 3 times with 5 mL of acetone until the solid material became colorless. The acetone was then evaporated at ambient temperature and samples were rediluted in 10 mL of acetone before analysis. The presence of usnic acid in the leachates was detected by high-performance liquid chromatography (HPLC; Stark et al. 2007) using a RP-18 Lichrocart 125-4 column, a mobile phase of 100% methanol and 0.9% phosphoric acid commercial, an injection volume of 20 µL and (+)-usnic acid as a standard (98%, Sigma-aldrich, Saint-Louis, MO). Usnic acid presence was detected using chromatogram at a wavelength of 270 nm and the lowest detectable usnic acid concentration was 1 mg.L^{-1}.

5.4.4 Analysis of the target pot soil

Samples of the potting soil used to fill the target pots were harvested before the experiment in May 2015 for soil analyses. Potting soil samples from the three control target pots (with no saplings) and from five target pots (containing saplings) per ground cover type were harvested at the end of the experiment in November 2015. Potting soil samples were first sieved at 6 mm to remove large roots and debris, dried at 60°C, then ground and sieved at 2 mm. NH4-N and NO3-N were extracted with a 2 M KCl solution and analyzed by spectrophotometry (QuikChem R8500 Series 2, Lachat Instruments, Milwaukee, WI). Phosphorus, potassium, calcium, magnesium and sodium were separated with a Mehlich extraction and analyzed by inductively coupled plasma (ICP) using an optical emission spectrometer (OES) (Optima 7300 DV, Perkin Elmer, Waltham, MA). Soil concentration in base cations was estimated by summing potassium, calcium, magnesium and sodium concentrations.

5.4.5 Statistical analysis

Seedling growth was estimated summing the biomasses of the five individual seedlings per pot while sapling relative growth was calculated as the difference of sapling biomass between the beginning and the end of the experiment divided by the initial sapling biomass. The effects of ground cover leachates on seedling and sapling growth were tested using linear models. For each experiment, treatment effects were tested on below and aboveground growth separately, total growth, and root allocation, i.e., the difference between final and initial belowground biomass divided by the difference between final and initial total biomass. The effects of ground cover type on final potting soil nutrients were analyzed using linear models.

When necessary, the dependent variables were transformed to respect linear model conditions (square root or log-transformation). When homoscedasticity was not verified for one factor, supplementary parameters were used to estimate the variance associated with each level of a factor and models were analyzed based on the maximum likelihood method. Finally, when data did not accurately fit into a specific distribution, we resorted to a bootstrap procedure in which treatment effect significance was deduced from the probability that the associated individual coefficient of the linear or generalized linear model was equal to zero considering the bootstrap confidence intervals (Fox and Weisberg 2012). We used contrasts to analyze the effects of ground cover *versus* bare soil in a first phase and to compare the effect of feather and lichens/*Sphagnum* spp. mosses in a second phase. All analyses were performed on R. 3. Software (R development core team 2014), using the packages ‘nlme’ (Pinheiro et al. 2014), ‘lme4’ (Bates et al. 2015), ‘car’ (Fox et al. 2016) and ‘MASS’ (Ripley et al. 2013).

5.5 Results

5.5.1 Leachate effects on seedling and sapling growth

In the pine experiment, the presence of a ground layer in the donor pot (feather mosses or lichens) had a negative effect on belowground, aboveground and total growth of the target pine seedlings, while effects of lichen and feather moss leachates on seedling growth were not significantly different (Table 5.1 and Fig. 5.2.a). The aboveground relative growth of the target pine saplings was not affected by ground cover treatment (Table 5.1 and Fig. 5.2.c). However, their belowground relative growth was reduced by the presence of a ground cover in the donor pot, especially when submitted to lichen leachates. In the spruce experiment, the different ground cover treatments had no differential effects on target spruce seedling and sapling growth (Table 5.1, Fig. 5.2.b and 5.2.c).

5.5.2 Leachate content

Dissolved inorganic nitrogen

In the two experiments, D.I.N. concentration of the leachates originating from feather mosses, *Sphagnum* spp., and, to a lesser extent, lichens, increased with time, while D.I.N content of the leachates originating from the control pots remained constantly low for all the duration of the experiment (Table 5.2 and Fig. 5.3). D.I.N. concentration of the feather moss leachates roughly stabilized in September and October 2015 and tended to be higher in the spruce than in the pine experiment. In the pine experiment, there was significantly more D.I.N. in feather moss than in lichen leachates regardless of the measurement date (Table 5.2). In the spruce experiment, *Sphagnum* spp. leachates tended to be less concentrated in D.I.N. than feather moss leachates -although the trend was not significant (Table 5.2)- and the two contained significantly more D.I.N. than the control pot leachates (Table 5.2 and Fig. 5.3).

Table 5.1 Leachate effect on pine and spruce seedling biomass and sapling relative growth. Treatment had no effect on root allocation.

	Belowground			**Aboveground**			**Total**		
	ß	t-value	p-value	ß	t-value	p-value	ß	t-value	p-value
Pine seedlings	*(sqrt)*			*(log)*			*(log)*		
Ground cover *vs* control	-1.02	-3.07	**0.0107***	-0.15	-2.54	**0.0276***	-0.15	-2.76	**0.0186***
Lichen *vs* feather moss	-0.85	-1.61	0.1366	-0.10	-1.04	0.3195	-0.13	-1.40	0.1894
Pine saplings	*(log)*						*(log)*		
Ground cover *vs* control	-0.08	-2.38	**0.0246***	-0.02	-0.30	0.7690	-0.05	-1.25	0.2220
Lichen *vs* feather moss	-0.16	-2.61	**0.0145***	0.07	0.62	0.5380	-0.05	-0.67	0.5070
Spruce seedlings	*(log)*			*(log)*			*(log)*		
Ground cover *vs* control	0.02	0.49	0.6314	0.05	0.37	0.7216	0.06	0.42	0.4666
Sphagnum vs feather moss	-0.09	-1.08	0.3037	-0.29	-1.22	0.2466	-0.26	-1.15	0.2736
Spruce saplings									
Ground cover *vs* control	0.03	0.63	0.5340	0.11	1.37	0.1840	0.06	1.14	0.2660
Sphagnum vs feather moss	0.03	0.17	0.8660	-0.10	-0.71	0.4860	-0.02	-0.23	0.8240

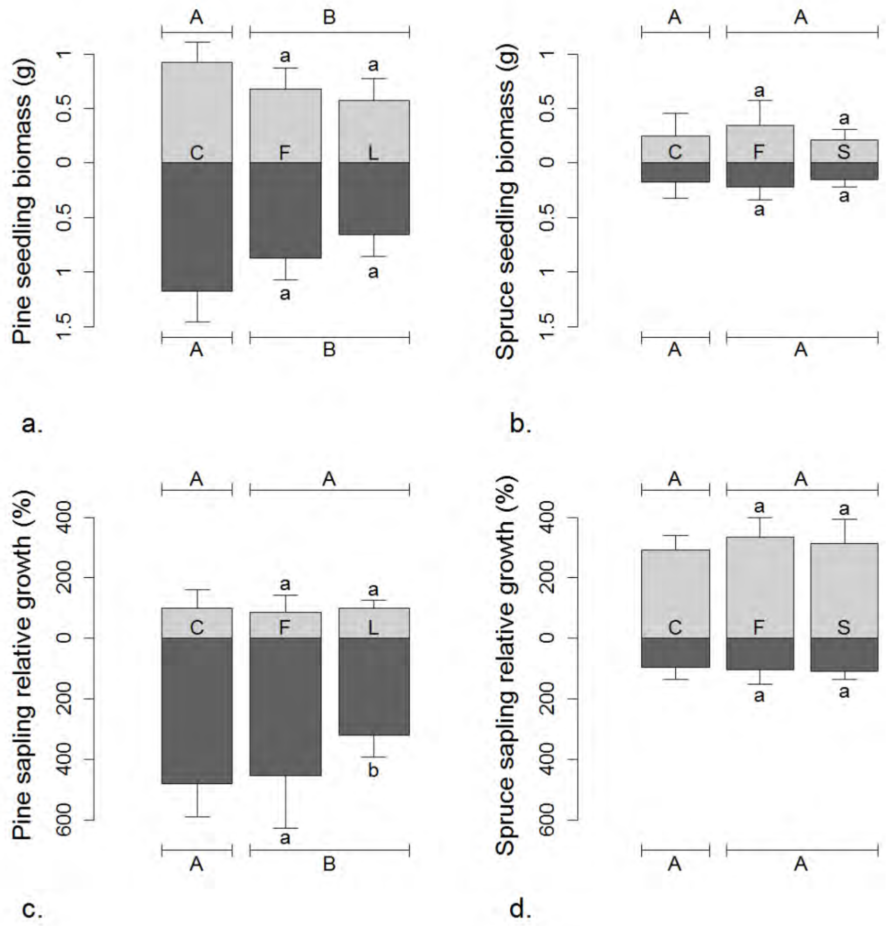

Figure 5.2 Effects of ground cover leachates on seedling (a and b) and sapling (c and d) growth including the effects of feather moss and lichen leachates on pine growth (a and c) and the effects of feather and *Sphagnum* spp. moss leachates on spruce growth (b and d). X-axis legend: C control, F feather moss, S *Sphagnum* spp. moss. Dark grey bars correspond to belowground biomass, light grey bars to aboveground biomass. Vertical lines correspond to standard deviations of the below- and aboveground biomass. Horizontal lines and letters indicate differences between ground cover types. Contrasts were used for the statistical analyses. The differences between ground cover and bare soil treatments are indicated by capital letters (A-B), while the differences between lichen and feather moss treatments are indicated by lower case letters (a-b).

Table 5.2 Effect of ground cover treatment on dissolved inorganic nitrogen content of the leachates (log-transformed).

	Pine experiment			**Spruce experiment**		
	β	t-value	p-value	β	t-value	p-value
Ground cover *vs* Control (1)	-0.10	-1.47	0.1576	0.22	2.74	**0.0127***
Lichens/*Sphagnum vs* feather mosses (2)	-0.47	-2.48	**0.0215***	-0.23	-1.68	0.1079
Date (3)	0.09	2.29	**0.0285***	0.25	12.69	**< 0.001*****
Interaction (1) x (3)	0.13	6.18	**< 0.001*****	-0.11	-7.51	**< 0.001*****
Interaction (2) x (3)	-0.08	-1.38	0.1773	-0.18	-7.80	**< 0.001*****

Coefficient estimates that are significantly different from zero are given in bold (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

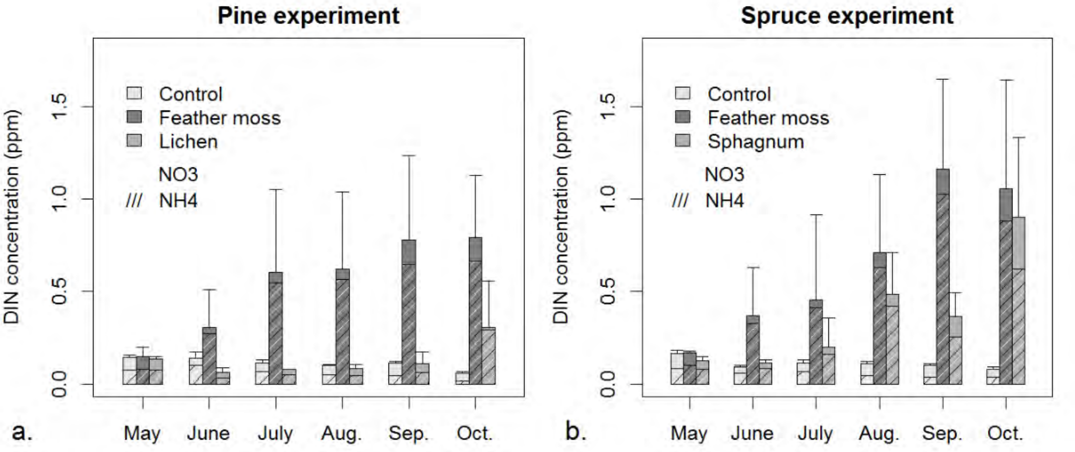

Figure 5.3 Dissolved inorganic nitrogen (D.I.N.) content of the leachates from the donor pots of (a) the pine experiment and (b) the spruce experiment. Vertical lines correspond to standard deviations of D.I.N. concentrations.

Polyphenol

In the two experiments, the leachates originating from the control pots had the lowest polyphenol content (Table 5.3 and Fig. 5.4). Lichen and *Sphagnum* spp. leachates tended to be less concentrated in polyphenol than feather moss leachates, especially at the second measurement date (October 2015).

Usnic acid content of the pine experiment leachates

The absorbance peak at 270 nm corresponding to the presence of usnic acid was associated with a migration time of 5.7 minutes in the HPLC analysis. This absorbance peak was absent in feather moss extracts and all the leachate samples originating from feather moss and control pots. However, lichen extracts and several samples of lichen leachates contained a substance that had the same migration time as the usnic acid standard.

5.5.3 Leachate effect on target pot soil

Contrary to the control target pots, there was no nitrate in the target pots that contained saplings (Table 5.4). Ground cover treatment had no differential effect on target pot soil in the pine experiment (Table 5.4). In the spruce experiment, target soil content in NH_4^+ tended to be higher under feather and *Sphagnum* spp. mosses than under control plots (+ 29.3 %, t = 2.11, p-value = 0.0568). Phosphorus content was the lowest in the target pots that were associated with the control donor pots (t = 2.92, p-value = 0.0129), and significantly lower in the target pots that were submitted to *Sphagnum* spp. than the ones that were submitted to feather moss leachates (- 37.6 %, t = -3.10, p-value = 0.0092).

Tableau 5.3 Polyphenol content of the leachates (mean +/- SE, expressed in mg.L^{-1}).

	Pine experiment				**Spruce experiment**			
	September 24th (n = 15)		**October 20th** (n = 33)		**September 24th** (n = 15)		**October 20th** (n = 33)	
Control	0.00 (+/- 0.07)	**A**	0.00 (+/- 0.00)	**A**	0.17 (+/- 0.09)	**A**	0.13 (+/- 0.03)	**A**
Feather mosses	2.79 (+/- 0.82) **a**	**B**	3.30 (+/- 0.40) **a**	**B**	7.76 (+/- 0.68) **a**	**B**	11.08 (+/- 0.92) **a**	**B**
Lichens	2.03 (+/- 0.57) **a**		0.44 (+/- 0.05) **b**		-		-	
Sphagnum mosses	-		-		3.86 (+/- 1.26) **a**		4.51 (+/- 0.41) **b**	

The values (or groups of values) that are followed by different letters are significantly different. Difference between ground cover treatments was analyzed based on a bootstrap analysis implying contrasts. The differences between ground cover and bare soil treatments are indicated by capital letters (A-B), while the differences between lichen and feather moss treatments are indicated by lower case letters (a-b).

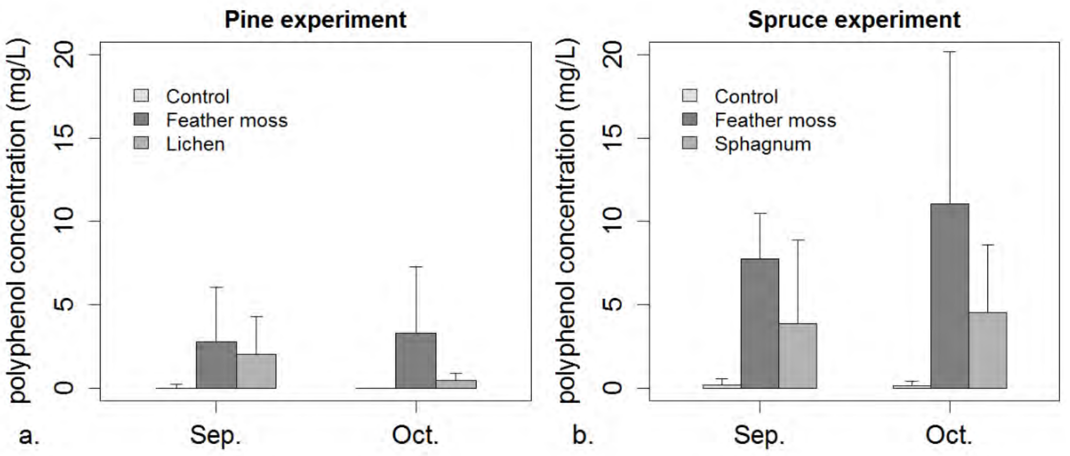

Figure 5.4 Polyphenol content of the leachates from the donor pots of (a) the pine experiment and (b) the spruce experiment. Vertical lines correspond to standard deviations of polyphenol concentrations.

Tableau 5.4 Leachate effect on the soil NH_4^+ content of the target pots at the end of the experiment. Soil concentrations in NH_4^+ and NO_3^- are given in ppm, soil concentration in P are given in $cmol.kg^{-1}$.

	May 2015			**November 2015**						
	Potting soil			**With sapling**				**Without sapling**		
Ground cover treatment	**NH_4^+**	**NO_3^-**	**P**	**NH_4^+**	**NO_3^-**	**P ($cmol.kg^{-1}$)**		**NH_4^+**	**NO_3^-**	**P**
Pine experiment										
Control	41.41 (± 1.53)	1.57 (± 0.06)	9.72 (± 0.15)	5.81 (± 1.20)	0	5.44 (± 0.79)		9.42	3.50	4.40
Feather mosses				5.10 (± 0.61)	0	6.82 (± 1.30)		21.17	12.23	8.11
Lichens				6.71 (± 0.62)	0	7.93 (± 0.94)		11.14	6.70	16.92
Spruce experiment										
Control	81.70 (± 7.40)	4.64 (± 0.28)	20.62 (± 3.11)	6.31 (± 0.82)	0	6.41 (± 0.59)	**A**	11.04	4.32	8.55
Feather mosses				8.64 (± 0.67)	0	12.67 (± 1.72) **a**	**B**	7.54	11.72	17.38
Sphagnum mosses				7.69 (± 0.66)	0	7.91 (± 0.50) **b**		21.55	2.45	8.89

Contrasts were used for the statistical analyses. The significant differences between ground cover and bare soil treatments are indicated by different capital letters (A-B), while the significant differences between lichen and feather moss treatments are indicated by different lower case letters (a-b).

5.6 Discussion

5.6.1 Effects of lichen and feather moss leachates on jack pine growth

Feather moss and lichen leachates had negative impacts on both below- and aboveground growth of the few month-old seedlings despite they were associated with higher D.I.N. concentrations than the control leachates. This suggests that the two types of ground cover modify soil solution chemistry in a way that is detrimental for early jack pine development. In contrast, pine sapling growth was reduced by lichen leachate only, and this negative effect was limited to the belowground parts of the trees. Besides being the first organs exposed to potential allelochemicals, pine sapling roots had grown much more than the aboveground organs for all the duration of the experiment, making treatment effects more visible on pine belowground parts as observed for direct plantation (Pacé et al. in preparation (a)).

The lower D.I.N. concentration of the lichen leachates compared to the feather moss leachates corroborates the hypothesis that lichens constitute a poorer quality substrate than feather mosses for pine development partly because they are associated with a lower nutrient availability (Wheeler et al. 2011; DeLuca et al. 2013). However, our experiment confirms that lichen effect on pine development does not only consist in reducing soil nutrient availability. Indeed, the pines that were submitted to lichen leachates were significantly smaller than the ones that were submitted to the control leachates although the control leachates were almost devoid of D.I.N. Similarly, we showed in a previous study (Pacé et al. in preparation (a)) that fertilization did not remove lichen effect on pine sapling growth, suggesting the existence of another unknown factor that may be related to chemical interferences. We found a substance that is likely to be usnic acid in the lichen leachates. Usnic acid is known to have antimicrobial properties (Crittenden, 2000), and to affect plant tissues by reducing chlorophyll and carotenoid concentrations (Romagni et al. 2000). Therefore, this substance might have contributed to the negative effect of lichen leachates on pine sapling growth.

Feather moss leachates did not affect the development of pine saplings despite the fact that they had a negative effect on few month-old seedlings. Contrary to pine seedling development that partly relied on seed nutrient reserves, the growth of the two year-old pine saplings was limited by nutrient availability in the surrounding soil (see fertilization effect in Pacé et al. in preparation (a)). Therefore, by stimulating pine sapling growth, the supply of nutrients *via* the feather moss leachates may have partly hidden any negative chemical effects from feather mosses when compared to the pine saplings submitted to the control leachates. In contrast, the low response of the few month-old seedlings to nutrient supply (Pacé et al. in preparation (a)) and their probable higher sensitivity to local soil conditions may explain why they react more negatively to the feather moss leachates than the two year-old saplings in our experiment.

5.6.2 Effects of *Sphagnum* spp. and feather moss leachates on black spruce growth

There was no significant effect of *Sphagnum* spp. and feather moss leachates on black spruce growth, despite their higher concentration in D.I.N. and polyphenols than the control leachates. The higher D.I.N. concentrations of the moss leachates might have counterbalanced any negative chemical effect from *Sphagnum* spp. and feather moss leachates. Black spruce growth was the same whether they were submitted to *Sphagnum* spp. or feather moss leachates, suggesting that the *Sphagnum* spp. effect we observed on black spruce growth in a previous study (Pacé et al. in preparation (b)) was more related to nutrient limitation than it was to differential chemical effects.

The D.I.N. and phenolic compounds we detected in the moss leachates are likely to originate from organic matter decomposition. Thus, the increasing D.I.N. concentration of the moss leachates with time may result from an increase of organic matter decomposition in the donor pot. The higher concentration in D.I.N. and polyphenols of the feather moss leachates compared to the *Sphagnum* spp. leachates suggests that decomposition and nitrogen mineralization were higher under feather mosses than under *Sphagnum* spp., as previously observed by Lang et al. (2009). Furthermore, *Sphagnum* spp. mosses have been shown to have a higher ion exchange capacity than feather mosses (Clymo, 1963; Chapin et al., 1987). Therefore, the lower nutrient concentration of the *Sphagnum* spp. leachates may have also partly resulted from nutrient absorption and retention by *Sphagnum* spp. mosses in the donor pots. These two potential mechanisms are also likely to explain the higher final phosphorus concentration of the target pots that were submitted to the feather moss leachates. This confirms that feather mosses are associated with higher concentrations of soil nutrients, including phosphorus, than *Sphagnum* spp., and thus constitute a more suitable substrate for black spruce growth.

Polyphenols and D.I.N. were more concentrated in the feather moss leachates of the spruce experiment than they were in the pine experiment, suggesting differences between the two feather moss covers originating from the two forest types. These contrasts include difference in terms of organic layer thickness, specific composition of the feather moss layer and possible intraspecific phenotypic plasticity.

5.6.3 Testing allelopathy

To establish evidence of allelopathy, an experiment must show that secondary substances are not only present in tissue extracts but also released in the environment at toxic levels for the neighbourhood organisms (Inderjit and Callaway 2003). In our experiment conducted in semi-natural greenhouse conditions, we showed that lichen affects pine seedling and sapling growth through chemical interference *via* the soil solution. Concurrently, we found a substance that may be usnic acid in the lichen leachates. This last result contrasts with thoose of Stark and Kytöviita (2007) who did not detect any usnic acid in lichen leachates collected from natural rainfall events. The regularity and the relatively high watering volume we applied daily in our *ex situ* experiment may have exacerbated substance release by lichens in the soil solution, and thus the chemical effects of lichen leachates on pine. Difference in water pH, which constitutes an important factor of usnic acid solubility, may also explain why usnic acid was detected in our study although it was not in the lichen leachates analyzed by Stark and Kytöviita (2007). Also temperature and humidity conditions of the greenhouse may have stimulated sapling growth and thus exacerbated leachate effect on pine development. Inversely, a part of the secondary metabolites released by mosses and lichens in the soil solution may have been retained in the donor pots, which may have reduced the chemical effect of cryptogams on jack pine compared to pines that directly grow in lichens.

5.7 Conclusion

In this study, we showed that early jack pine growth was reduced by lichen leachates and, to a lesser degree, by feather moss leachates. The effect of lichen leachates seemed to be associated with the release of usnic acid in the soil solution suggesting that this secondary metabolite might have been partly responsible for the detrimental effect of lichen leachates on jack pine seedling and sapling growth. Furthermore, our results confirm that the presence of a feather moss cover contributes to increased soil nutrient availability for jack pine and black spruce, and that lichens and *Sphagnum* spp. mosses are associated with lower nitrogen mineralization rates than feather mosses.

5.8 Aknowledgements

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CHAPITRE VI

GROUND LAYER COMPOSITION MAY LIMIT THE POSITIVE IMPACT OF PRECOMMERCIAL THINNING ON BOREAL FOREST STAND PRODUCTIVITY

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6.1 Abstract

In the boreal forest, ground layer composition may modulate the effects of precommercial thinning (PCT) on stand productivity by affecting tree growth conditions. Based on data from 15 years of PCT monitoring in black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) stands, the objectives of this study were to investigate (1) the effects of PCT on ground layer composition and (2) the way ground layer composition is related to tree growth, stand productivity and PCT impact on stand productivity. PCT favored lichen expansion in xeric sites. Positive impact of PCT on stand productivity after 15 years was lower in sites with high year-one lichen cover, suggesting that the aboveground positive effect of PCT on growth may have been mitigated by a belowground negative feedback resulting from lichen expansion in xeric sites. Although *Sphagnum* spp. cover was not affected by PCT, 15-year increase in stand productivity was lower in sites with high year-one *Sphagnum* spp. cover. These results suggest that xeric stands with high lichen cover should not be targeted for PCT because of either null or negative effects on stand productivity. Subhydric stands with high *Sphagnum* spp. cover should also be avoided because of lower potential stand productivity.

Keywords: Lichen, *Sphagnum*, feather moss, jack pine, black spruce, *Cladonia*, understory, tree growth, merchantable tree, forest cover.

6.2 Résumé

En forêt boréale, la strate au sol peut moduler les effets de l'éclaircie précommerciale (EPC) sur la productivité du peuplement en affectant les conditions de croissance des arbres. Basé sur des données provenant d'un suivi sur 15 ans des effets de l'EPC sur des peuplements d'épinettes noires (*Picea mariana*) et de pins gris (*Pinus banksiana*), les objectifs de cette étude sont de déterminer (1) les effets de l'EPC sur la composition de la strate au sol, et (2) la manière dont la composition de la strate au sol est liée à la croissance ligneuse, la productivité du peuplement et l'impact de l'EPC sur la productivité du peuplement. L'EPC a favorisé l'expansion des lichens dans les sites excessivement drainés. L'impact positif de l'EPC sur la productivité du peuplement après 15 ans était inférieur sur les sites avec un fort recouvrement en lichens à l'année 1, suggérant que l'effet positif de l'EPC sur la croissance a pu être atténué par une rétroaction négative résultant de l'expansion des lichens dans les sites xériques. Bien que le couvert de sphaignes n'ait pas été affecté par l'EPC, l'augmentation de la productivité du peuplement sur 15 ans était plus faible dans les sites avec un fort recouvrement en sphaignes à l'année 1. Ces résultats suggèrent que les sites xériques avec un fort recouvrement en lichens ne devraient pas être ciblés pour l'EPC dans la mesure où ils sont peu enclins à y répondre favorablement. Les sites subhydriques avec un fort recouvrement en sphaignes devraient également être évités du fait de leur plus faible potentiel productif.

Mots-clés : Lichen, sphaigne, mousses hypnacées, pin gris, épinette noire, *Cladonia* spp., sous-bois, croissance ligneuse, arbres marchands, couvert forestier.

6.3 Introduction

Precommercial thinning (PCT) is a common silvicultural treatment in conifer stands (Boulay 2015) that reduces density-dependent competition for light in young, high-density stands by mechanically eliminating some of the regenerating saplings. High competition for light and space alters fiber quality by favoring the formation of curved stems. The objective of PCT is to reduce rotation time and improve fiber quality by pre-empting the natural process of self-thinning and redistributing the space and growth resources to the remaining trees, which will form the mature stand. Consequently, PCT is supposed to increase stem diameter and accelerate stand operability by rapidly increasing the proportion of merchantable trees (Pothier 2002, Gravel et al. 2016). PCT has also been proposed as a method to increase the proportion of softwood trees in the boreal mixed forest where logging tends to favor deciduous tree species (Prévost and Gauthier 2012). In addition to its positive effects on light availability for the remaining trees, PCT has been shown to accelerate nitrogen mineralization and enhance balsam fir (*Abies balsamea* (L.) Mill.) nutritional status by favoring light transmission through the canopy and increasing temperature of the forest's surface soil (Thibodeau et al. 2000).

In the boreal forest, the ground layer is mainly composed of three important groups of cryptogams, i.e., feather mosses (mostly *Pleurozium schreberi* (Brid.) Mitt.), *Sphagnum* spp. mosses and terricolous lichens, which influence ecosystem processes through their effects on soil physical, chemical and biological properties (Sedia and Ehrenfeld 2003, Fenton et al. 2006, Cornelissen et al. 2007). Full light exposure and associated microclimatic conditions tend to favor *Sphagnum* spp. mosses (Bisbee et al. 2001) or lichens (Boudreault et al. 2013) depending on site moisture regime (*Sphagnum* spp. in subhydric conditions, lichens in xeric conditions). In contrast, feather mosses tend to be restricted to shady microsites in closed-crown forests when *Sphagnum* spp. mosses or lichens are present (Bisbee et al. 2001, Haughian and Burton 2015), likely because of competitive exclusion (Sulyma and Coxson 2001, Fenton and Bergeron 2006). Several studies have suggested that lichens and *Sphagnum* spp. mosses offer less favorable tree growth conditions than feather mosses. Compared to a cover of feather mosses, lichens have been shown to reduce the growth of black spruce (Wheeler et al. 2011) and jack pine (Pacé et al. in preparation) likely through their effects on soil micro-organisms and nutrient availability (Ohtonen and Väre 1998, Sedia and Ehrenfeld 2005, 2006). Similarly, *Sphagnum* spp. mosses reduce spruce growth through their effects on water table, soil oxygenation, temperature and nutrient availability (Fenton et al. 2006, Simard et al. 2007, Lafleur et al. 2011). Thus, by affecting tree growth conditions, ground layer composition may constitute an important factor of variability in PCT effects on stand productivity.

Fire usually leads to high regeneration density that favors the rapid establishment of a closed canopy, which in turn favors the colonization of the understory by feather mosses (Foster 1985). In contrast, clear-cut followed by PCT leads to lower regeneration density (Pothier 2002) and a more open canopy that may favor lichen or *Sphagnum* spp. dominance (Bisbee et al. 2001, Boudreault et al. 2013), especially in sites with extreme moisture regimes, i.e. excessively (xeric) and poorly (subhydric to hydric) drained sites. This change in understory composition may have a negative feedback effect on tree growth and thus limit the positive impact of PCT under extreme moisture regimes. Maintaining closed-canopy stands and avoiding a transition in productive stands to either open lichen woodlands (Jasinski and Payette 2005) or open paludified forest (Simard et al. 2007) remains a cause of concern in the management of boreal stands, especially at the northern limit of the managed forest where a recent expansion of open canopy stands has been documented (Girard et al. 2008). Based on data from 15 years of PCT monitoring in black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) stands, the main objectives of this study were to investigate (1) the effects of PCT on ground layer composition and (2) the way ground layer composition is related to tree growth, stand productivity and PCT impact on stand productivity 15 years after treatment. We hypothesized that PCT was likely to favor lichen and/or *Sphagnum* spp. expansion at the expense of feather mosses under extreme moisture regimes (xeric and subhydric conditions), and that this change in ground layer composition would have a negative feedback effect on tree growth, thus mitigating the direct positive effect of PCT.

6.4 Material and methods

6.4.1 Study Area and Design

This study is part of a larger study established between 1995 and 1999 by the *Ministère des Forêts, de la Faune et des Parcs du Québec*, which included the whole province of Québec (Laflèche and Tremblay 2008). For this study, we retained data from the regions of Abitibi-Témiscamingue and Nord-du-Québec, which roughly corresponds to the western spruce-moss and the balsam fir-white birch bioclimatic regions (Laflèche and Tremblay 2008, Saucier et al. 2011). Average annual temperatures (1981-2010) follow a north-south gradient, from 0.0°C (Joutel, QC) to 3.1°C (Ville-Marie, QC; Environment Canada 2017). Average annual precipitation varies from 885.9 (Lac Berry, QC) to 995.8 mm (Chapais, QC). Within these regions, data was collected from fifty young post-fire or post-harvest stands (Table 6.1) composed primarily of black spruce (*Picea mariana* [Mill.] B.S.P.) and jack pine (*Pinus banksiana* Lamb.). Balsam fir (*Abies balsamea* (L.) Mill.) was also abundant in some stands. *Pleurozium schreberi* (Brid.) Mitt., *Dicranum* spp., *Hylocomium splendens* (Hedw.) Schimp., *Polytrichum* spp. and *Sphagnum* spp. were the most frequent bryophyte species. Terricolous lichens were mainly represented by *Cladonia stellaris* (Opiz) Pouzar & Vězda, and *C. rangiferina* (L.) F.H. Wigg.

Table 6.1 Stand characteristics by moisture regime (mean ± SE).

Moisture regime	Xeric	Mesic	Subhydric
Drainage code[1]	1-2	3-4	5-6
Number of stands	10	25	12
Dominant tree species	*Pinus banksiana*	*Picea mariana*	*Picea mariana*
Percentage of dominant species stems	51 ± 6	67 ± 5	92 ± 2
Codominant tree species (average percentage of stems)	*Picea mariana* (34 ± 7)	*Pinus banksiana* (21 ± 5) *Abies balsamea* (7 ± 2)	*Abies balsamea* (4 ± 1)
Surface soil type	Mineral	Mineral	Mineral or organic
Organic layer thickness[2] (mm)	75 ± 10	150 ± 15	280 ± 25
Thinning intensity[3] (%)	55.7 ± 12.5	43.4 ± 8.3	51.5 ± 6.6
Initial density[4] (stems.ha^{-1})	3881 ± 1110	3681 ± 365	4379 ± 293
Initial basal area[4] (m^2.ha^{-1})	5.66 ± 1.10	3.17 ± 0.46	1.74 ± 0.17
Average study tree age at t_1 (years)	12 ± 1	16 ± 1	21 ± 1
Average study tree size at t_1			
- dbh (cm)	5.90 ± 0.47	4.53 ± 0.29	4.19 ± 0.38
- Height (m)	4.97 ± 0.42	4.02 ± 0.18	3.64 ± 0.23

[1] According to MFFP classification (2011)

[2] Stands had not been scarified before tree establishment

[3] Thinning intensity was estimated as the relative difference in tree basal area at t_1 between the thinned and control plots of each pair, and thus corresponds to the proportion of tree basal area that was removed by PCT.

[4] Initial density and basal area correspond to control plot density and basal area at t_1.

The area treated by PCT was randomly chosen in each stand, i.e. there was no difference between control and treated areas before treatment. Pairs of control (unthinned) and thinned plots were established in each stand the year after PCT intervention by forest companies. The two plots of a unique pair presented similar site physical characteristics, as well as similar pre-thinning stand structure, age and composition. Control plots were established in unthinned areas that were at least 50 m x 50 m in size in order to avoid border effects. A thinned plot was localized as close as possible, but with a minimum of 20 m from the edge of the unthinned area. PCT was completed following current inventory standards, including a target spacing of 2 m between trees and an average density of 2500 trees.ha^{-1} (Ministère des Ressources naturelles, de la Faune et des Parcs du Québec 2003). Nested circular plots 400 m^2 and 100 m^2 in area were established. Non-merchantable trees (diameter at breast height (dbh) $\leq$ 9 cm) that were at least 60 cm tall were counted by species and 2-cm dbh class (0, 2, 4, 6 and 8 cm) inside the 100 m^2 subplot, while merchantable trees (dbh > 9 cm) were counted by species and dbh class (2-cm dbh class from 10 to 24 cm) in the main 400 m^2 plot. Basal area (m^2·ha^{-1}) and density (trees·ha^{-1}) were estimated for each plot including both merchantable and non-merchantable trees. Twenty study trees that were representative of the dominant and codominant trees of the stand and that were evenly distributed were selected in the 400 m^2 plots. Their dbh (cm) and height (m) were measured, and their age was established either by counting the whorls, evaluating the time since the last major disturbance (fire or logging), or counting tree rings based on non-destructive cores. The composition and percent cover of the moss and lichen layer were visually assessed inside each 400 m^2 plot. In the field, species cover was assessed by using eight cover classes. The average value of each cover class was used as a numerical estimation of species cover. Cover per species group (lichens, feather and *Sphagnum* spp. mosses) was then calculated by adding the covers of each component species. Moisture regime was evaluated for each 400 m^2 plot following an intensity scale (from 1: rapid to 6: very poor; Berger et al. 2008). All tree and understory measurements were repeated four times, i.e., every 5 years from the 1st year after PCT (t_1) to the 15th year (t_{15}).

6.4.2 Statistical Analyses

Plots for which we lacked information on ground cover composition at t_1 were not considered and uncomplete pairs were removed. Therefore, of the 50 pairs of plots that were available for the study area, only 47 were retained for the statistical analyses. As feather moss cover is likely to be inversely correlated to lichen and *Sphagnum* spp. cover, this ground cover type was not considered in the following analyses.

To address objective 1, PCT effects on lichen and *Sphagnum* spp. cover were tested using repeated measure models based on the four measurement periods (1, 5, 10 and 15 years after treatment). As lichen and *Sphagnum* spp. abundance depends on site moisture regime (Carleton et al. 1990, Bisbee et al. 2001), this parameter was also included in the models. Plot pairing was considered in the model by introducing stand as a random factor. Since the data did not accurately fit a specific distribution, we applied a bootstrap procedure in which treatment effect significance was deduced from the probability that the associated individual coefficient of the linear model was equal to zero considering the bootstrap confidence intervals (Sánchez-Espigares and Ocaña 2009, Fox and Weisberg 2012).

In order to address objective 2, we assumed that the rate of tree growth and sensitivity to surface soil conditions decreased with age. Therefore, the effects of ground layer composition on tree growth are likely to be crucial soon after treatment (t_1) with the accumulation of consequences of these effects becoming visible 15 years after treatment (t_{15}). This is why we considered lichen and *Sphagnum* spp. cover 1 year after treatment (t_1) to investigate the way ground layer composition was related to tree growth, stand productivity, and PCT impact on stand productivity 15 years after treatment.

Tree growth over 15 years was estimated as tree relative growth in dbh between the 1st and the 15th year after PCT (expressed in % of increase). Since jack pine and black spruce do not have the same growth rate, the relationship between ground cover composition at t_1 and 15-year growth of the study trees was analyzed separately for the two species. All the study trees were considered in the analysis (N = 308 pines and N = 1135 spruce). Data distribution was not normal, and relationships between study tree growth in dbh, initial study tree dbh and ground layer composition at t_1 for the whole 400 m^2 plot were analyzed using a bootstrap procedure applied to a mixed regression model (Sánchez-Espigares and Ocaña 2009, Fox and Weisberg 2012), in which stand and plot (nested in stand) were introduced as random factors.

In addition to the tree-level analyses mentioned above, stand-level relationships between lichen and *Sphagnum* spp. cover at t_1 and stand characteristics 15 years after treatment were investigated using model selection, since the error distribution was normal. Analyses were conducted on four stand properties: basal area of the merchantable trees (dbh > 9 cm, BA_{MT}), total stand basal area (BA_{tot}), density of the merchantable trees ($Dens_{MT}$), and total stand density ($Dens_{tot}$). Model selection was based on the comparison of corrected Akaike information criteria (AICc), which are well adapted for small sample sizes (N = 47 for a maximum of seven parameters) using the package 'AICcmodavg' (Mazerolle 2016). Since jack pine, which was the second most abundant tree species in the sampled stands, is a faster-growing species than black spruce, its abundance in the stand was likely to have a large influence on stand characteristics after 15 years. Jack pine stand density was also a good indicator of site moisture regime and fertility in our study (Table 6.1). Therefore, jack pine density per hectare was introduced as a covariate in the models (JP).

To estimate PCT impact on stand productivity 15 years after treatment, we calculated a thinning efficiency index (TEI) based on the comparison of basal area of the merchantable trees (BA_{MT}) 15 years after treatment in the thinned plots *versus* the control plots:

$$[1]\quad \mathrm{TEI} = \log\left[\frac{(\mathrm{BA}_{\mathrm{MT}})_{\mathrm{thinned}}}{(\mathrm{BA}_{\mathrm{MT}})_{\mathrm{control}}}\right]$$

If TEI < 0, PCT had a negative effect on $\mathrm{BA}_{\mathrm{MT}}$; if TEI = 0, PCT had no effect on $\mathrm{BA}_{\mathrm{MT}}$; if TEI > 0, PCT had a positive effect on $\mathrm{BA}_{\mathrm{MT}}$, and the higher the TEI, the higher the positive effect of PCT on $\mathrm{BA}_{\mathrm{MT}}$. The relationships between this index and the initial ground layer composition of the thinned plot were analyzed using model selection based on AICc (Table 6.2). As the two tree species were likely to respond differently to PCT, especially because of the difference in growth rate and light dependence, jack pine density per hectare was introduced as a covariate in the models (JP). This covariate also reflected variations in site moisture regime and fertility across stands (Table 6.1).

When necessary, the dependent variables were transformed to improve homoscedasticity (square root or log-transformation). The strength of the correlation between each pair of explanatory variables was verified before conducting analyses ($r < 0.7$). All analyses were performed on R software (R Core Team 2014), using the packages ‘nlme’ (Pinheiro et al. 2014), ‘lme4’ (Bates et al. 2014), ‘car’ (Fox and Weisberg 2011) and ‘MASS’ (Venables and Ripley 2002).

6.5 Results

6.5.1 Effect of PCT on Ground Layer Composition

Reduced cover of lichen and *Sphagnum* spp. tended to be associated with greater feather moss cover (Figure 6.1). Lichen cover was significantly higher in the thinned plots, especially in xeric sites (Figure 6.1 and Table 6.3), and this effect was the same for all the measurement periods. Although lichen cover was poorly related to moisture regime in the control plots, the positive effect of PCT on lichen cover was visible in xeric-sites only, as suggested by the highly significant effect of the interaction between treatment and moisture regime (Table 6.3). In contrast, thinning treatment did not affect *Sphagnum* spp. cover whose distribution was related to site moisture regime only

(Figure 6.1 and Table 6.3). In the thinned plots of the xeric sites, the lichen cover remained relatively high for 10 years and tended to decrease slightly 15 years after PCT. *Sphagnum* spp. cover did not change with time in any of the moisture regime classes (Figure 6.1).

Table 6.2 Explanatory variables and models used to explain stand characteristics 15 years after treatment.

	#	Explanatory variables	Model meaning
BA_{MT} $Dens_{MT}$ BA_{tot} $Dens_{tot}$	**1**	Treat + JP + BA_1 + $Lich_1$ + $Spha_1$ + (1|Site)	Complete model
	2	Treat + JP + BA_1 + (1|Site)	Not related to ground layer composition
	3	Treat + JP + BA_1 + $Lich_1$ + (1|Site)	Only related to lichen cover
	4	Treat + JP + BA_1 + $Spha_1$ + (1|Site)	Only related to *Sphagnum* spp. cover
TEI	**1**	JP * $Lich_1$ + JP * $Spha_1$	Complete model
	2	JP	Not related to ground layer composition
	3	JP * $Lich_1$	Only related to lichen cover
	4	JP * $Spha_1$	Only related to *Sphagnum* spp. cover

BA: Basal area; Dens: density; $_{MT}$: merchantable trees; $_{tot}$: total; TEI: Thinning Efficiency Index; Treat: treatment; $Lich_1$: lichen cover at t_1; $Spha_1$: *Sphagnum* spp. cover at t_1; BA_1: basal area at t_1; JP: jack pine tree density per hectare.

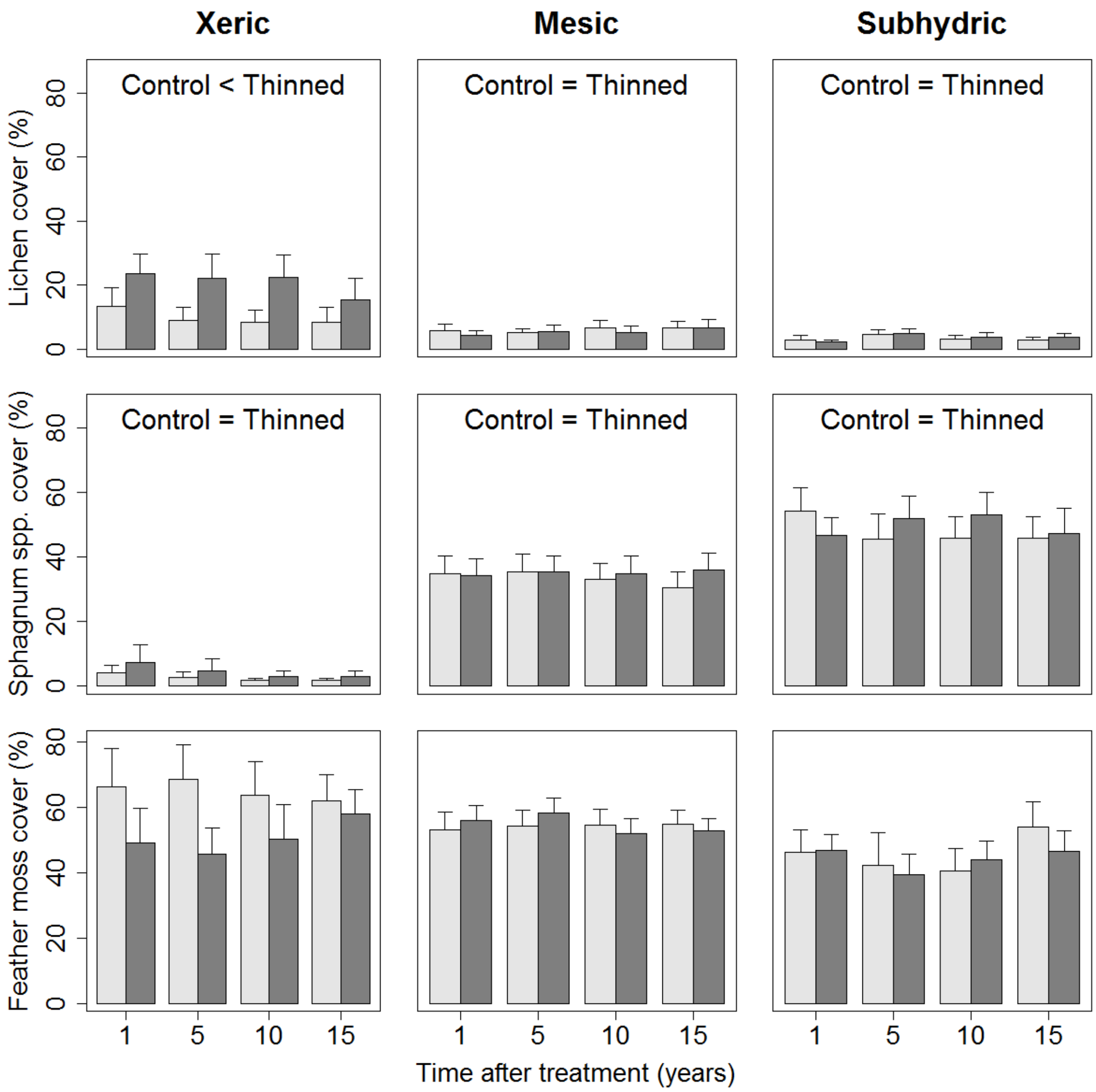

Figure 6.1 Temporal variations in lichen, *Sphagnum* spp. and feather moss cover by thinning treatment. Data are presented by moisture regime, i.e. xeric (1-2), mesic (3-4), and subhydric (5-6). Light and dark grey bars correspond to control and thinned plots, respectively.

Table 6.3 Thinning effect on the composition of the ground layer by moisture regime and measurement period. *p*-values were estimated following a bootstrap procedure. The coefficients that are significantly different from 0 are indicated by a *p*-value in bold. The interaction between treatment and year was not significant (ns) in any of the models.

	Lichen[1]		*Sphagnum* spp.[2]	
	Coefficient	*p*-value	Coefficient	*p*-value
Treatment	18.59	< **0.001**	4.84	ns
Moisture regime	-0.18	ns	1.20	< **0.001**
Year 5	0.76	ns	-0.77	ns
Year 10	0.32	ns	-1.53	ns
Year 15	-0.09	ns	-2.64	ns
Treatment x moisture regime	-0.43	< **0.001**	-0.05	ns

[1] Repeated measure models with uncorrelated random intercept and random slope within the stands.

[2] Repeated measure models with correlated intercept and random slope within the stands.

6.5.2 Ground Layer Composition and 15-Year Growth of the Study Trees

PCT treatment had a positive impact on both jack pine and black spruce growth in dbh (Figure 6.2 and Table 6.4). Study tree growth in dbh was inversely proportional to initial tree size. Relationships between tree dbh growth and lichen cover differed between the two tree species (Figure 6.2a and 6.2c). While jack pine growth was positively correlated to year-one lichen cover (Figure 6.2 and Table 6.4), the inverse tended to be true for the study black spruce trees that were small at the time of the treatment (Table 6.4). Neither jack pine nor black spruce dbh growth was related to year-one *Sphagnum* spp. cover (Figure 6.2c and 6.2d). As the effect of the interaction between treatment and ground cover composition was not significant in any of the two models, this parameter was not conserved.

6.5.3 Ground Layer Composition and Stand Characteristics 15 Years after Treatment

The two best models explaining BA_{MT} at t_{15} (weight > 0.40) included *Sphagnum* spp. cover at t_1, or did not include any of the ground layer parameters (Table 6.5). The best models explaining $Dens_{MT}$ and $Dens_{tot}$ at t_{15} included *Sphagnum* spp., but not lichen cover at t_1, while the best model explaining BA_{tot} at t_{15} did not include any of the ground layer parameters (Table 6.5). Although BA_{tot} and $Dens_{tot}$ of the thinned plots were still lower than BA_{tot} and $Dens_{tot}$ of the control plots 15 years after treatment, PCT had a significant positive effect on BA_{MT} and $Dens_{MT}$ (Figure 6.3 and Table 6.6). Except for $Dens_{tot}$, stand characteristics at t_{15} (BA_{MT}, BA_{tot} and $Dens_{MT}$) were primarily influenced by total stand basal area at t_1 (Table 6.6). Jack pine density was positively associated with BA_{MT} and $Dens_{MT}$, and negatively associated to $Dens_{tot}$ (Table 6.6). Finally, *Sphagnum* spp. cover at t_1 was negatively related to BA_{MT} and $Dens_{MT}$ at t_{15}, and positively related to $Dens_{tot}$ at t_{15} (Figure 6.3 and Table 6.6).

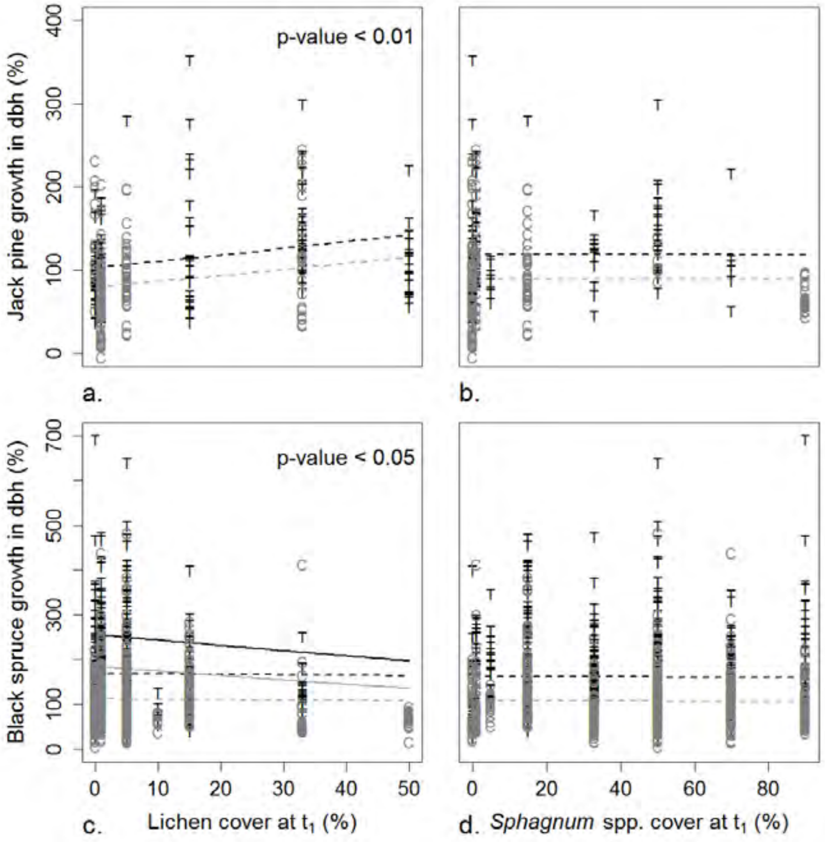

Figure 6.2 Relative growth in dbh of the study trees as a function of tree species and ground cover composition at t_1. **a.** Jack pine x lichen cover (N = 308); **b.** Jack pine x *Sphagnum* spp. cover (N = 308); **c.** Black spruce x lichen cover (N = 1135); **d.** Black spruce x *Sphagnum* spp. cover (N = 1135). Grey "C" and black "T" correspond to control and thinned plots, respectively. Grey and black dashed lines correspond to the predictions of the models given in Table 4 for control and thinned plots, respectively, considering an average dbh at t_1, i.e. 6 cm dbh for jack pine (a and b) and 4 cm dbh for black spruce (c and d). As the relationship between black spruce growth and lichen cover was tree size-dependent, model predictions for 1.5 cm dbh at t_1 are also given for each treatment in Figure c (grey and black solid lines for control and thinned plots, respectively). Significant relationships are indicated by the corresponding *p*-value threshold.

Table 6.4 Relationships between relative growth and dbh at t_1 of jack pine and black spruce, and ground cover composition at t_1.

	Coefficient	*p*-value
Pine relative growth in dbh (sqrt[1])		
Treatment	1.2	**< 0.01**
dbh at t_1 (cm)	-0.46	**< 0.001**
Lichen at t_1 (%)	9.8×10^{-2}	**< 0.01**
Sphagnum spp. at t_1 (%)	-7.2×10^{-3}	ns[2]
dbh at t_1 * Lichen at t_1	-1.0×10^{-2}	**< 0.001**
dbh at t_1 * *Sphagnum* spp. at t_1	1.2×10^{-3}	ns
Spruce relative growth in dbh (sqrt)		
Treatment	2.4	**< 0.001**
dbh at t_1 (cm)	-1.2	**< 0.001**
Lichen at t_1 (%)	-5.9×10^{-2}	**< 0.05**
Sphagnum spp. at t_1 (%)	3.5×10^{-3}	ns
dbh at t_1 * Lichen at t_1	1.4×10^{-2}	**< 0.001**
dbh at t_1 * *Sphagnum* spp. at t_1	-2.9×10^{-3}	**< 0.05**

[1] sqrt: square root transformed ; [2] ns: non-significant.

Tableau 6.5 Degrees of freedom (Df), corrected Akaike information criteria (AICc), differences in AICc compared with the best model (ΔAICc), and weights of the models used to explain stand characteristics 15 years after treatment. Acronyms of the explanatory variables are given in Table 6.2.

#	Explanatory variables	Df	AICc	ΔAICc	Weight
Basal area of merchantable trees at t$_{15}$ (sqrt)					
4	**Treat + JP + Spha$_1$ + BA$_1$**	**87**	**312.8**	**0**	**0.57**
2	**Treat + JP + BA$_1$**	**88**	**313.4**	**0.7**	**0.41**
3	Treat + JP + Lich$_1$ + BA$_1$	87	321.1	8.4	0.01
1	Treat + JP + Lich$_1$ + Spha$_1$ + BA$_1$	86	321.7	8.9	0.01
Total basal area at t$_{15}$					
2	**Treat + JP + BA$_1$**	**88**	**590.6**	**0**	**0.84**
3	Treat + JP + Lich$_1$ + BA$_1$	87	594.1	3.5	0.14
4	Treat + JP + Spha$_1$ + BA$_1$	87	598.7	8.1	0.01
1	Treat + JP + Lich$_1$ + Spha$_1$ + BA$_1$	86	602.6	12.0	0.00
Merchantable tree density at t$_{15}$ (sqrt)					
4	**Treat + JP + Spha$_1$ + BA$_1$**	**87**	**690.4**	**0**	**0.72**
2	Treat + JP + BA$_1$	88	693.1	2.7	0.18
1	Treat + JP + Lich$_1$ + Spha$_1$ + BA$_1$	86	695.1	4.7	0.07
3	Treat + JP + Lich$_1$ + BA$_1$	87	696.8	6.4	0.03
Total stand density at t$_{15}$ (sqrt)					
4	**Treat + JP + Spha$_1$ + BA$_1$**	**87**	**905.2**	**0**	**0.56**
2	Treat + JP + BA$_1$	88	906.6	1.4	0.27
1	Treat + JP + Lich$_1$ + Spha$_1$ + BA$_1$	86	908.6	3.4	0.10
3	Treat + JP + Lich$_1$ + BA$_1$	87	909.5	4.2	0.07
Thinning Efficiency Index					
2	**JP**	**45**	**149.7**	**0**	**0.47**
3	**JP * Lich$_1$**	**43**	**149.8**	**0.1**	**0.44**
1	JP * Lich$_1$ + JP * Spha$_1$	41	154.2	4.5	0.05
4	JP * Spha$_1$	43	154.5	4.8	0.04

sqrt: square root transformed

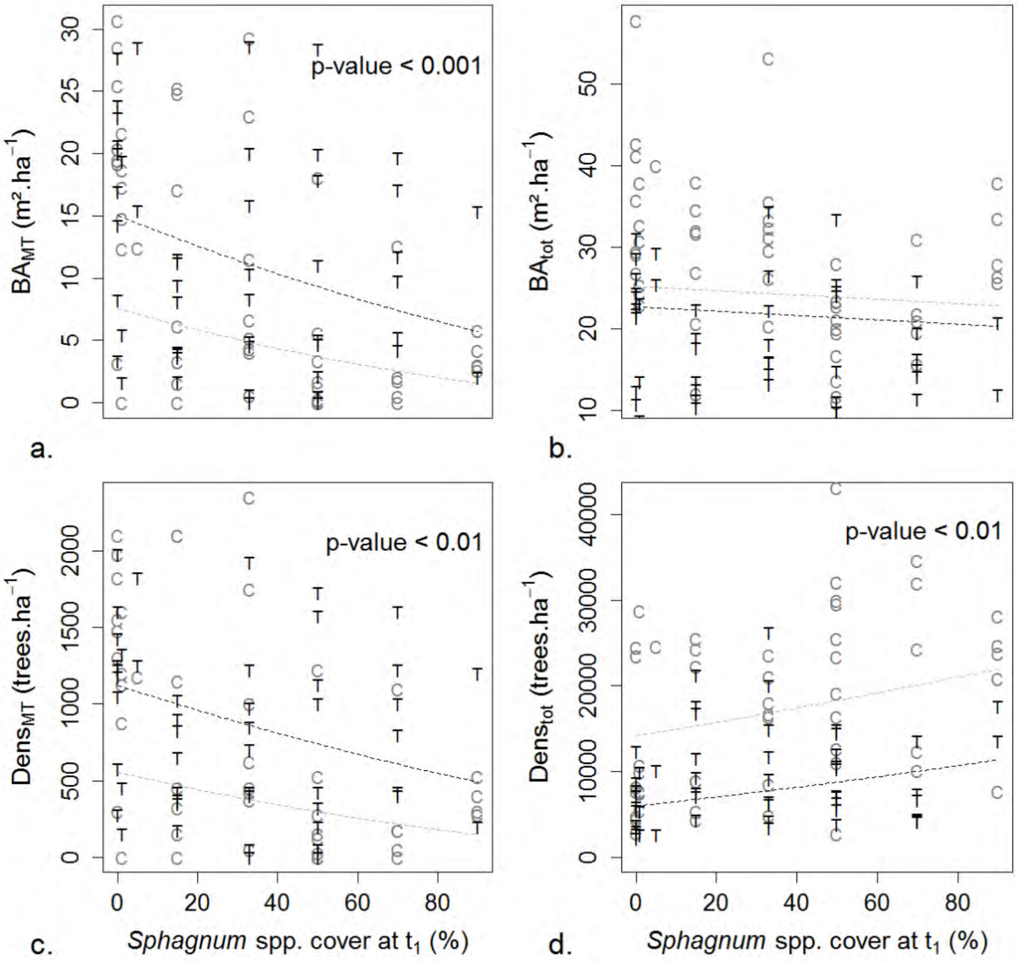

Figure 6.3 Stand characteristics at t_{15} in relation to *Sphagnum* spp. cover at t_1. **a.** Basal area of the merchantable trees; **b.** Total basal area of the stand; **c.** Density of the merchantable trees; **d.** Total density of the stand. Grey “C” and black “T” correspond to control and thinned plots, respectively. Grey and black dashed lines correspond to the predictions of the models given in Table 6.6 for control and thinned plots, respectively, considering an average basal area at t_1 (8 m².ha^{-1}) and an average pine density (1900 trees.ha^{-1}). Significant relationships are indicated by the corresponding *p*-value threshold.

Table 6.6 Analysis of the best models to explain stand characteristics 15 years after treatment. Coefficients that are significantly different from 0 are indicated by a *p*-value in bold. The stand, which was included as a random factor in the first four models, explained more than half of the total variance of the stand characteristics. This contributed to increase the values of the pseudo R^2 associated with these models.

		Coefficient		Model
	Estimate	*t*-value	*p*-value	Pseudo R^2
Basal area of merchantable trees at t_{15} (sqrt)				
Treatment	1.13	6.54	**< 0.001**	0.86
JP	1.3×10^{-4}	2.71	**0.0095**	
Basal area at t_1	6.7×10^{-2}	3.54	**0.0010**	
Sphagnum spp. at t_1	-1.6×10^{-2}	-3.69	**< 0.001**	
Total basal area at t_{15}				
Treatment	-3.16	-3.22	**0.0024**	0.91
JP	-1.8×10^{-4}	-0.72	0.4724	
Basal area at t_1	1.12	10.96	**< 0.001**	
Merchantable tree density at t_{15} (sqrt)				
Treatment	9.96	6.66	**< 0.001**	0.68
JP	1.2×10^{-3}	2.95	**0.0051**	
Basal area at t_1	0.67	4.13	**< 0.001**	
Sphagnum spp. at t_1	-0.13	-3.37	**0.0016**	
Total stand density at t_{15} (sqrt)				
Treatment	-41.5	-1.63	**< 0.001**	0.83
JP	-6.2×10^{-3}	-4.63	**< 0.001**	
Basal area at t_1	0.45	7.02	0.4343	
Sphagnum spp. at t_1	0.32	2.77	**0.0126**	
Thinning Efficiency Index				
JP	-4.9×10^{-4}	-2.28	**0.0277**	0.19
Lichen at t_1	-5.0×10^{-2}	-2.07	**0.0447**	
JP * Lichen at t_1	2.2×10^{-5}	1.38	0.1762	

6.5.4 Ground Layer Composition and PCT Impact on Stand Productivity 15 Years after Treatment

The two best models explaining TEI 15 years after treatment (weight > 0.40) included lichen cover at t_1, or did not include any of the ground layer parameters (Table 6.5). TEI was negatively associated with jack pine density in the stand and negatively related to the proportion of lichen cover in the thinned plots 1 year after treatment (Figure 6.4 and Table 6.6).

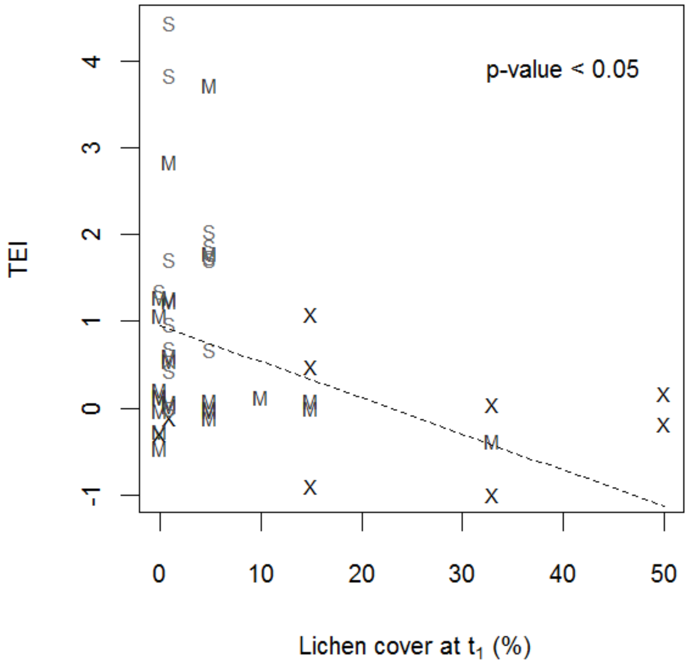

Figure 6.4 Thinning Efficiency Index (TEI) in relation to lichen cover at t_1. X, M and S correspond to xeric, mesic and subhydric stands, respectively. Dashed line corresponds to the prediction of the model presented in Table 6.6 considering an average pine density (1900 trees.ha^{-1}).

6.6 Discussion

6.6.1 PCT Effect on Ground Layer Composition Depends on Site Moisture Regime

We expected that PCT to favor lichen and *Sphagnum* spp. expansion at the expense of feather moss cover by opening up the canopy and changing the light and microclimatic conditions at the ground layer (Bisbee et al. 2001, Boudreault et al. 2013). In this study, it seems that PCT did favor lichen cover, but only in xeric sites. No more than 1 year after the PCT treatment, lichen cover was already much higher in the thinned than in the unthinned plots. This large difference may not only result from the effect of PCT on the degree of canopy closure, but also to some degree from the effect of ground cover trampling by the workers at the time of the PCT. As lichens regenerate well from fragmentation (Crittenden 2000) and in open canopy conditions (Boudreault et a. 2013), understory trampling during PCT and post-PCT advantageous microclimatic conditions may have accelerated lichen expansion at the expense of feather moss cover (Sulyma and Coxson, 2001). However, as lichen cover was visually assessed in the 400 m^2 plot, we can also suppose that lichen fragmentation by trampling may have contributed to an overestimation of year-one lichen cover in the thinned plots. This may explain why the difference observed between treatments was surprisingly high considering the growth potential of lichens (Crittenden 2000, Coxson and Marsh 2001, Boudreault et al. 2013). PCT effect on lichen cover tended to diminish with time since treatment in the thinned plots, presumably because of the gradual reclosing of the stand (Coxson and Marsh 2001). In contrast, lichen cover remained constantly low in the control plots where canopy continuity and ground layer integrity were not disturbed over the 15 years.

In contrast to lichens, the expansion of *Sphagnum* spp. mosses was not favored by PCT, even in the sites characterized by mesic to subhydric conditions. The absence of effect of PCT on the *Sphagnum* spp. cover may have resulted from the already high proportion of *Sphagnum* spp. mosses in the ground layer before treatment, as suggested by the abundant *Sphagnum* spp. cover in the unthinned plots (≈ 40% in the mesic sites, 60% in the subhydric sites). The subhydric sites investigated in this study were characterized by high *Sphagnum* spp. cover, high organic layer thickness, and low initial tree basal area, which may indicate that they probably were already paludified at the time of the PCT treatment. Furthermore, initial tree basal area of the sites characterized by subhydric to mesic conditions was lower than that in xeric sites, suggesting that the degree of canopy closure before PCT was also lower in those stands. Therefore, PCT effect on light availability and microclimatic conditions may have been less significant in those sites, which would explain why PCT had no effect on *Sphagnum* spp. expansion while it had a non-negligible effect on lichen cover in the xeric sites.

6.6.2 The Positive Effect of PCT is Reduced in Sites with High Lichen Cover

At the tree scale, relationships between tree growth and lichen cover differed according to tree species. As the study area included a large range of environmental conditions, jack pine growth may have been positively associated with lichen cover because of similar environmental preferences between the two species, especially in terms of moisture regime and surface deposits. In contrast, the proportion of lichens in the ground layer soon after PCT tended to be negatively correlated to the growth of the study black spruce trees that were small at the time of treatment. Lichens have been shown to reduce black spruce sapling growth (Brown and Mikola 1974, Wheeler et al. 2011), and it has been suggested that they may affect tree fine root growth through their effects on soil nutrients (Pacé et al. 2017). Therefore, black spruce growth may have been negatively affected by the environmental conditions associated with lichen cover, especially small trees that are likely to be more dependent on surface soil conditions.

As the relationship between tree growth and lichen cover was tree species-dependent, and thus varies with stand composition, we were not able to establish any correlation at the stand scale between lichen cover and stand productivity. However, each pair of plots (thinned and control) used to estimate TEI was homogeneous in terms of tree species composition. Therefore, while the relationship between lichen cover and basal area of merchantable trees varied according to tree species in the stand, TEI expresses the way PCT has improved productivity in a given stand independently of stand composition. The negative relationship we observed between pine density and TEI may partly result from jack pine's association with low-fertility xeric sites, where the effect of PCT was likely to be less beneficial. In addition to this effect, the impact of PCT on the basal area of merchantable trees 15 years after treatment was weaker, and even tended to be negative in stands with a high proportion of lichen cover 1 year after treatment. This result suggests that the aboveground effect of PCT on tree growth may have been mitigated by belowground negative feedback resulting from lichen expansion on xeric sites.

6.6.3 Stand Productivity Depends on *Sphagnum* spp. Cover

Although *Sphagnum* spp. cover was not related to the growth of the study trees, it was negatively associated with the basal area and density of merchantable trees at the stand scale 15 years after treatment. *Sphagnum* spp. impact on surface soil conditions mainly affect the growth of trees that are rooted in the fibric layer (Simard et al. 2007; Saint-Denis et al. 2010). As study trees were sampled among the biggest individuals of the plot at the time of thinning, they may have been sufficiently large and deeply rooted in the mineral soil that their growth was not related to *Sphagnum* spp. cover. However, by affecting the growth of the smallest trees and, eventually, that of the new seedlings, the dominance of *Sphagnum* spp. in the ground layer of some stands may have reduced the number of trees that reached 9 cm in dbh, resulting in a reduction of the basal area and density of merchantable trees at the stand scale 15 years after treatment.

The positive relationship between *Sphagnum* spp. and total stand density may result from the positive impact of this ground cover type on germination (Ohlson and Zackrisson 1992, Groot and Adams 1994, Hörnberg et al. 1997) and spruce layering (Stanek 1961). Slow growth of trees in *Sphagnum* spp. mosses may also have resulted in slow self-thinning in high-density stands. Several of the subhydric stands with high *Sphagnum* spp. cover that we investigated in this study were probably paludified. In these stands, regeneration of black spruce is relatively abundant, but saplings tend to remain small because of unfavorable growth conditions (Saint-Denis et al. 2010; Lafleur et al. 2011). This high density of small trees associated with high *Sphagnum* spp. cover resulted in a total tree basal area that was not significantly different from that of the stands with low *Sphagnum* spp. cover.

TEI was not related to year-one *Sphagnum* spp. cover in the thinned plots, suggesting that PCT impact on stand productivity was the same regardless of *Sphagnum* spp. cover at the time of thinning. As PCT did not favor *Sphagnum* spp. expansion, it likely did not make *Sphagnum* spp. effect on tree growth conditions worse when compared to unthinned plots. Therefore, a high cover of *Sphagnum* spp. had neither a negative nor a positive effect on TEI. Since the sensitivity to *Sphagnum* spp. impact on soil conditions is inversely proportional to root depth (Simard et al. 2007), as suggested by the absence of *Sphagnum* spp. effect on the growth of the study trees, we can hypothesize that part of the trees benefited from the increase in space, light and soil resource availability associated with PCT even in stands with high *Sphagnum* spp. cover. However, because those stands were overall less productive, the growth increase due to PCT was lower than in the other stands.

6.7 Conclusion

Precommercial thinning favored lichen expansion in xeric sites, while it had no effect on *Sphagnum* spp. cover, which was related to site moisture regime. In contrast to jack pine, the growth of the black spruce trees that were small at the time of thinning was lower in the sites with high lichen cover. This negative relationship was visible at the stand scale, where the positive effect of PCT on stand productivity was negatively related to the proportion of lichens in the ground layer 1 year after treatment. Although no relationship was established between *Sphagnum* spp. cover and the growth of the study trees in this study, *Sphagnum* spp. cover was negatively associated with the basal area and density of merchantable trees at the stand scale. These contrasting results between the two scales probably result from the size-dependent sensitivity of trees to *Sphagnum* spp. effects on the forest soil.

6.8 Management Implications

High lichen cover at the time of thinning may indicate that the stand is less susceptible to respond efficiently to a PCT treatment, especially in black spruce-dominated stands. Therefore, it may be more appropriate to plan PCT in mesic stands with a low cover of lichens. Precaution should be taken, especially in xeric sites where PCT is more likely to favor ground layer colonization by lichens. As feather mosses outcompete lichens in closed-canopy conditions only, scarification before tree establishment is not likely to control lichen expansion in these sites.

Although the increase in *Sphagnum* spp. cover did not seem to affect deeply rooted trees, it was associated with a reduction in the basal area and density of merchantable trees at the stand scale, suggesting that it offers less appropriate growth conditions for saplings. Therefore, precaution should also be taken in the subhydric sites that are already advanced in the paludification process in order to avoid tree growth problems that would result in long-term forest productivity loss. Furthermore, although PCT impact might be positive even in sites with high *Sphagnum* spp. cover, it is probably more profitable, considering the cost for this forest treatment, to target more promising sites for PCT.

6.9 Aknowledgements

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6.10 References

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CHAPITRE VII

CONCLUSION GÉNÉRALE

L'objectif principal de cette thèse était d'élucider le rôle de la strate des mousses et lichens dans l'établissement et le maintien de milieux ouverts stables en forêt boréale. L'approche corrélative menée sur le terrain (chapitre 2) nous a d'abord permis de vérifier les liens entre le degré d'ouverture du couvert et la composition de la strate des mousses et lichens à l'échelle de la station forestière. Ces résultats, ainsi que ceux d'études précédentes (Sulyma et Coxson, 2001 ; Fenton et Bergeron, 2006), corroborent l'hypothèse selon laquelle l'ouverture du couvert forestier sur les sites caractérisés par des conditions extrêmes de drainage tend à favoriser les lichens ou les sphaignes aux dépens des mousses hypnacées dans le parterre forestier. Dans une première partie, nous reviendrons sur les résultats des chapitres 2, 3, 4 et 5 de manière à faire le point sur les effets des mousses hypnacées, des lichens et des sphaignes sur la germination et la croissance du pin gris et de l'épinette noire. Dans un second temps, nous discuterons de ce que ces résultats nous révèlent sur les processus écosystémiques à l'origine de l'établissement et du maintien de milieux ouverts stables en forêt boréale. Enfin, nous discuterons de l'implication de ces résultats pour l'aménagement forestier en revenant notamment sur les résultats du chapitre 6 et tenterons d'établir des suggestions utiles pour l'aménagement écosystémique.

7.1 Effets des mousses hypnacées, des lichens et des sphaignes sur la germination et la croissance ligneuse

La série d'expériences réalisées dans le cadre de cette thèse (chapitres 2 à 5) ont permis de tester les effets des mousses hypnacées, des lichens et des sphaignes sur 4 stades de développement du pin gris et de l'épinette noire (Figure 7.1.), c.-à-d. la germination (chapitres 3 et 4), la croissance des plantules (0 - 6 mois, chapitres 2, 3 et 4), la croissance des jeunes plants (2 - 3 ans, chapitres 3, 4 et 5), et la biomasse de racines fines utilisées comme indicateur de la qualité des conditions de croissance d'arbres adultes (20 - 40 ans, chapitre 2). Ces quatre chapitres ont révélé que les effets des mousses hypnacées, des lichens et des sphaignes sur la germination et la croissance des arbres sont associés à des processus différents pouvant impliquer trois types de facteurs environnementaux : des facteurs physiques tels que l'humidité (H_2O), l'oxygénation (O_2), la température (T°C) ou la disponibilité en lumière (Lum.) ; des facteurs chimiques tels que la disponibilité des nutriments (NPK) ou l'émission de composés chimiques dans la solution du sol (Sub.) ; ou encore des facteurs biologiques tels que le degré de mycorhization (Myc.) et la diversité des morphotypes ectomycorhiziens associés aux racines. Les effets (positifs, négatifs ou neutres) de chaque type de couvert au sol ont été testés relativement à l'absence de couvert (modalité contrôle).

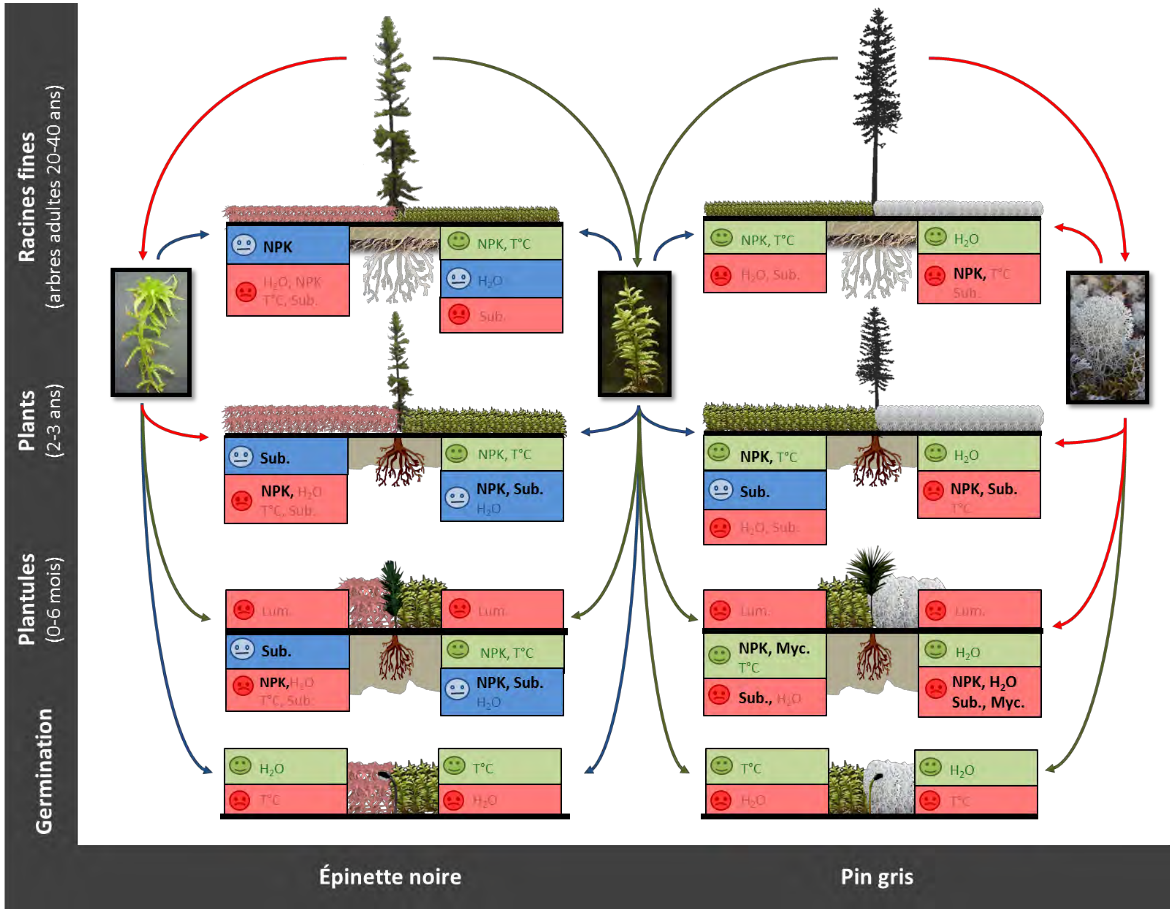

Figure 7.1 Effets principaux des mousses hypnacées, des lichens et des sphaignes à différents stades du développement de l’épinette noire et du pin gris (légende : voir précisions sur la page suivante).

Notes concernant la figure 7.1 : Les flèches vertes et rouges sont associées à chaque stade de développement de l'arbre et correspondent à des effets positifs et négatifs, respectivement. Les flèches bleues indiquent une absence d'effet. Pour chaque stade de développement de l'arbre, les facteurs environnementaux influencés par la composition de la strate des mousses et lichens sont indiqués dans les cases vertes, bleues ou rouges suivant l'effet qu'ils induisent sur le développement de l'arbre (positif, neutre ou négatif, respectivement). Les facteurs environnementaux ayant été identifiés comme responsables des effets de la mousse ou du lichen dans le cadre de cette thèse sont indiqués en noir. Les autres correspondent à des facteurs soupçonnés ou mis en évidence dans d'autres études (références citées dans le texte). Un même facteur environnemental peut apparaitre dans plusieurs catégories (positif, négatif ou neutre) en cas de résultats contradictoires dans la littérature. H_2O : humidité du substrat ; Lum. : disponibilité en lumière ; Myc. : mycorhization des racines ; NPK : disponibilité des nutriments ; O_2 : oxygénation du substrat ; Sub. : interférences chimiques *via* l'émission de composés dans la solution du sol ; T°C : température du substrat.

7.1.1 Effets des mousses hypnacées sur le pin gris et l'épinette noire

En comparaison de l'absence de couvert au sol, la présence d'un couvert de mousses hypnacées tend soit à favoriser, soit à avoir un effet neutre sur la germination et la croissance du pin gris et de l'épinette noire (Figure 7.1). Le contenu en azote inorganique dissous des lessivats de mousses hypnacées était plus grand que celui des lessivats de sol nu, de lichens ou de sphaignes (chapitre 5), suggérant que l'effet positif des mousses hypnacées sur la croissance des arbres provient de son influence positive sur la disponibilité des nutriments dans le sol. Cette hypothèse semble d'ailleurs se vérifier sur le terrain (chapitre 3) où ce type de couvert au sol est généralement associé à des sols plus riches que le lichen (Ohtonen et Väre, 1998 ; Wheeler et al., 2011 ; DeLuca et al., 2013) ou la sphaigne (Lavoie et al., 2007 ; Lafleur et al., 2011). Le couvert de mousses hypnacées a également eu un effet très positif sur la mycorhization et la diversité des morphotypes ectomycorhiziens associés aux racines des plantules de pin gris, et ce probablement du fait de l'effet positif de la présence de matière organique sur les communautés fongiques du sol (chapitre 3).

L'effet négatif des lessivats de mousses hypnacées sur la croissance des plantules de pin gris (chapitre 5) suggère que ce type de couvert interfère chimiquement avec la croissance des arbres *via* la solution du sol. Ce résultat vient compléter ceux d'expériences précédentes basées sur l'analyse d'extraits de tissus de bryophytes (Steijlen et al., 1995 ; Michel et al., 2011) en suggérant que les substances inhibitrices de la croissance des arbres ne sont pas uniquement contenues dans les tissus muscinaux mais peuvent se retrouver également dans la solution du sol. L'existence d'interférences chimiques pourrait contribuer à expliquer pourquoi la croissance des épinettes fertilisées était moindre dans les mousses hypnacées que dans les sphaignes, bien que l'inverse ait été vrai lorsque les plants étaient limités par les nutriments. L'effet positif des mousses hypnacées sur la croissance ligneuse *via* l'augmentation de la disponibilité des nutriments dans le sol forestier tendrait à dissimuler tout effet d'interférence chimique lié à l'émission de composés dans la solution du sol.

7.1.2 Effets des lichens sur le pin gris

Mis à part leur effet positif sur la germination des graines en serre, les lichens ont inhibé la croissance du pin gris à chacun des stades de développement analysés (chapitres 3 et 5). De même, l'augmentation de la biomasse de racines fines suite à la suppression du lichen (chapitre 2) témoigne d'une amélioration à court-terme des conditions nutritives locales, et donc potentiellement d'un effet positif de la suppression du lichen sur la croissance des pins gris adultes. D'après nos résultats, les effets du lichen sur la croissance du pin gris seraient liés non seulement à une disponibilité moindre des nutriments dans le sol forestier (chapitres 2 et 3), mais aussi à l'existence d'effets chimiques plus directs (chapitres 3 et 5). Ces effets peuvent relever entre autres de processus allélopathiques et/ou antimicrobiens (Brown et Mikola, 1974 ; Crittenden, 2000 ; Sedia et Ehrenfeld, 2003 ; Molnár et Farkas, 2010), comme le suggère la présence probable d'acide usnique dans les lessivats de lichens (chapitre 5). La présence de lichens était également associée à une mycorhization moindre des racines de plantules (chapitre 3), possiblement en raison de l'émission par le lichen de composés antimicrobiens et de leur impact sur les communautés fongiques. Nos résultats ne permettent cependant pas d'affirmer avec certitude que les effets observés sur les arbres soient directement liés à l'émission de composés issus du métabolisme secondaire des lichens. En d'autres termes, ils ne constituent pas une preuve de l'existence d'effets allélopathiques du lichen sur la croissance du pin gris.

Dans le cadre de nos expériences, les effets du lichen sur la croissance ligneuse ont été testés soit sous couvert forestier (chapitres 2 et 3), soit en chambre de culture (chapitres 3 et 5), c.-à-d. dans des conditions d'humidité relativement favorables. Or, le lichen est également connu pour maintenir un taux d'humidité suffisante à la surface des sols forestiers fortement drainés des clairières ouvertes (Kershaw et Rouse, 1971 ; Bonan et Shugart, 1989), notamment parce qu'il est associé à un taux d'évapotranspiration plus faible que celui des mousses (Lafleur et Schreader, 1994). Ainsi, dans des conditions de sécheresse plus intenses, il est possible que le lichen facilite plus qu'il n'inhibe l'établissement et la croissance des plantes vasculaires (Steijlen et al., 1995), ces processus étant plus limités par les conditions d'humidité du sol que par les nutriments ou par le milieu chimique. Ces conditions extrêmes s'appliquent peu à notre région d'étude. Certaines années plus sèches peuvent affecter la croissance du pin gris de manière ponctuelle, mais leur impact reste limité sur la croissance à long-terme. On peut ainsi raisonnablement penser que les impacts négatifs du lichen prédominent dans les pinèdes grises considérées dans cette étude.

7.1.3 Effets des sphaignes sur l’épinette noire

La présence de sphaignes n’a pas affecté la germination des graines d’épinette noire. Elle a cependant eu des effets contrastés sur la croissance des arbres, dépendamment du stade de développement et des conditions environnementales auxquelles les plants étaient soumis au cours de leur croissance. De la même manière que la présence d’un couvert de mousses hypnacées, la présence de sphaignes a eu un effet positif sur la croissance des plantules d’épinette noire (chapitre 4). Ce type de couvert a cependant inhibé la croissance en serre des plants âgés de 2 à 3 ans, bien qu’il n’ait pas eu d’effet significatif sur le terrain (chapitre 4). De la même façon, l’analyse de pistes réalisée dans le chapitre 1 et les analyses corrélatives entre productivité et couvert en sphaignes menées dans le chapitre 6 ont souligné le rôle clé de la sphaigne dans la réduction de la productivité des stations forestières sujettes à la paludification. Nos résultats confirment ainsi les observations selon lesquelles la sphaigne affecte moins l’établissement que la croissance des arbres (Saint-Denis et al., 2010). Ces effets différentiels selon le stade de développement ont été particulièrement visibles dans les placettes paludifiées du chapitre 6 où le couvert en sphaignes était lié à une diminution de la densité des arbres marchands bien qu’associée à une augmentation de la densité totale des arbres sur la station.

En serre, la fertilisation a plus fortement stimulé la croissance des plants dans la sphaigne que dans les mousses hypnacées ou sur un sol nu, suggérant que l’effet négatif de la sphaigne sur la croissance des plants était lié à une disponibilité moindre des nutriments dans le sol forestier (chapitre 4). Ces résultats sont cohérents avec ceux de Lavoie et al. (2007) qui ont mesuré des concentrations foliaires en azote et phosphore plus faibles dans des plants ayant poussé dans de la sphaigne que dans des plants ayant poussé dans des mousses hypnacées. La prédominance de ce mécanisme d’inhibition de la croissance ligneuse pourrait expliquer pourquoi l’établissement et la croissance des plantules n’ont été que peu ou pas affectés par la sphaigne. En effet, puisque les besoins en nutriments de l’arbre augmentent au cours de son développement, ces derniers étaient moins limitants pour les plantules qu'ils ne l'étaient pour des arbres à des stades de développement plus avancés. Les bonnes conditions de croissance associées à l'environnement de la serre ont permis d'obtenir une réponse rapide des jeunes plants aux contrastes de disponibilité des nutriments associée au sol nu, aux mousses hypnacées et à la sphaigne. On peut supposer cependant que la durée de l'expérience de plantation sur le terrain n'était pas suffisamment longue pour permettre une accumulation visible des effets de la limitation par les nutriments sur la croissance des épinettes. En effet, la faible réponse des arbres à la fertilisation *in situ* (chapitre 4) suggère qu'à ce stade de développement, la croissance des plants était plus limitée par d'autres facteurs de stress tels que la température ou l'humidité qu'elle ne l'était par le contenu nutritif du sol. Ce délai plus long dans la réponse des plants *ex situ* est sans doute lié à un plus fort choc de transplantation en conditions naturelles (Struve, 2009). Ce que les résultats obtenus en serre à partir de la transplantation d'une fine couche muscinale révèlent également, c'est que les sphaignes n'affectent pas seulement la croissance de l'épinette *via* leurs effets à long-terme sur l'accumulation de litière et le régime hydrique (Lavoie et al., 2005 ; Fenton et al., 2005, 2006 ; Fenton et Bergeron, 2006 ; Simard et al., 2007), mais aussi par des effets plus directs sur la disponibilité des nutriments dans le sol forestier.

7.2 Rôle de la strate des mousses et lichens dans l'établissement et le maintien de milieux ouverts stables en forêt boréale

Compte-tenu des effets contrastés des différents types de couvert au sol sur la germination et la croissance ligneuse, il parait tout à fait probable que le remplacement des mousses hypnacées par les lichens ou les sphaignes en cas d'ouverture du couvert forestier contribue à la dégradation des conditions de croissance du pin gris et de l'épinette noire. Nos résultats tendent donc à supporter l'hypothèse selon laquelle les changements qui s'opèrent dans la strate des mousses et lichens constituent un moteur de l'établissement et de la stabilisation des milieux ouverts en forêt boréale, en intervenant comme un facteur aggravant du déficit de régénération ligneuse. Les mécanismes diffèrent cependant entre les deux transitions. Alors que l'établissement d'une lande à lichens provient d'une succession de perturbations poussant le système vers un état d'équilibre secondaire, l'établissement d'une tourbière à sphaignes n'est rendue possible que par l'absence prolongée de perturbations sévères du système. Ceci souligne les caractères différents de ces deux types de transition : alors que l'une est déclenchée par des facteurs exogènes, l'autre est régie par des mécanismes endogènes à la communauté végétale. Par ailleurs, le déficit de régénération à l'origine de la formation d'une lande à lichens est d'abord lié à une réduction de la banque de graines (Payette et Delwaide, 2003 ; Pinno et al., 2013), quand celui observé dans les tourbières à sphaignes résulte plus d'un déficit de croissance de la régénération ligneuse que d'un déficit de recrutement (Saint-Denis et al., 2010). Dans ce second cas, la réduction de la banque de graines est une conséquence de l'entourbement (Van Bogaert et al., 2015) au même titre que le déficit de croissance ligneuse, et ne constitue donc pas la cause première du défaut de régénération. Ces considérations sont importantes puisqu'elles soulignent les rôles contrastés du lichen et de la sphaigne dans l'établissement et le maintien de milieux ouverts stables : alors que le lichen joue surtout un rôle dans la stabilisation de l'état de lande à lichens, la sphaigne intervient comme un élément moteur de la transition vers un état de tourbière boisée.

L'installation du lichen, bien que n'étant pas l'élément déclencheur de la transition, est un facteur important du basculement et de la stabilisation de l'état ouvert alternatif. L'ouverture prolongée du couvert forestier favorise la formation d'un épais tapis de lichens sur le sol forestier (Boudreault et al., 2013). Ce dernier contribue à dégrader les conditions d'établissement et de croissance des arbres en régénération (chapitres 2, 3 et 5) en limitant l'accès à la lumière pour les plantules (Crittenden, 2000) et en favorisant la réduction à long-terme de la disponibilité des nutriments dans le sol forestier (Sedia et Ehrenfeld, 2005 ; Deluca et al., 2013). Les effets négatifs du couvert de lichens sur la mycorhization des racines de plantules (chapitre 3) indiquent également que ce type de couvert au sol est susceptible de fragiliser le pin gris vis-à-vis des conditions climatiques extrêmes telles que le gel ou la sécheresse. Sur les sites excessivement drainés, l'absence de couvert forestier peut également constituer un facteur aggravant du déficit de régénération dans la mesure où elle peut accentuer la sécheresse du substrat (Von Arx et al., 2013) et donc altérer les conditions microclimatiques nécessaires à l'établissement et à la croissance des arbres. Supprimer la couche de lichens ou bien la remplacer par un couvert de mousses hypnacées pourrait tendre dans ces conditions à empirer les conditions de croissance pour les plantes vasculaires en aggravant les conditions de sécheresse à la surface du sol (Kershaw et Rouse, 1971 ; Bonan et Shugart, 1989). L'ouverture du couvert forestier peut également favoriser certaines Ericacées dont *Kalmia angustifolia* et *Rhododendron groenlandicum* (Hébert et al., 2010). Or, ces espèces sont connues pour constituer un facteur supplémentaire de dégradation des conditions de croissance des résineux (Mallik, 1987 ; Thiffault et al. 2006, 2012). Dans la mesure où nos expériences ont été réalisées dans des conditions favorables d'humidité (sous couvert forestier), l'application d'un ombrage n'a pas eu d'effet positif sur la croissance des plants et des racines fines (chapitres 2 et 3).

Contrairement à l'établissement d'une lande à lichens, l'établissement d'une tourbière à sphaignes est régi par des mécanismes endogènes à la communauté végétale. Passé un certain stade de la succession forestière, la trajectoire de l'écosystème n'est plus dictée par le couvert forestier mais par les effets de la strate muscinale sur les conditions physico-chimiques et biologiques du sol (analyse de pistes du chapitre 2). Nos résultats expérimentaux révèlent que l'effet négatif de la sphaigne sur la croissance ligneuse est susceptible d'intervenir assez rapidement après le remplacement des mousses hypnacées par les sphaignes, avant même d'être associé à l'accumulation d'une épaisse couche organique sur le sol forestier (chapitre 4). Le parterre de sphaignes n'intervient pas uniquement comme élément stabilisateur mais aussi et surtout comme moteur principal de la transition vers un état de tourbière ouverte. L'impact de ces organismes ingénieurs sur le sol est à l'origine d'une réduction de la production de graines par les arbres (Van Bogaert et al. 2015), et donc de l'éventuelle stabilisation à long-terme de l'état de tourbière à sphaignes en cas de perturbation tardive. En effet, la pluie de graines post-perturbation n'est pas suffisante pour permettre le rétablissement d'un peuplement forestier fermé, et la suppression des tiges par le feu ou la coupe empêche toute possibilité de reproduction par marcottage. Dans ce cas spécifique, la transition vers un état de tourbière à sphaignes peut prendre une tournure définitive dans la mesure où l'absence de reproduction par graines ou marcottage, associée à la piètre qualité des conditions de croissance, annihilent toute possibilité de réinitialisation de la succession forestière.

7.3 Implications des résultats pour l'aménagement écosystémique

7.3.1 Prévention des risques

Nos résultats soulignent le rôle non négligeable de la composition de la strate des mousses et lichens dans la survenue d'accidents de régénération en forêt boréale et améliorent notre compréhension des mécanismes sous-jacents. L'analyse attentive des caractéristiques de la strate de sous-bois peut être utilisée de façon à : (i) mieux prévenir les accidents de régénération imputables aux travaux sylvicoles en évitant d'intervenir dans des peuplements à risque ; (ii) mieux anticiper les effets de l'augmentation de la fréquence de feux à venir sur l'expansion des milieux ouverts, et donc mieux appréhender la capacité future de la forêt boréale à intervenir comme un puits de carbone. Il reste encore beaucoup d'inconnues quant aux effets du remplacement de la forêt fermée par des clairières ouvertes de type lande à lichens ou tourbière à sphaignes sur la capacité de la forêt à séquestrer le carbone. Il est en effet possible que le puits de carbone associé à la productivité forestière soit substitué par l'accumulation à long-terme de la matière organique peu décomposée dans les sols des forêts paludifiées (Ziegler et al., 2017). Par ailleurs, le remplacement des étendues d'épinettes noires, de couleur foncée, par des étendues blanches de lichens engendre un changement important de réflectance et favorise un effet de refroidissement dans l'atmosphère (Bernier et al. 2013). Ainsi, il est possible que les effets de la perte nette de productivité liée au basculement de la forêt fermée vers un état de lande à lichens ouverte soient atténués par l'effet d'albédo du lichen (Bernier et al. 2013).

Les pratiques sylvicoles qui ouvrent le couvert forestier sont susceptibles d'influencer la composition de la strate des mousses et lichens. Les résultats du chapitre 6 montrent que l'ouverture du couvert forestier par éclaircie pré-commerciale (EPC) tend à favoriser l'expansion des lichens sur les sites excessivement drainés. En revanche, ils ne nous ont pas permis de rendre compte de la dynamique temporelle de l'envahissement du sous-bois par les sphaignes suite à l'EPC, dans la mesure où plusieurs des placettes échantillonnées étaient déjà largement colonisées par les sphaignes au moment du traitement. Par ailleurs, nous ne disposions pas d'informations sur l'épaisseur de la couche de sphaignes, ce qui ne nous a pas permis de vérifier les effets de l'EPC sur la croissance verticale du tapis muscinal. Selon nos résultats, ces changements de composition ont des répercussions négatives sur la croissance ligneuse. De ce fait, ils confirment que la pratique de la coupe sur des stations forestières à risque est susceptible de favoriser l'expansion de milieux ouverts stables dans la matrice forestière aménagée.

Les pratiques sylvicoles telles que l'EPC visent à augmenter le rendement marchand d'une station forestière. Ces interventions engendrent des coûts, et nécessitent un retour sur investissement. Il n'y a donc aucun intérêt à les pratiquer là où elles ne fonctionnent pas. Nos résultats suggèrent que les sites fortement drainés à lichens et les sites à drainage lent avec un fort recouvrement initial en sphaignes ne devraient pas être ciblés (chapitre 6) dans la mesure où ils sont moins enclins à répondre favorablement à l'EPC et plus à risque de transiter vers une clairière ouverte stable (Figure 7.2.). Une autre solution serait de réduire la quantité de bois récolté pour maintenir une plus grande densité de tiges résiduelles et permettre le maintien d'un couvert forestier suffisant pour ne pas favoriser l'expansion du lichen ou de la sphaigne aux dépens des mousses hypnacées.

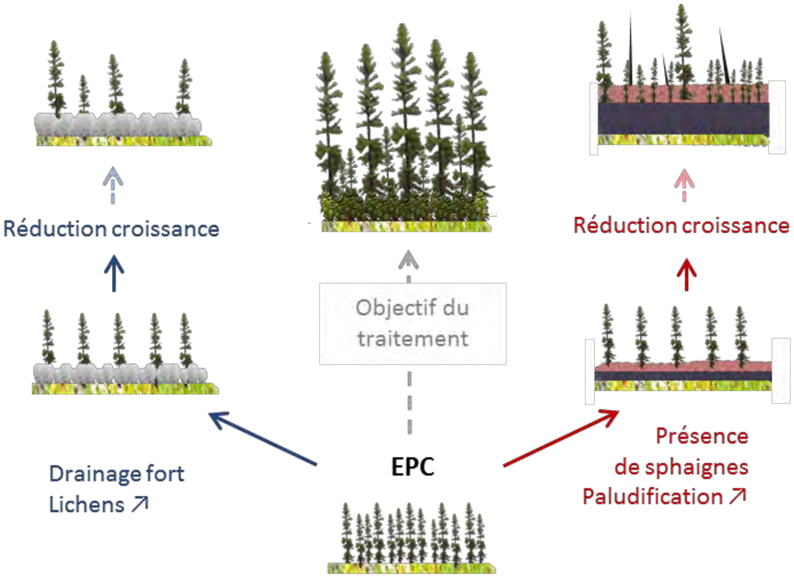

Figure 7.2 Les effets de l'éclaircie précommerciale sur la productivité du peuplement varient suivant les conditions de site et la composition initiale de la strate des mousses et lichens.

En conditions de drainage excessif, le basculement vers l'une ou l'autre des configurations stables de la communauté (forêt fermée à mousses ou clairière à lichens) dépend du pool d'espèces, ainsi que de leur capacité de reproduction et de dispersion après perturbation. En d'autres termes, il est important pour éviter les accidents de régénération subséquents à la survenue d'un feu sur un site récemment récolté d'adapter la configuration de coupe de façon à optimiser la ressource en graines disponibles, notamment sur les sites caractérisés par des conditions de drainage excessif. La rétention d'îlots matures dans le paysage de coupe permettrait par exemple de favoriser la résilience de l'état de forêt fermée en augmentant le nombre de graines disponibles en cas de feu subséquent à la coupe.

Les coupes avec protection de la régénération et des sols, ainsi que les coupes partielles qui ne perturbent pas suffisamment la strate muscinale et la couche organique du sol sont à proscrire sur les sites de fin de succession où la sphaigne est déjà bien présente. Il s'agirait de préconiser dans ce cas des méthodes de récolte ayant des effets plus sévères sur le sol et la végétation de sous-bois de façon à réduire la profondeur de la couche organique et limiter la dominance de la sphaigne dans le parterre forestier. Bien que le défaut de croissance observé sur ces sites soit principalement lié à l'épaisseur de la couche organique au sol, le chapitre 4 nous indique qu'une couverture peu épaisse de sphaignes peut également avoir des effets à court-terme sur la disponibilité des nutriments et donc limiter le potentiel de croissance ligneuse du peuplement forestier.

7.3.2 Restauration de la productivité forestière

L'établissement de milieux ouverts stables dans le paysage forestier boréal est le fruit de processus naturels. Leur présence dans le paysage forestier est importante pour le maintien de la diversité structurale des forêts et la biodiversité à l'échelle du paysage (Crittenden, 2000 ; Littlewood, 2010). La restauration de la productivité forestière ne doit donc pas être systématique mais seulement encouragée dans les forêts aménagées, plus spécifiquement sur les sites modifiés par les interventions anthropiques. Puisque l'établissement et le maintien de landes à lichens et de tourbières à sphaignes reposent sur des mécanismes différents, le rétablissement d'un couvert forestier sur ces deux types de site nécessite des solutions sylvicoles différentes.

La suppression du lichen a stimulé localement la production de racines fines sous couvert forestier (chapitre 2). De la même façon, Hébert et al. (2006) ont fait état d'un effet positif de la préparation de sol sur la croissance du pin gris dans des conditions de drainage bon à modéré. Il est cependant possible que la perturbation du couvert de lichens à grande échelle sur des sites plus sujets à la sécheresse ait des répercussions négatives sur les conditions d'humidité du sol (Kershaw et Rouse, 1971 ; Rouse et Kershaw, 1971 ; Bonan et Shugart, 1989), notamment en cas d'absence de couvert forestier. Par conséquent, il semble que la meilleure façon d'encourager le rétablissement de la productivité à long-terme sur les sites de lande à lichens soit de favoriser une fermeture rapide du couvert forestier de façon à améliorer les conditions microclimatiques du sous-bois et à favoriser l'installation des mousses hypnacés dans le parterre forestier. L'établissement de landes à lichens stables est d'abord le fruit d'une réduction de la banque de graines suite à une ou plusieurs perturbations. Ainsi, malgré l'effet négatif des lichens sur la croissance ligneuse (chapitres 3 et 5), l'ensemencement et la plantation à forte densité constitue sans doute la manière la plus efficace de rétablir un couvert forestier sur ces sites (Sirois, 1993; Tremblay et al., 2013).

L'impact négatif de la sphaigne sur la croissance ligneuse résulte principalement de ses effets sur l'accumulation de litière et le régime hydrique (Lavoie et al. 2005 ; Fenton et al., 2005, 2006 ; Fenton et Bergeron, 2006 ; Simard et al. 2007). Ainsi, la meilleure manière de rétablir la productivité d'un site entourbé est de réduire l'épaisseur de la couche de matière organique accumulée sur le sol forestier en recourant notamment au brûlage dirigé (Lavoie et al. 2005) ou à la préparation de sol (Fenton et al., 2009 ; Henneb et al. 2015 ; Lafleur et al. 2016). Ces pratiques permettent d'augmenter la quantité et la qualité des lits de germination tout en améliorant les conditions de croissance de la régénération. Ces traitements, s'ils sont suivis d'un ensemencement ou d'une plantation à forte densité favorisant une fermeture rapide du couvert forestier et la colonisation du sous-bois par les mousses hypnacées, devraient être en mesure de rétablir la productivité forestière à long-terme sur les sites sujets à l'entourbement. De la même manière, la coupe totale, puisqu'elle a des effets plus sévères sur le sol et la végétation de sous-bois, serait plus adaptée que la coupe avec protection de la régénération et des sols dans les stations forestières paludifiées (Lafleur et al., 2010 ; Lafleur et al., 2016).

ANNEXE A

SUPPORTING INFORMATION FOR MATERIAL AND METHODS

Chapitre 3: Lichens contribute to open woodland stability in the boreal forest through detrimental effects on pine growth and root ectomycorrhizal status

Living material and substrate

Pinus banksiana Lamb. seeds and saplings originated from provincial nurseries of the *Ministère des Ressources Naturelles du Québec*. Seeds (germination success = 97 %; germinative value = 74 %) were produced in the forest seed centre of Berthier (Sainte-Geneviève de Berthier, QC, Canada). Trees originated from the provincial nurseries of Guyenne and Trécesson (Abitibi, QC, Canada), where they had grown in greenhouses for 2 years. No chemicals were applied to pine trees prior to the experiments. Their growth in nurseries was stimulated by the application of fertilisers.

Mineral sand, lichens and feather mosses were harvested in May 2015 in the boreal forest of western Québec (spruce-moss bioclimatic domain, Bergeron et al. 1999), in a pure *Pinus banksiana* Lamb.-lichen stand located on fluvioglacial coarse-grain deposits (49° 19’ N; 79° 11’ W). Ground covers were harvested with their associate poorly to well-decomposed dead organic matter, and Ericaceae (above- and belowground parts) were entirely removed from the moss and lichen layers. Harvested lichens mainly were *Cladonia stellaris* (Opiz) Pouzar & Vězda, with some *C. rangiferina* (L.) F.H. Wigg. and *C. mitis* Sandst. Feather mosses were mainly represented by *Pleurozium schreberi* (Brid.) Mitt., with some *Dicranum polysetum* Swartz*, D. undulatum* Schrad. ex Brid. and *Ptilidium ciliare* (L.) Hampe.

Pot watering, temperature and air humidity in the greenhouse experiments

Seedling pots were watered with demineralised water twice a day (10 mL per pot) throughout summer 2015. Watering was progressively reduced to 10 mL once a day in September 2015 and 10 mL three times a week in October and November 2015. Sapling pots were watered twice a day at a daily rate of 60 mL per pot from May to August 2015. Watering was reduced to 30 mL per day in September 2015 and 30 mL three times a week in October and November 2015.

For each greenhouse experiment, temperature and air humidity were recorded hourly from May to November 2015 using HOBO® data loggers (HOBO® U23 PRO V2, Onset Data Loggers, Bourne, MA, USA).

Environmental conditions of the field experiment

Average annual precipitation in the field experiment site was 909.1 mm (Joutel, QC, Environment Canada, 2010). Air temperature and humidity were recorded hourly from July 2014 to October 2015 using HOBO® data loggers. Understorey plant species, including mosses, lichens and Ericaceae, were the same as those mentioned above. Before planting, aboveground parts of Ericaceae were removed by cutting at the soil surface. Ericaceae roots were not removed to avoid ground cover disturbance.

To account for a possible bias in light availability due to the preference of lichens for high light levels, canopy closure was measured in July 2014 using fish-eye photos at each sapling location. Photos were analyzed in terms of percentage of pixels attributable to trees using Adobe Photoshop Elements software. This analysis revealed an average canopy closure of 60% with no significant differences between cover types (F-value = 1.38, *p*-value 0.2506).

Ectomycorrizha analysis

Contrary to the saplings, which spent 2 years in the nursery before the experiment and were almost exclusively colonised by greenhouse opportunistic fungi, seedlings were chosen for ectomycorrhiza analysis because they had completed their early development in natural substrates and may thus have been colonised by fungal associations that were closer to the ones found in natural pine forests. Fresh seedling root samples were gently rinsed in demineralised water and analysed under a dissecting microscope. Ectomycorrhizal morphotypes were identified according to macroscopic characteristics such as colour, general tip shape, branching and structure, as well as microscopic attributes. Colonised root tips were gently squashed under a cover slip and viewed under high magnification (x 400-630) using a light microscope. Details on rhizomorphs, mantle cells, emanating hyphae and cystidia were noted to identify ectomycorrhizal morphotypes using descriptions by Agerer (1987-2008) and Ingleby et al. (1990).

ANNEXE B

SUPPLEMENTARY DATA

Chapitre 3: Lichens contribute to open woodland stability in the boreal forest through detrimental effects on pine growth and root ectomycorrhizal status

Table S1 Dry biomass increase by ground cover type (non-fertilised trees only, mean ± SE)

		Biomass increase (mg)		
		Belowground	**Aboveground**	**Total**
Greenhouse seedlings (6 months)	Bare soil	161 +/- 15	97 +/- 4	258 +/- 18
	Feather mosses	392 +/- 26	260 +/- 19	652 +/- 44
	Lichens	143 +/- 23	102 +/- 14	245 +/- 36
Greenhouse saplings (7 months)	Bare soil	7910 +/- 2110	1240 +/- 390	9070 +/- 2060
	Feather mosses	7310 +/- 520	1910 +/- 310	9220 +/- 720
	Lichens	4870 +/- 560	1190 +/- 320	6560 +/- 700
Field saplings (18 months)	Bare soil	720 +/- 140	1430 +/- 630	2150 +/- 750
	Feather mosses	1260 +/- 200	2550 +/- 450	3810 +/- 540
	Lichens	850 +/- 160	1750 +/- 360	2600 +/- 460

Table S2 General characteristics and environmental conditions associated with the four experiments

	Location	**Duration**	**Additional treatment**	**Period**	**Temperature**			**Air humidity**		
					Mean	Range	SD	Mean	Range	SD
Germination	Greenhouse	3 weeks	-	May 2015	21.2 ˚C	11.9-33.6 ˚C	3.7 ˚C	60.8%	13.3-100.0%	23.7%
Seedling growth	Greenhouse	6 months	Fertilisation (2 levels)	June 2015 to Nov. 2015	21.2 ˚C	11.9-33.6 ˚C	3.7 ˚C	60.8%	13.3-100.0%	23.7%
Sapling growth	Greenhouse	7 months	Fertilisation (2 levels)	May 2015 to Nov. 2015	21.5 ˚C	12.6-39.6 ˚C	4.1 ˚C	60.2%	10.8-100.0%	24.4%
	Field	18 months	Shading (2 levels)	July 2014 to Oct. 2014	10.8 ˚C	-8.9-39.2 ˚C	7.7 ˚C	92.0%	27.7-100.0%	14.0%
				Nov. 2014 to May 2015	-0.8 ˚C	-11.9-32.4 ˚C	5.5 ˚C	89.9%	23.1-100.0%	10.6%
				May 2015 to Oct. 2015	15.0 ˚C	-4.0-39.8 ˚C	7.1 ˚C	85.2%	17.5-100.0%	18.1%

Table S3 Substrate available nutrient concentrations at the end of the two sapling experiments by treatment and ground cover type (mean ± SE)

Experiment	**Soil**	**Treatment**	**Ground cover**	**NH_4^+** (mg.kg^{-1})	**NO_3^-** (mg.kg^{-1})	**P** (cmol.kg^{-1})	**Major base cations** (cmol.kg^{-1})
Greenhouse	Mineral	Unfertilised	Bare soil	0.77 ± 0.05	0.50 ± 0.10	57.43 ± 1.03	0.13 ± 0.01
			Feather mosses	0.90 ± 0.04	0.41 ± 0.05	58.85 ± 2.47	0.16 ± 0.01
			Lichens	0.96 ± 0.08	0.38 ± 0.01	58.95 ± 1.25	0.16 ± 0.01
		Fertilised	Bare soil	0.89 ± 0.10	0.68 ± 0.17	62.63 ± 1.06	0.11 ± 0.01
			Feather mosses	0.86 ± 0.03	0.36 ± 0.01	59.03 ± 1.81	0.14 ± 0.01
			Lichens	1.25 ± 0.26	0.54 ± 0.18	57.49 ± 1.74	0.15 ± 0.01
Field	Mineral	No-shade	Bare soil	1.35 ± 0.01	0	2.85 ± 0.57	0.19 ± 0.00
			Feather mosses	1.52 ± 0.09	0	4.29 ± 0.81	0.26 ± 0.01
			Lichens	1.39 ± 0.02	0.08 ± 0.06	0.52 ± 0.37	0.13 ± 0.06
	Organic	No-shade	Bare soil	75.3 ± 7.9	0	87.6 ± 8.4	6.63 ± 0.42
			Feather mosses	120.4 ± 16.0	0	146.9 ± 18.0	9.3 ± 0.32
			Lichens	156.4 ± 6.0	0	45.8 ± 8.3	5.91 ± 0.76
		Shade	Bare soil	48.20 ± 15.7	0	121.6 ± 16.9	7.02 ± 0.19
			Feather mosses	137.6 ± 17.9	0	166.6 ± 28.7	11.24 ± 0.53
			Lichens	83.0 ± 7.3	0	90.7 ± 15.5	5.40 ± 0.41

Table S4. Description of the ectomycorrhizal morphotypes discriminated under microscope

Morphotype	Main morphological characteristics
Cenecoccum sp.	Black large hyphae (3-5 µm), ornamentation, sclerotia, no rhizomorphs, no stamps
Thelephora cf. terrestris	Dark to light brown, smooth, shiny, monopodial pinnate, no ornamentation, cystidia with basal clamps, dark brown rhizomorphs
Rhizopogon sp.	Tuberculate, dark brown pigmentation on the mantle and the hyphae, enlarged septa, no clamps
Unknown 1	Cremish white, smooth, shiny, branching in Y, hyphae with septa and clamps, white rhizomorphs
Unknown 2	Cremish white to light brown, smooth, shiny, pinnate, some in Y, rhizomorphs, septa but no clamps, mantle cells = 3-6 µm
Unknown 3	Narrow hyphae (1-2 µm), dark pigmentation in the mantle, no clamps
Unknown 4	Beige, cremish yellow, smooth, shiny, branching in Y, cells of the prosenchyma and emanating hyphae = 2-4 µm, septa and clamps, yellow cristalls

Table S5**.** Closest sequences recorded from the NCBI GenBank database matching the 11 OTUs recorded from the root tips analysis and occurrence of the OTUs by ground cover type.

OTUs (number of tips amplified)	Total occurrence (seedling number and proportion[1])	Occurrence per ground cover type (seedling number and proportion[2])			Coverage (%)	Similarity (%)	BLAST match
		Bare soil (N = 20)	Feather mosses (N = 20)	Lichens (N = 15)			
OTU 1 (20)	34 (0.62)	20 (1.00)	6 (0.30)	8 (0.53)	100	99	*Wilcoxina mikolae* voucher HMJAU27330, KU061020
OTU 2 (14)	18 (0.33)	0	16 (0.80)	2 (0.13)	100	100	Uncultured *Cantharellaceae* clone 5041-1201, HM146798
OTU 3 (5)	4 (0.07)	2 (0.10)	1 (0.05)	1 (0.07)	100	99	*Amphinema* aff. *byssoides* UC2022834, KP814528
OTU 4 (3)	2 (0.04)	0	2 (0.15)	0	62	91	*Rhizopogon truncatus* voucher OSC 144019, JX310376
OTU 5 (3)	2 (0.04)	0	0	2 (0.13)	100	100	*Thelephora terrestris* isolate ML-7, KT447173
OTU 6* (3)	25 (0.45)	2 (0.10)	18 (0.90)	5 (0.33)	100	99	*Cenococcum geophilum*, LC095204
OTU 7 (2)	1 (0.02)	0	1 (0.05)	0	100	99	*Suillus* sp. RT-2012 isolate FFP350, JQ711787
OTU 8 (2)	2 (0.04)	0	1 (0.05)	1 (0.07)	100	99	*Cortinarius cinnamomeus* voucher F15447, FJ157025 *Cortinarius tillamookensis* MICH 139446, NR_131857 *Cortinarius aurantiobasis* voucher SAT03-305-07, HM068560
OTU 9 (1)	1 (0.02)	0	1 (0.05)	0	100	99	*Tomentellopsis* sp. BB-2010, HM190011
OTU 10 (1)	1 (0.02)	0	0	1 (0.07)	100	100	*Amanita muscaria* strain RET289-3, EU071901
OTU 11 (1)	1 (0.02)	0	1 (0.05)	0	100	99	*Helotiaceae* sp. V GK-2010 strain ARSL 190907, HQ157876

[1] Proportion relative to the total number of seedlings (N_{tot} = 55 seedlings)

[2] Proportion relative to the number of seedlings per ground cover type

* The ITS region of *Cenococcum cf. geophilum* was difficult to amplify (40 % of success), nevertheless it was easy to recognise by microscopy based on its morphological characters.

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