UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

ÉVALUATION DES IMPACTS DES PERTURBATIONS SYLVICOLES SUR LA QUALITÉ DES MICROSITES ET LES FACTEURS AFFECTANT LA CROISSANCE DES PLANTATIONS EN FORÊT BORÉALE

THÈSE

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À mes parents, frères et soeurs

AVANT-PROPOS

Cette thèse est rédigée sous forme d'articles scientifiques, le premier article a été publié, le deuxième article a été accepté avec corrections mineures et le troisième article est en cours de préparation pour soumission. La thèse est complétée par une introduction générale et une conclusion générale. Je suis le principal responsable de l'étude, de la collecte des données, de leur analyse et de la rédaction des articles. Mes directeurs et codirecteurs ont contribué à la conception de l'étude et m'ont assisté dans l'interprétation des résultats. Ils ont aussi révisé de manière critique et constructive le contenu des articles.

Chapitre I. Introduction générale.

Chapitre II. Henneb, M., Valeria, O., Thiffault, N., Fenton, N., Bergeron, Y. 2019. Effects of mechanical site preparation on microsite availability and on growth of planted black spruce in Canadian paludified forests. *Forests* 10(8): 670.

Chapitre III. Henneb, M., Valeria, O., Thiffault, N., Fenton, N. 2019. Black spruce seedling growth response in conrolled organic and organic-mineral substrates. *Silva Fennica* 53(4).

Chapitre IV. Henneb, M., Thiffault, N., Valeria, O. 2020. Regional climate, edaphic conditions and establishment substrates interact to influence initial growth of black spruce and jack pine planted in the boreal forest. *Forests* 11(2): 139.

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RÉSUMÉ

La forêt boréale de l'Est canadien présente un fort potentiel de production ligneuse; l'industrie forestière y réalise des activités importantes de récolte et d'aménagement forestier. Les résineux, notamment les épinettes (*Picea* spp.) et les pins (*Pinus* spp.), sont les principales essences commerciales récoltées et utilisées pour le sciage et la pâte à papier. Dans le domaine bioclimatique de la pessière noire à mousses, certaines régions sont caractérisées par une faible productivité dans les sites paludifiés. La paludification est un phénomène naturel par lequel la matière organique s'accumule graduellement sur le sol minéral en absence de feu sévère. Ce phénomène est accéléré par plusieurs facteurs climatiques (climat froid) et édaphiques (imperméabilité du sol, topographie plane, faible drainage). La paludification mène à une baisse de croissance et à des taux de mortalité élevés de la régénération pré-établie due à la mauvaise qualité des substrats organiques surfaciques, souvent gorgés d'eau et pauvres en éléments nutritifs. Le reboisement précédé par une perturbation des horizons organiques, via la préparation mécanique du sol (PMS), a été proposée comme une solution prometteuse pour limiter la paudification et remettre en production les sites paludifiés. Cependant, peu d'informations sont disponibles concernant les conditions sous lesquelles certains traitements sylvicoles peuvent s'avérer efficaces à faciliter la remise en production des sites paludifiés.

La préparation mécanique du sol (PMS) vise à créer des conditions favorables à l'établissement des plants dans des microsites propices afin de maximiser leur chance de survie et leur croissance initiale. En effet, la croissance initiale des plants est déterminée par des variables environnementales à plusieurs échelles, qui incluent le climat régional (température, précipitations et humidité de l'air), les caractéristiques édaphiques à l'échelle du peuplement (drainage, dépôt de surface, pente), et le microenvironnement des plants à l'échelle du microsite (substrat d'établissement, température du substrat, position de mise en terre, épaisseur de l'humus). L'objectif général de cette thèse était d'analyser un ensemble de facteurs environnementaux qui déterminent la survie et la croissance des plants installés sur des sites ayant subi des perturbations sylvicoles à différentes intensités. Pour ce faire, via 3 chapitres, l'analyse

s'est réalisée à trois différentes échelles dans la forêt boréale de l'Est canadien, soit à l'échelle régionale, du peuplement et du microsite.

Une caractérisation des microsites et un suivi de croissance de jeunes plants d'épinette noire (hauteur, diamètre) ont été réalisés sur un réseau de 15 placettes disposées aléatoirement sur des sites paludifiés et préparés mécaniquement dans l'Est canadien. Nos résultats ont confirmé que la PMS (scarificateur, herse forestière) était efficace pour établir une cohorte de régénération productive dans les sites paludifiés. Également, à court terme, la PMS permettait un contrôle adéquat des éricacées. Lors des opérations de reboisement, il convient de privilégier les microsites argileux et mélangés (organo-argileux et argileux-humiques) afin de garantir une disponibilité suffisante en eau et en nutriments. Pour assurer une remise en production efficace des sites paludifiés, il est important de distinguer préalablement les zones faiblement-modérément paludifiées des zones fortement paludifiées; ceci permettra d'utiliser les traitements de PMS (scarificateur, herse forestière) adéquats pour chaque zone et d'exposer davantage de microsites propices à l'établissement des plants.

Dans une expérience de six mois sous serre (milieu contrôlé : accès illimité en eau, températures favorables), nous avons déterminé les effets des substrats extraits de sites paludifiés, tels que : organiques et mélanges organiques, minéraux et mélanges organo-minéraux sur la croissance et le développement racinaire de 130 plants d'épinette noire pendant une saison de croissance. Les résultats ont montré que les substrats ont eu un effet significatif sur la croissance des plants et leurs concentrations foliaires en nutriments (N, P, K). L'accroissement en hauteur et en diamètre était supérieur dans les substrats argileux et organique-mésique respectivement. Nous n'avons pas noté d'effet significatif des substrats sur l'accroissement de la biomasse totale et sur la biomasse racinaire finale. Les concentrations foliaires en nutriments (N, P, K) étaient relativement élevées dans les plants établis sur les substrats mésiques et relativement faibles dans ceux établis sur les substrats argileux. De ce fait, à court terme, pour garantir le succès d'établissement des plants, nous recommandons l'utilisation de techniques de PMS aptes à exposer davantage de microsites argileux et organiques-mésiques sur les sites présentant un accès limité et illimité en eau dans le sol, respectivement.

Dans le but de déterminer l'influence des variables climatiques (échelle régionale), édaphiques (échelle du peuplement), locales (échelle du microsite) et les conditions de reboisements sur le substrat d'établissement et la croissance initiale des plants d'épinette noire (*Picea mariana* (Mill.) B.S.P) et de pin gris (*Pinus banksiana* Lamb.), un suivi a été réalisé sur 29 parterres de coupe reboisés (5 placettes/parterre) par la

Direction de la recherche Forestière (DRF, Québec), et répartis sur un gradient climatique (précipitations et température) d'est en ouest, dans les domaines de la sapinière et de la pessière à mousse de l'Est canadien. Les résultats ont montré que les substrats d'établissement de types minéraux, organo- minéraux et organiques avaient des effets mitigés sur la croissance des plants selon l'influence et l'interaction des variables climatiques régionales, édaphiques à l'échelle du peuplement et locales à l'échelle du microsite. Cette étude a permis, à terme, de mieux comprendre les conditions d'établissement de la régénération en forêt paludifiée et les interactions existantes entre la croissance initiale des plants et les conditions environnementales à différentes échelles (régionale, peuplement et microsite) suite à leur mise en terre, et ce, afin d'assurer le maintien de la productivité des sites forestiers récoltés. Les recommandations sylvicoles de cette étude permettront aux aménagistes forestiers d'adapter les pratiques de reboisement aux conditions climatiques régionales dans l'est canadien, notamment dans le contexte des changements climatiques.

Ce travail a permis de mieux comprendre les conditions d'établissement de la régénération en forêt boréale de l'Est canadien. L'aménagement des sites reboisés dans les différentes régions bioclimatiques de l'Est canadien, dépend des caractéristiques édaphiques à l'échelle du peuplement et locales (types de substrats d'établissement ou de mise en terre) à l'échelle du microsite. La PMS est un traitement sylvicole que les aménagistes forestiers pourraient considérer dans l'aménagement des sites boréaux, notamment les sites paludifiés. Après la PMS, le choix des microsites et des substrats propices à l'établissement lors des opérations de reboisement est indispensable pour garantir une meilleure croissance et survie des plants dans les sites boréaux aménagés.

Mots clés : Croissance, Épinette noire, Facteurs environnementaux, Microsite, Nutrition, Paludification, Pin gris, Préparation mécanique du sol.

ABSTRACT

The boreal forest in eastern Canada has a high potential for wood production. This region is subject to heavy harvesting and forest management activities by the forest industry. Softwoods, especially spruce (*Picea* spp.) and pine (*Pinus* spp.), are the main commercial species harvested and used for sawing and pulp. In the black spruce-moss bioclimatic domain, some regions are characterized by low productivity on paludified sites. Paludification is a natural phenomenon by which organic matter accumulates gradually on the mineral soil in the absence of severe fire. This phenomenon is accelerated by climatic (cold climate) and edaphic factors (soil impermeability, flat topography, poor drainage). Paludification leads to lower growth and high mortality of advance regeneration due to the poor quality of surface organic substrates, which are often waterlogged and poor in nutrients. Reforestation preceded by a disturbance of organic horizons by mechanical soil preparation (MSP), has been proposed as a promising solution to limit paludification and restore the productivity of paludified sites. However, little information is available on the conditions under which some silvicultural treatments can prove effective in facilitating the restoration of paludified sites.

Mechanical soil preparation aims to create favorable conditions for the establishment of seedlings in suitable microsites in order to maximize their chance of survival and their initial growth. Indeed, the initial growth of seedlings is determined by environmental variables at several scales, which include the regional climate (temperature, precipitation and air humidity), the edaphic characteristics at the stand scale (drainage, surface deposits, slope), and the microenvironment of plants on the microsite scale (establishment substrate, substrate temperature, planting position, humus thickness). The general objective of this thesis was to analyze a set of environmental factors that determine the survival and growth of seedlings planted on sites that have sustained silvicultural disturbances at different intensities. Through 3 chapters, the analysis was carried out at three different scales in the boreal forest of Eastern Canada, notably at the regional, stand and microsite scales.

Microsite characterization and growth monitoring of black spruce seedlings (height, diameter) were performed on 15 plots randomly placed on prepared paludified sites in eastern Canada. Our results confirmed that MSP was effective in establishing a

productive regeneration cohort in paludified sites. Also, MSP allowed adequate control of Ericaceae species in the short term. During planting operations, clay and mixed microsites (organo-clay and clay-humic) should be favored to ensure sufficient availability of water and nutrients. To ensure effective restoration of paludified sites, it is necessary to identify the low-moderate paludified areas and highly paludified areas; this will allow the appropriate MSP treatments to be applied to each area and expose more favorable microsites for seedlings establishment.

In a six-month greenhouse experiment (controlled conditions: unlimited access to water, favorable temperatures), we determined the effects of substrates collected from paludified sites, such as: organic and organic-mix, mineral and organo-mineral mix substrates, on the growth and root development of 130 black spruce seedlings during a growing season in a controlled conditions. The results showed that the substrates had a significant effect on seedlings growth and foliar nutrient concentrations (N, P, K). The increase in height and diameter were better with clay (mineral) and mesic substrates respectively. We did not observe any significant effect of the substrates on the increase in total biomass and on the final root biomass. Foliar nutrient concentrations (N, P, K) were relatively high in seedlings established on mesic substrates and relatively low in those established on clay substrates. Therefore, to ensure successful seedlings establishment in the short term, we recommend the use MSP techniques able to expose more clay and organic-mesic microsites in sites with limited and unlimited access to water in the soil respectively.

To determine the influence of climatic variables (regional scale), edaphic variables (stand scale), local variables (microsite scale) and planting conditions on establishment substrate and initial growth of black spruce seedlings (*Picea mariana* (Mill.) BSP) and jack pine seedlings (*Pinus banksiana* Lamb.), A Monitoring was conducted on 29 reforested cutting patches (5 plots / cutting patch) by the *Direction de Recherche Forestière (DRF, Québec)*, and distributed over a climatic gradient (precipitation and temperature) from east to west, particularly in the Balsam-fir and spruce-moss domains in eastern Canada. The results showed that mineral, organo-mineral, and organic establishment substrates had variable effects on seedling growth depending on the influence and interaction of regional climatic variables, stand edaphic variables and local variables at the microsite scale. This study eventually led to a better understanding of the conditions for establishment of regeneration in paludified forest and the interactions between the initial growth of seedlings and environmental conditions at different scales (regional, stand and microsite) after planting, in order to maintain the productivity of the harvested forest sites. This study issued silvicultural recommendations for forest managers to adapt reforestation practices to regional climatic conditions in eastern Canada, particularly in the context of climate change

This work provided a better understanding of the conditions for establishing regeneration in the boreal forest of eastern Canada. Planting management in the different bioclimatic regions of eastern Canada depends on the edaphic characteristics at the stand scale and local characteristics (establishment and planting substrate type) at the microsite scale. Mechanical soil preparation (MSP) is a silvicultural treatment that forest managers could consider in the management of boreal sites, including paludified sites. After MSP, the choice of microsites and suitable substrates for establishment during planting operations is essential to ensure better growth and survival of seedlings in boreal sites.

Key words: Growth, Black spruce, Environmental factors, Microsite, Nutrition, Paludification, Jack pine, Mechanical soil preparation.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Forêt boréale

La zone circumboréale englobe les forêts les plus septentrionales du monde. C'est le plus vaste biome terrestre (couvre environ 14 % de la surface terrestre) comprenant 32% (14 millions km^2) du couvert forestier mondial (Burton et al., 2003). Le climat boréal se caractérise par des hivers froids et neigeux et une courte saison de croissance (Burton et al., 2010). Les températures moyennes journalières supérieures à 10 °C s'étalent seulement sur 30 à 120 jours par année et les températures sous 0 °C s'étalent sur 6 à 8 mois (Walter, 1985). Bien que les précipitations varient fortement à travers des gradients longitudinaux, ces dernières restent relativement faibles, en moyenne 150 à 450 mm/an (Walter, 1985). Les sols de la forêt boréale sont relativement humides et froids à cause des températures fraîches et de la faible évapotranspiration, sauf au milieu de la saison estivale où les températures peuvent atteindre 30 °C, causant l'assèchement des sols forestiers (incluant la végétation) et des feux de forêt (Johnson, 1992). Les feux de forêt constituent le principal type de perturbation dans la forêt boréale et sont le principal processus qui organise les attributs physiques et biologiques de ce biome. Les feux contribuent également à façonner la diversité des paysages et à influencer les flux d'énergie et les cycles biogéochimiques, en particulier le cycle du carbone (Weber et Flannigan, 1997). La forêt boréale est caractérisée par une faible diversité d'espèces d'arbres, les espèces d'arbres les plus répondus étant les conifères, espèces bien adaptées au climat froid, aux sols minces et acides (Ressources Naturelles Canada, 2005). Les conifères les plus répondus de la forêt boréale sont les genres *Pinus* (pins), *Picea* (épinettes), *Abies* (sapins) et *Larix* (mélèzes), et pour les feuillus de début de succession, les espèces des genres *Populus* (peupliers), *Betula* (bouleaux), *Salix* (saules), *Alnus* (aulnes), et *Sorbus* (sorbiers). Toutes ces essences boréales ont des distributions spatiales relativement larges (Zasada et al., 1997).

Bien que la productivité annuelle soit faible, la forêt de la zone circumboréale détient 45% du stock de bois mondial (Davidenko, 1998; Kuusela, 1992). De plus, les forêts boréales ont la capacité à la fois de piéger le carbone et de le conserver pendant une longue période dans la biomasse et le sol (Burton et al., 2010). Cependant, afin de maintenir cette fonction importante dans cette zone, en particulier la productivité forestière, des inquiétudes ont été soulevées par la communauté scientifique, notamment dans l'est du Canada. Dans cette région, on observe la perte des forêts matures qui dominaient les paysages forestiers naturels, la perte de grands paysages forestiers en raison de leur fragmentation, l'absence de feu comme catalyseur au recyclage des nutriments dans certaines régions, l'ouverture des couverts forestiers causée par le phénomène de la paludification et le remplacement des sites forestiers par des espèces de mousses (en particulier les sphaignes) et d'éricacées (Fenton et al., 2005; Gluck et Rempel, 1996; Wardle et al., 2004).

Afin de trouver des solutions potentielles à ces inquiétudes, diverses pratiques d'aménagement ont été proposées par les aménagistes pour optimiser la productivité forestière dans la zone boréale, telles que l'augmentation de l'espacement entre les zones de coupe afin de maintenir les grandes zones de forêt continue, l'inclusion de durées de révolutions variables pour les coupes, l'augmentation de la rétention en bloc des coupes, l'optimisation des densités de reboisement, l'utilisation de fertilisants dans les sites pauvres, la sélection génétique des essences productives, et enfin l'utilisation de la préparation du site, via la préparation mécanique du sol (PMS, p. ex. scarifiage) et le brûlage dirigé. La préparation de terrain permet l'amélioration des conditions environnementales (nutriments, humidité, température) nécessaires au développement des plants (dans les sites reboisés) tout en minimisant l'effet de la végétation concurrente pouvant influencer négativement la croissance sur les sites reboisés (Angelstam et Kuuluvainen, 2004; DeLong, 2002).

1.2 Productivité forestière et facteurs influençant la productivité

La productivité forestière est essentiellement exprimée en unité de volume (m^3) ligneux récolté par unité de surface (hectare) (Barnes et al., 1997). Les mesures directes de la productivité les plus utilisées par les aménagistes forestiers sont : la surface terrière, le volume et la biomasse (Evans, 1985). Il existe des mesures indirectes de la productivité forestière telles que l'indice de qualité du site (IQS, i.e. hauteur des arbres dominants à un âge spécifique) qui fournissent des mesures de la productivité qui sont assez précises et très utilisées pour la gestion forestière (Evans, 1985).

Malgré une faible productivité annuelle, la forêt boréale détient un potentiel ligneux (arbres en place) assez important, d'où l'importance de maintenir ce potentiel qui joue un rôle primordial pour l'industrie forestière régionale et mondiale, mais également dans la séquestration du carbone terrestre (Davidenko, 1998; Kuusela, 1992). Le maintien de la productivité forestière nécessite systématiquement une bonne gestion des forêts productives; ceci nécessite une bonne connaissance des facteurs environnementaux qui influencent la productivité forestière à multiples échelles en région boréale (Messier et al., 1999). Ces facteurs environnementaux peuvent être séparés en deux groupes, soient les facteurs extrinsèques et intrinsèques.

1.2.1 Facteurs extrinsèques

Selon Barnes et al. (1997), Field et al. (1995), O'Neill (1981) et Westman et Whittaker (1975), les facteurs extrinsèques influençant la productivité forestière en forêt boréale incluent le climat, la topographie et la géologie zonale ou régionale. Ces facteurs extrinsèques peuvent changer ou varier au fil du temps, mais ne sont pas influencés par la présence ou l'absence de la végétation. Ces facteurs influencent directement la croissance des arbres, via l'humidité, la disponibilité des éléments nutritifs, la température de l'air et du sol. La productivité forestière tend à être faible lorsque l'un ou plusieurs de ces facteurs sont limités. C'est pour cela que la productivité potentielle est faible dans les environnements froids tels que la zone boréale et la toundra en raison des faibles températures.

Le climat semble exercer un effet majeur sur l'expression régionale de la végétation en zone boréale, le climat ayant une influence directe sur l'humidité de l'air, la température de l'air et les régimes de lumière, et une influence indirecte sur la disponibilité des nutriments (Barnes et al., 1997; Lieth, 1975). La topographie est essentiellement le résultat de l'histoire géologique et climatique (p. ex. mécanismes de gel et dégel) d'une région. Plusieurs études ont démontré que des gradients de la productivité nette étaient liés à l'élévation associée aux positions topographiques (Chen et al., 2007; Grant, 2004). La position topographique (p. ex. haut vs. bas de pente) peut avoir des effets importants sur le microclimat et les conditions édaphiques du sol (Graham et Wurtz, 2003), notamment sur le drainage et le lessivage des éléments nutritifs.

1.2.2 Facteurs intrinsèques

Selon Chen et al. (2002), McKenney et Pedlar (2003) et Ung et al. (2001), il existe une multitude de facteurs intrinsèques qui sont influencés par les processus des écosystèmes et qui sont sujets à des modifications par les perturbations naturelles ou humaines. Parmi les principaux facteurs intrinsèques, nous distinguons les propriétés physico-chimiques et biologiques du sol, le microclimat du site et la quantité de lumière interceptée. Contrairement aux facteurs extrinsèques, les facteurs intrinsèques sont influencés par l'aménagement forestier et ils peuvent augmenter ou diminuer de manière significative le potentiel productif des peuplements forestiers. Les facteurs intrinsèques les plus importants à prendre en compte sont les propriétés du sol, car ils peuvent influencer significativement la productivité forestière. Les propriétés du sol qui influencent la productivité forestière et la croissance des plantes sont : l'humidité du sol, la disponibilité des éléments nutritifs dans le sol et la porosité du sol (Barnes et al., 1997; Carmean, 1975). Donc, un sol humide, bien drainé, bien aéré et riche en éléments nutritifs influencerait positivement la croissance des arbres et la productivité forestière (Barnes et al., 1997). Dans un peuplement où la quantité de lumière est limitée, les essences tolérantes à l'ombre ont un meilleur taux de survie que celles étant intolérantes (Kobe et Coates, 1997; Stancioiu et O'Hara, 2006). Ceci est expliqué en partie par le fait que les espèces tolérantes à l'ombre nécessitent moins d'énergie pour maintenir une surface foliaire constante (King, 1994). Plus une espèce est tolérante à l'ombre, plus ses adaptations morphologiques et physiologiques au manque de lumière sont grandes (Stancioiu et O'Hara, 2006).

1.2.3 Productivité forestière et modèles conceptuels

Il existe plusieurs modèles conceptuels qui mettent en relation la productivité forestière et les facteurs influençant cette dernière. À titre d'exemple, Bonan (1989) a mis en place un schéma conceptuel (Figure 1.1) dans un modèle de simulation de la dynamique de la forêt boréale qui regroupe les facteurs intrinsèques et extrinsèques pouvant influencer la régénération, la croissance et la mortalité des arbres dans les forêts de conifères, de feuillus et mixtes dans plusieurs sous-régions bioclimatiques de la zone boréale nord-américaine. Ces facteurs comprenaient le climat, le rayonnement solaire, l'humidité du sol, la température du sol, la couche organique du sol forestier, la disponibilité des nutriments, les incendies de forêt et les épidémies d'insectes. Également, dans les schémas conceptuels d'Austin et Smith (1990) et Barnes et al. (1997), les facteurs environnementaux (intrinsèques et extrinsèques) ont un effet direct sur les processus physiologiques des arbres et sur leur réponse en regard de la productivité (Figure 1.2).

Dans la forêt boréale aménagée, il existe d'autres facteurs, dits "facteurs d'aménagement" qui peuvent interagir avec d'autres facteurs intrinsèques (p. ex. sol forestier) et influencer significativement la productivité forestière à l'échelle du site. Ces facteurs sont la fertilisation, la sélection génétique des essences, le contrôle de la végétation concurrente, le contrôle de la densité de reboisement, la taille et l'état des plants (Figure 1.3) (Richardson et al., 1999). À titre d'exemple, en forêt boréale russe, on a fixé une certaine densité de plants de pins pour maintenir une productivité optimale dans les zones à régénérer. Le nombre recommandé de plants est de 3 000 à 4 000 par hectare (Karvinen et al., 2011). Par ailleurs, en Alaska, les plus faibles taux de survie de l'épinette blanche (25% à 40%, faible productivité) étaient liés à la présence de végétation concurrente, telle que la calamagrostide du Canada (*Calamagrostis canadensis* (Michx.) Beauv.) et l'épilobe à feuilles étroites (*Chamaenerion angustifolium* (L.) Scopoli subsp. *angustifolium*) (Graham et Wurtz, 2003). Des études réalisées dans des sites reboisés en forêt boréale canadienne ont montré que les plants de taille importante avaient des taux de survie et de croissance plus élevés que les petites plantules et étaient susceptibles de maximiser la productivité forestière du futur peuplement (Hamel et al., 2004; Sutherland et Day, 1988; Thomson et McMinn, 1989). Généralement, les caractéristiques du sol (fertilité, texture, structure, humidité) sont parmi les facteurs les plus influents, car elles peuvent influencer significativement la productivité forestière du site. Donc, toute pratique d'aménagement pouvant détériorer le continuum sol-plante aura des conséquences néfastes (p. ex. érosion, lessivage des nutriments, compactage du sol, envahissement du site par la végétation concurrente) sur la productivité future du site (Austin et Smith, 1990; Bonan, 1989; Richardson et al., 1999).

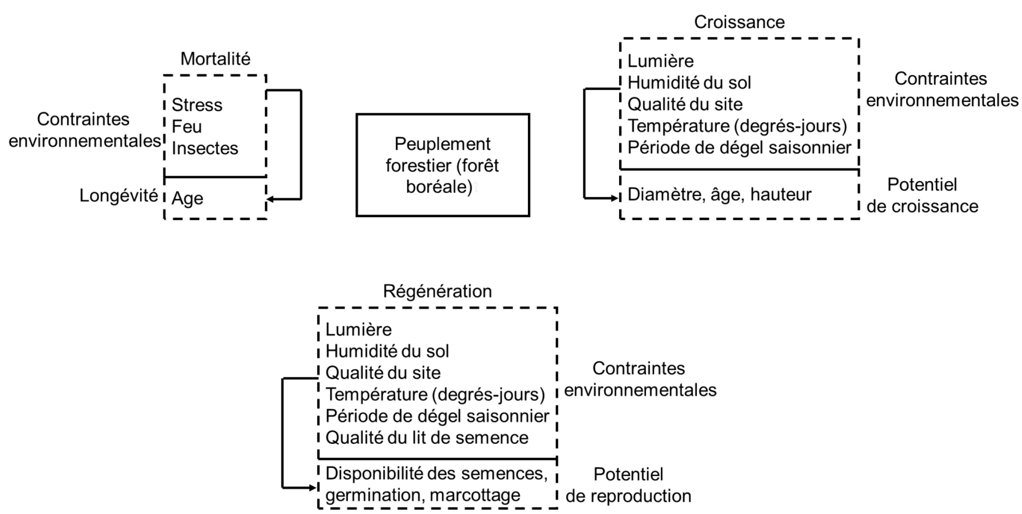

Figure 1.1 Représentation schématique du modèle de croissance de la forêt (Bonan, 1989, modifié).

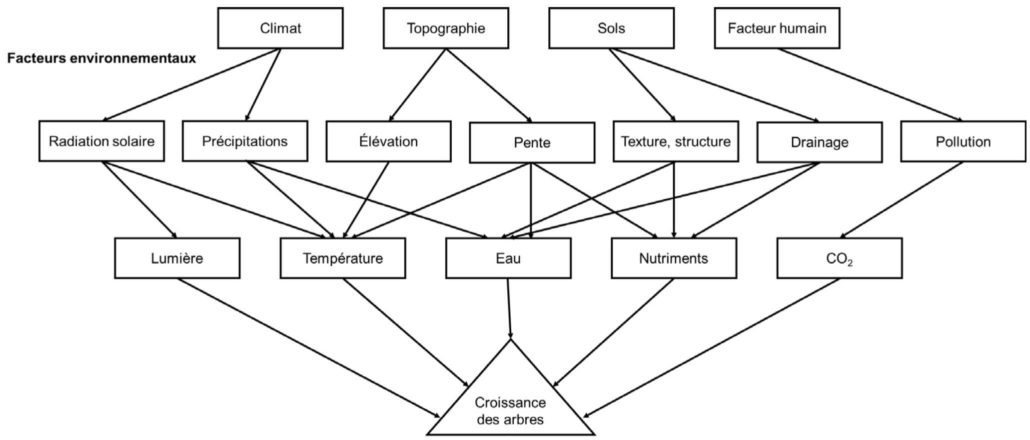

Figure 1.2 Relations générales entre les facteurs environnementaux et la productivité forestière (Barnes et al., 1997; Austin et Smith, 1990, modifié).

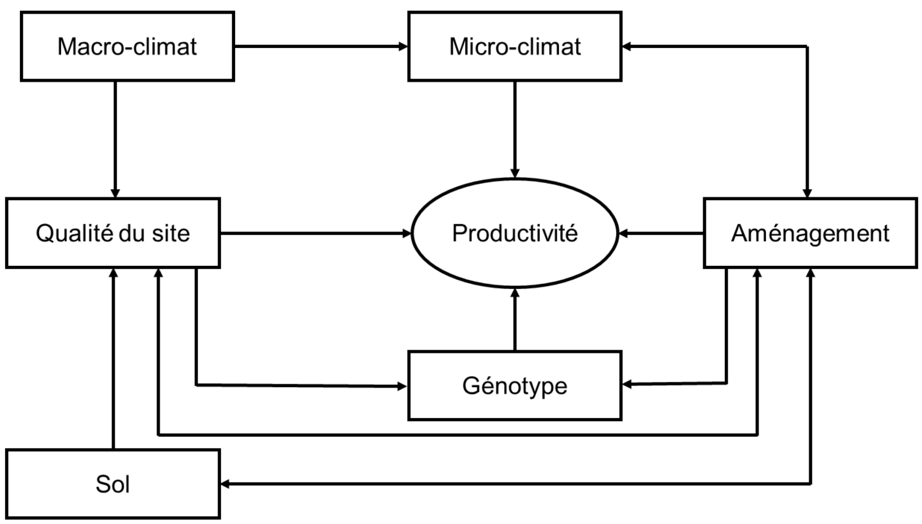

Figure 1.3 La relation entre la productivité forestière, les facteurs environnementaux et l'aménagement forestier (Richardson et al., 1999, modifié).

1.3 Relation sol-plante-productivité dans la forêt boréale

Dans la région boréale, il existe une diversité de sols (minéraux et organiques) répartis le long du gradient climatique nord-sud. Ces sols sont relativement acides, pauvres en nutriments, principalement en azote (N), considéré comme l'un des principaux facteurs limitants de la croissance des arbres et donc de la productivité forestière dans la zone boréale (Tamm, 1991). En forêt boréale, la composition en espèces des communautés végétales est fortement liée à l'approvisionnement en N (Tamm, 1991), car il permet d'augmenter la photosynthèse, la surface foliaire, la croissance et la formation du bois (Lupi et al., 2013). Les diminutions de la productivité induites par les limitations nutritionnelles, notamment en N, ont été abondamment démontrées dans la forêt boréale, notamment dans les peuplements paludifés d'épinette noire de l'est du Canada (Fenton et al., 2005; Lafleur et al., 2010a, b; Lafleur et al., 2011; Simard et al., 2007). En effet, dans des sites paludifiés en forêt boréale, il a été démontré que la croissance de l'épinette noire diminuait avec l'augmentation accrue de l'humidité du sol et de l'épaisseur de la couche organique (ÉCO) sur le sol minéral (Cleve et al., 1990; Yamasaki et al., 2002).

1.4 Forêts paludifiées de l'Est canadien

La forêt boréale de l'Est canadien présente un fort potentiel de production ligneuse, notamment dans le domaine bioclimatique de la pessière noire à mousses. Toutefois, cette région est caractérisée par une faible productivité dans les sites paludifiés. La paludification (entourbement) est un phénomène naturel où l'épaisseur de la couche organique augmente graduellement jusqu'à excéder, voire largement dépasser 30 cm menant graduellement à la formation d'une forêt tourbeuse (Bernier et al., 2008; Payette et Rochefort, 2001). Ce milieu est caractérisé par une saturation en eau du sol, conduisant à un milieu anaérobique froid, qui diminue l'activité microbiologique (Comont, 2006). Ces conditions limitent la minéralisation des éléments nutritifs et leur absorption par les plantes (Gower et al., 1996; Murty et al., 1996; Prescott et al., 2000) causant une diminution de la croissance et une hausse de la mortalité des arbres en place, ainsi qu'une faible régénération (Simard et al., 2009, 2007). Selon Fenton et al. (2005, 2010) et Greene et al. (2006), le processus de paludification est lié à une multitude de facteurs qui peuvent le contrôler ou l'accentuer. La sévérité des feux de forêt et leurs fréquences, le type de peuplement, la topographie et le niveau de la pente sont parmi ces facteurs. Par exemple, les feux sévères et les pentes inclinées (bon drainage) permettent de freiner le processus de la paludification (Simard et al., 2007). Selon Payette et Rochefort (2001), il existe deux principaux types de processus de paludification, la paludification édaphique et la paludification successionelle. La paludification édaphique, également appelée paludification des dépressions humides, opère où la topographie joue un rôle déterminant dans le maintien de la nappe phréatique proche de la surface du sol. La paludification successionelle, également appelée paludification des sites bien drainés, opère où la succession forestière est le principal moteur du processus (Simard et al., 2007). Sur le terrain, ces deux processus sont confondus mais leurs différences sont importantes pour l'aménagement forestier (Laamrani et al., 2004a, b). La paludification successionelle est un phénomène potentiellement réversible, tandis que la paludification édaphique est fortement liée aux propriétés intrinsèques du site dont la modification nécessiterait des ressources considérables (p. ex. drainage forestier) (Simard et al., 2009).

La paludification est très répandue dans la pessière à mousses de l'Est canadien, notamment dans les pessières à mousses de l'Ouest québécois en raison du relief plat, du climat froid et à la présence de sols argileux à drainage lent (Gauthier et Vaillancourt, 2008; Mansuy et al., 2018). Ces conditions diminuent la capacité de drainage (conditions hydromorphes et anaérobiques) et l'activité microbienne à cause des conditions d'anaérobies du sol. À leur tour, ces conditions diminuent le taux de décomposition de la matière organique accumulée sur le sol argileux (Fenton et al., 2005). La paludification crée des conditions défavorables pour la croissance de la régénération de l'épinette noire due à la mauvaise qualité des substrats organiques (microsites) surfaciques dominés par un tapis de sphaignes, souvent gorgées d'eau et pauvres en éléments nutritifs (Lavoie et al., 2007a; Fenton et al., 2005). La productivité ligneuse des pessières noires peut diminuer de 50 à 80 % sur plusieurs centaines d'années; cette perte de productivité s'observe particulièrement entre 100 et 200 ans après feu (Drobyshev et al., 2010; Simard et al., 2009, 2007). Durant cette période, l'épaisseur de la couche organique passe graduellement de 20 à 40 cm. La zone d'enracinement de l'épinette noire, laquelle est superficielle, migre alors du sol minéral à la couche organique saturée et pauvre en éléments nutritifs (Lavoie et al., 2007a, 2007b; Simard et al., 2007). Dans les pessières à mousses de l'Est canadien, les perturbations des pratiques sylvicoles actuelles ne permettent pas de limiter le processus de paludification. Parmi ces pratiques sylvicoles, on note la coupe avec protection de la régénération et des sols (CPRS), fréquemment utilisée au Québec, qui conserve la couche organique et le couvert de sphaignes entre les sentiers de débardage (Bernier et al., 2008; Lafleur et al., 2010a, b). Les coupes hivernales sont particulièrement problématiques dans les sites paludifiés, car la couche de neige ne permet pas de perturber (et de mélanger) le sol sous-jacent (Lafleur et al., 2010a). De plus, durant la saison estivale, ces sites récoltés sont difficilement accessibles pour la remise en production via le reboisement, à cause des conditions hydromorphes du sol (orniérage) qui limitent la circulation de la machinerie sylvicole (p. ex. enfouissement des roues dans les sols très humides). Néanmoins, dans les sites paludifiés, les sylviculteurs doivent déployer des efforts importants (p. ex. préparation mécanique du sol (PMS)) pour assurer la remise en production de ces sites, notamment en augmentant la disponibilité des microsites propices à la croissance (Bergeron et al., 2007; Lavoie et al., 2005).

1.5 Préparation mécanique du sol (PMS)

La PMS (p. ex. scarifiage, hersage) est la forme de préparation de terrain la plus répondue à travers toute la zone boréale, notamment au Canada (Bock et Van Rees, 2002; Thompson et Pitt, 2003). La PMS est un traitement qui consiste à rendre le terrain favorable à la mise en terre d'une quantité optimale de plants dans des microsites propices au reboisement (Figure 1.4) ou à favoriser l'implantation d'une régénération naturelle (Sutherland and Foreman, 1995; Von der Gönna, 1992). Le but de la PMS est de recréer des lits de germinations, dont les conditions sont similaires à celles générées par les perturbations naturelles, telles que les feux de forêt (Örlander et al., 1998). La PMS est généralement considérée comme une méthode efficace pour favoriser l'établissement des plants. Ce traitement améliore notamment les conditions de température, d'humidité et de fertilité du sol, et réduit l'abondance de la végétation (Maynard et al., 2014; Örlander et al., 1990; Sutherland et Foreman, 2000; Sutton, 1993), d'où la recommandation de planter sur un sol préparé en forêt boréale (Prévost et Dumais, 2003; Thiffault et al., 2005).

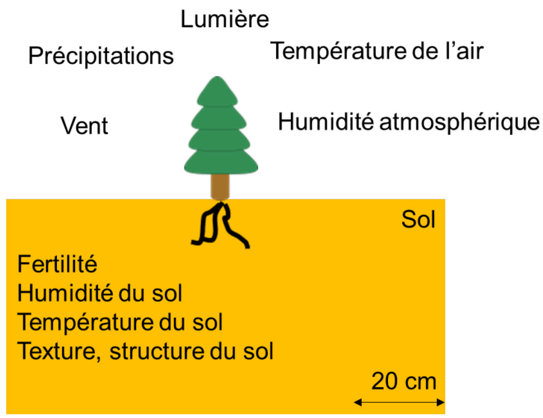

Figure 1.4 Représentation schématique d'un microsite de reboisement et des facteurs environnementaux influençant l'établissement d'un plant de régénération (Sutherland et Forman, 1995, modifié).

Les effets bénéfiques de la PMS sont généralement liés à l'exposition de microsites ou substrats (sol minéral ou mélanges organo-minéraux riches en éléments nutritifs) propices à la croissance des semis (Sutherland et Foreman, 1995). Cependant, dans des sites paludifiés de l'Est canadien, la PMS serait aussi un moyen efficace pour limiter la paludification, tout en générant des microsites propices à la croissance des plants (Lafleur et al., 2010a; Thiffault et al., 2004a, b). Or, en conditions paludifiées, l'application de ces traitements sylvicoles reste problématique, car nous ignorons : 1) l'effet de leur perturbation sur la disponibilité des microsites propices au reboisement, 2) la relation existante entre le climat régional, les caractéristiques édaphiques à l'échelle du peuplement, la qualité des substrats exposés à l'échelle du microsite et la croissance des plants, 3) l'influence des microsites ou des substrats d'établissement (organiques, organo-minéraux et minéraux) exposés sur la disponibilité des éléments nutritifs essentiels à la croissance et au développement racinaire, 4) l'effet de la compétition (particulièrement par les éricacées) sur la croissance, et 5) l'effet de la technique de reboisement sur le succès d'établissement sur ce type de sites.

1.6 Objectifs de la thèse

L'objectif général de cette thèse est de déterminer les effets de certains facteurs édaphiques (teneur en eau du sol, disponibilité des éléments nutritifs du sol nécessaires à la croissance : N, P, K, Ca, Mg, épaisseur de la couche organique) et certains facteurs environnementaux et topographiques (disponibilité et qualité des microsites, compétition interspécifique, pente, orientation, position d'établissement du plant) sur la survie et la croissance (hauteur et diamètre) des plants de reboisement installés sur des sites ayant subi une altération des horizons organiques et minéraux par différentes intensités de perturbations créées par plusieurs traitements sylvicoles. Pour ce faire, l'analyse se réalisera sur trois échelles, notamment à l'échelle du microsite, à l'échelle du peuplement et à l'échelle régionale. Ces travaux permettront, à terme, de mieux comprendre les conditions d'établissement de la régénération artificielle en forêt boréale de l'Est canadien, notamment en forêts paludifiées; et les interactions entre la croissance des plants et leur environnement (à l'échelle du microsite, du peuplement et de la région) suite à leur mise en terre, et ce, afin d'assurer le maintien de la productivité des sites boréaux et paludifiés récoltés. Le chapitre II de la thèse a pour objectif d'évaluer la disponibilité et la qualité des microsites (incluant le type de substrats) influençant l'établissement et la croissance des plants d'épinette noire mis en terre sur des sites paludifés suite aux perturbations générées par trois traitements sylvicoles (coupe totale (CPRS), PMS par le scarificateur mécanique T26, PMS par la herse forestière). Dans le chapitre III, nous avons déterminé l'effet des substrats minéraux, organiques et organo-minéraux sur la croissance des plants d'épinette noire en milieu contrôlé. Dans le chapitre IV, nous avons identifié les facteurs climatiques (échelle régionale), édaphiques (échelle du peuplement) et locaux (échelle du microsites) influençant la survie et la croissance initiale des plants d'épinette noire *Picea mariana* (Mill.) B.S.P et de pin gris (*Pinus banksiana* Lamb.). Dans le chapitre V, nous récapitulons la contribution de la thèse dans l'avancement de connaissances et proposons des pistes d'aménagement forestier et de sylviculture qui permettent de garantir de meilleures conditions d'établissement des plants dans les sites boréaux aménagés et une remise en production efficace des sites paludifiés de l'Est canadien.

CHAPITRE II

EFFECTS OF MECHANICAL SITE PREPARATION ON MICROSITE AVAILABILITY AND GROWTH OF PLANTED BLACK SPRUCE IN CANADIAN PALUDIFIED FORESTS

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2.1 Abstract

Low productivity caused by paludification in some parts of the closed black spruce (*Picea mariana* (Mill.) B.S.P) dominated boreal forest threatens the provision of ecosystem services, including wood fiber production. The accumulation, over time, of organic matter in paludified soils leads to an anaerobic environment that reduces microbial activity, decelerates decomposition of organic matter, and generates nutrient-poor microsites for regeneration. Consequently, it results in significant impacts on site productivity. Considering its ability to disturb the soil, mechanical site preparation (MSP) is viewed as a potential treatment that can help restore productivity of paludified sites following harvesting. We conducted a field experiment to verify if (1) the availability of microsites conducive to reforestation varies with MSP, microtopography (slope and aspect) and initial OLT conditions; (2) the growth of planted seedlings depends on the intensity of mechanical disturbance of the organic layer, type of microsite, planting density, presence of Ericaceae, and the planting position and depth; (3) there are direct and indirect causal relationships between microsites availability after MSP, OLT, microtopography, planting quality and seedlings growth; and (4) if mechanical site preparation and microsite type exposed affect the Ericaceae cover after planting. Our results confirmed that MSP is effective in establishing conditions that permit a productive regeneration cohort on these paludified sites. To ensure successful establishment of plantations on these sites, it is necessary, however, to distinguish between those that are slightly or moderately paludified from those that are highly paludified, as treatment effectiveness of different MSP types depends on organic layer thickness. Our results also show that preference should be given to some microsite types as clay and mixed-substrate microsites for planting to ensure sufficient availability of water and nutrients for seedlings.

2.2 Résumé

La faible productivité causée par la paludification dans certaines zones de la forêt boréale fermée dominée par l'épinette noire (*Picea mariana* (Mill.) B.S.P) menace la l'apport de services écosystémiques, y compris la production de fibre de bois. L'accumulation, au fil du temps, de matière organique dans les sols paludifiés crée un environnement anaérobique qui réduit l'activité microbienne, ralentit la décomposition de la matière organique et génère des microsites pauvres en nutriments pour la régénération. Par conséquent, il en résulte des impacts importants sur la productivité du site. Compte tenu de sa capacité à perturber le sol, la préparation mécanique du site (PMS) est considérée comme un traitement potentiel pouvant aider à rétablir la productivité des sites paludifiés après la récolte. Nous avons mené une expérience sur le terrain pour vérifier si (1) la disponibilité des microsites propices au reboisement variait en fonction de la PMS, de la microtopographie (pente et aspect) et des conditions initiales de l'épaissaur de la couche organique (ÉCO); (2) la croissance des plants mis en terre dépend de l'intensité de la perturbation mécanique de la couche organique, du type de microsite, de la densité de plantation, de la présence d'éricacées, ainsi que de la position et de la profondeur de plantation; (3) il existe des relations causales directes et indirectes entre la disponibilité des microsites après PMS, ÉCO, microtopographie, la qualité de la plantation et la croissance des plants; et (4) la préparation mécanique du site et le type de microsite exposé affectent la couverture des éricacées après la plantation. Nos résultats ont confirmé que la PMS est efficace pour créer des conditions permettant une cohorte de régénération productive sur les sites paludifiés. Pour que les plantations soient bien établies sur ces sites, il est toutefois nécessaire de distinguer les sites qui sont légèrement ou modérément paludifiées de ceux qui sont très paludifiées, car l'efficacité des différents types de PMS dépend de l'ÉCO. Nos résultats montrent également que la croissance des plants est privilégiée par certains types de microsites

tels que les microsites d'argile et de substrats mixtes, afin de garantir une disponibilité suffisante en eau et en nutriments pour les semis.

2.3 Introduction

Forests dominated by black spruce (*Picea mariana* (Mill.) B.S.P) occupy a large portion of the boreal biome of northeastern Canada, and are an important source of wood for the lumber, and pulp and paper industries (Rossi et al., 2015). In addition to their economic role, black spruce-dominated forests play key ecological functions, for example as a significant carbon sink (Kurz et al., 2013); however, the low productivity caused by paludification in some parts of this ecosystem threatens the provision of ecosystem services (Harper et al., 2003; Munson et Timmer, 1989). Paludification is a natural phenomenon characterized by an accumulation, over time, of organic layers (from top to bottom: fibric, mesic, humic) above the mineral soil (Canadian Agricultural Services, 1998; Siren, 1955). Consequently, paludified soils have an organic layer thickness that exceeds 40 cm, and in some cases, 100 cm (Henneb et al., 2015).

On the Clay Belt of northeastern Canada, the long fire interval permits the accumulation of thick organic layers in this region (Fenton et al., 2005; Lavoie et al., 2005) and the relatively cold climate and poorly drained soils (Jutras et al., 2007) leads to an anaerobic soil environment that reduces microbial activity and decomposition of organic matter (Bergeron et al., 2007; Fenton et al., 2005; Lavoie et al., 2005). The resulting gradual accumulation of organic matter is often associated with *Sphagnum* species on the forest floor (Salemaa et al., 2008), leading in the long run to nutrient-poor microsites for regeneration (Gower et al., 1996; Prescott et al., 2000), an abundance of such microsites contributes to reduced growth of trees, both mature and regenerating (Simard et al., 2007), with significant impact on site productivity.

Successful establishment and growth of conifer plantations on paludified sites depends on the type of microsite, the microtopography, the presence of competing species (notably ericaceous shrubs) and the quality of planting (planting position, seedling verticality, planting depth) (Prévost, 1996; Prévost et Dumais, 2003; Thiffault et al., 2004). The effect of planting quality on seedling growth has not been fully documented in paludified sites; this knowledge is necessary to ensure stand resilience in these ecosystems. For example, microtopography is expected to have significant effects on the availability of microsites following mechanical soil preparation (MSP), as well as on microclimate and environmental conditions at the seedling level (Henneb et al., 2015). Moreover, ericaceous shrubs are significant competitors for soil resources (Thiffault et al., 2012); they can impair the successful establishment of conifers and delay the growth and survival of planted seedlings (Thiffault et al., 2013). Soil disturbance through MSP, such as scarification (Thiffault et al., 2005), appears effective in reducing the negative effect of ericaceous competition on seedling growth. However, microsites created by scarification are quickly re-invaded by ericaceous plants (Thiffault et al., 2012); therefore, the beneficial impact of the treatment can be short term. Given that thick organic layers favor the vegetative reproduction of ericaceous species (Hébert et Thiffault, 2011; Mallik, 1993), it is important to verify how MSP impacts ericaceous re-colonization of disturbed paludified sites.

The thickness of the organic layer may affect the establishment of planted seedlings, even after MSP (Henneb et al., 2015; Lafleur et al., 2011). MSP through light or intense scarification appears to be effective in reducing organic layer thickness and competing plant cover while creating microsites that are conducive to good rooting (Sutherland et

Foreman, 2000; Sutton, 1993). MSP has mixed effects on the availability of nutrients for regeneration, apparently depending on the treatment used and the extent of disturbance ((Prévost et Dumais, 2003; Smith et al., 2000). However, little information is available about the types of microsites created by MSP on paludified sites. Such knowledge is needed to assess the potential for silvicultural treatments to maintain or increase productivity on sites subjected to paludification and to identify microsites that should be favored during planting.

Our objectives were thus: (1) to assess how mechanical disturbances caused by three post-harvest MSP treatments (scarification with several parallel passes; plowing with two perpendicular passes, and no MSP as a control) affect microsite type availability in paludified areas; (2) to determine how the three treatments and the microsites thus created affect the growth of planted seedlings; (3) to assess how the organic layer thickness (OLT), presence of Ericaceae, microtopography and quality of planting affect the success of seedling establishment; and (4) to identify the possible relationships among MSP treatment, type of microsite exposed, and the presence of post-planting Ericaceae (Thiffault et al., 2004; Yamasaki et al., 2002) on long-term forest productivity ((Bradley et al., 1997; Mallik, 2003). To these ends, we established an experimental design to test the following hypotheses: (1) the availability of microsites conducive to reforestation varies with MSP, microtopography (slope and aspect) and initial OLT conditions; (2) the growth of planted seedlings depends on the intensity of mechanical disturbance of the organic layer, type of microsite, planting density, presence of Ericaceae, and the planting position and depth (Thiffault et al., 2004a, b); (3) there are direct and indirect causal relationships between microsites availability after MSP, OLT, microtopography, planting quality and seedling growth; and (4) mechanical site preparation and microsite type exposed affect the Ericaceae cover after planting.

2.4 Materials and Methods

2.4.1 Study Site and Experimental Design

The study was located about 80 km northeast of the village of Villebois (49°06′ N, 79°08′ W), within the spruce-moss bioclimatic domain of Quebec, Canada (Saucier et al., 2009) (Figure 2.1), more specifically in the most northerly portion of the Clay Belt (which corresponds to the distal margin of the final Cochrane surge) (Veillette, 1994). The clay soil is associated with extensive peatlands and topography is relatively flat. The average annual temperature is 0.1 °C and the average annual precipitation is 782 mm (Environment Canada, 2017). Black spruce and jack pine (Pinus banksiana Lamb.) dominate forest composition, accounting for 79% and 16%, respectively, of the forest cover, followed by trembling aspen (*Populus tremuloides* Michx), tamarack (*Larix laricina* [Du Roi] K. Koch), balsam fir (*Abies balsamea* [L.] Miller) and white birch (*Betula papyrifera* Marshall) (Laamrani et al., 2013). The forest floor is covered with Sphagnum species (*Sphagnum capillifolium*, *Sphagnum russowii*, *Sphagnum angustifolium*), feather mosses (mainly *Pleurozium schreberi* [Brid.] Mitten) and shrubs (mainly Ericaceae such as *Kalmia angustifolia* L. and *Rhododendron groenlandicum* (Oeder) Kron & Judd) (Harper et al., 2003; Laamrani et al., 2014a).

We marked off nine cut-blocks averaging 32 ha each. The cut-blocks were harvested in the fall of 2010 using careful logging around advance growth (CLAAG, or Coupe avec Protection de la Régénération et des Sols (CPRS) in Quebec (Groot et al., 2005). In the summer of 2011, each cut-block was systematically sampled for organic layer thickness at intervals of 20 m with a graduated probe, along eight parallel geo-referenced transects that were about 400 m long and 20 m apart, and oriented perpendicular to the logging trails. Microtopographical variables (slope and aspect

[North, East, South, West, NE, NW, SE, SW]) were obtained from the Digital Terrain Model (DTM) (1 m resolution) derived from Lidar available data using ArcGIS software (ESRI, 2015). Post-harvest OLT of in the plots varied between 0 and 100 cm.

In the fall of 2011, six of the nine cut-blocks underwent mechanical site preparation. Three of the six were treated by plowing (two perpendicular passes) using a custom forest plow, and three were treated by disc trenching (parallel passes) using a T26 scarifier (Bracke Forest AB, Bräcke, Sweden). The three remaining cut-blocks served as controls, i.e., CLAAG but no mechanical preparation (Figure 2.1). During the summer of 2012, the sector was planted and each cut-block had two initial densities: single (2200 stems per ha) and double (5000 stems per ha) (Figure 2.1). All cut-blocks were planted with black spruce seedlings (initial average height = 20 cm) that had been produced in containers of 45 cells with a 110 cm3 volume. During summer 2014, 15 circular sampling plots (5 per treatment), each having a radius of 8 m, were located in the cut-blocks in order to identify the availability of regeneration microsites and monitor seedling growth (Figure 2.1).

2.4.2 Data Collection

In summer 2014 and summer 2015 (the second and third growing seasons after planting), we measured the height (cm) and ground-level diameter (mm) of 600 black spruce seedlings in the 15 sampling plots (40 seedlings per plot) (Figure 2.1a, b). Sampling plots were distributed to include both classes of paludification (low to moderate, and high paludification) (Annexe A). Five seedlings (two in CLAAG, two in CLAAG + plowing, and one in CLAAG + scarifier) were found dead in 2015 as a result of frost heaving. We continued to monitor the 595 remaining seedlings, characterizing microsites at the same time (Annexe A).

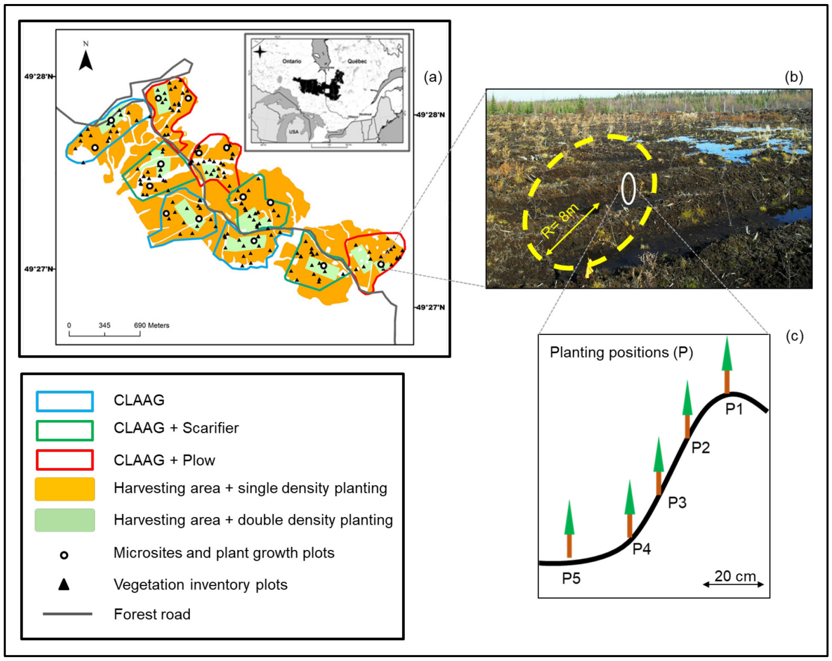

Figure 2.1 (a) Location of the study area (inset), distribution of the silvicultural treatments (careful logging around advance growth (CLAAG) without mechanical site preparation (MSP), CLAAG + scarifier, CLAAG + plowing), distribution of microsite and plant growth plots, and vegetation plots over the nine main cut block, and planting densities single (2200 stem per ha) and double (5000 stem per ha) ; (b) An inventory plot 8 m in radius; (c) Planting positions along a furrow (P1 higher to P5 lower) after mechanical site preparation.

To this end, we determined (i) the degree of decomposition of the organic matter using the Von Post Scale [38]; (ii) the verticality of the seedlings (a vertical seedling is one whose inclination is within ±30° from the vertical; otherwise the seedling is deemed non-vertical ((MFFP (Ministère des Forêts, de la Faune et des Parcs), 2016)) and the position of seedling along the furrows formed by mechanical site preparation (Figure 2.1c); (iii) the depth (in cm) of planting by measuring the position of the collar with respect to ground level; iv) the existence of obstacles (stumps, rocks, etc.) near the seedlings; (v) the thickness (in cm) of the humus at the bottom of the furrows created by the scarifier or the plow, and (vi) the width (in cm) and the depth (in cm) of the furrows with respect to ground level. We also measured the distance (in cm) between the seedlings and the nearest ericaceous plant (Thiffault et al., 2012).

A parallel study followed the evolution in the vegetation (Ericaceae cover) in a set of 120 sampling plots (radius 11.28 m) randomly distributed across the cut-blocks (Figure 2.1a). Within these 400 m2 plots, percent recovery of Ericaceae was measured in five 1 m2 quadrats located in the north, east, south, west and center of each sampling plot.

2.4.3 Data Analysis

All analyses were conducted in the R software environment version 3.5.1 (R Core Team, 2018). To test hypothesis (1) (availability of microsites), a non-parametric regression tree method was used (rpart, tree and mvpart packages of the R environment), in order to partition the data and identify the complex interactions among the silvicultural treatments, microtopography (slope and aspect), initial paludification conditions (post-CLAAG OLT) and the availability of microsites for seedling growth. The regression tree method, frequently used in soil science (e.g., (Häring et al., 2012; Johnson et al., 2009), works by binary splitting of the response variables into small homogeneous groups (terminal nodes) based on the numerical and categorical explanatory variables (De'ath et Fabricius, 2000).

We used seedling height and diameter to calculate the relative growth rate in volume index (RGRV) (Avery et Burkhart, 2015). The volume index (V) in cm3 of each seedling was determined using the equation for the volume of a cone:

$$V = \pi \times (D/2)2 \times (H/3) \quad (1)$$

where D is ground-level diameter (cm) and H is height (cm) of the seedlings. The relative growth rate was then calculated as:

$$RGRV = [\ln (V1) - \ln (V0)]/[t1 - t0] \quad (2)$$

where V1 and V0 are seedling volumes at time t1 (2015 growing season) and t0 (2014 growing season) (Margolis et Brand, 1990).

To test hypothesis (2) (seedling growth), sixteen explanatory variables were incorporated in a general linear mixed model and underwent stepwise, backward-forward selection of variables and their interactions (all two-way and three-way interactions between variables) based on the Akaike Information Criterion (AIC) (stepAIC, MASS packages of the R environment) to identify the best predictive model that explains seedling growth. The variables were assigned to five groups: (1) the "treatment" variables (scarifier, plow and CLAAG alone); (2) the "environmental conditions" variables, i.e., types of microsite exposed, microtopography (slope and aspect) and presence of competing species (planting density and distance from Ericaceae); (3) the "planting quality" variables (planting position, seedling verticality, planting depth); (4) the "initial paludification conditions" variables post-CLAAG (Henneb et al., 2015): class 1 (low to moderate paludification with post-CLAAG OLT ≤ 40 cm) and class 2 (high paludification with post-CLAAG OLT > 40 cm) (Henneb et al., 2015; Mansuy et al., 2018) ; (5) "% OLT reduction" after each treatment calculated as:

$$\% \text{ OLT reduction} = (\text{post-treatment OLT} - \text{post-CLAAG OLT})/(\text{post-CLAAG OLT}) \times 100\% \quad (3)$$

where a negative value indicates a reduction in OLT after mechanical site preparation, and a positive value indicates an increase. We used an analysis of variance (ANOVA) to evaluate the effect of the selected variables on RGRV; a Tukey's test (multicomp package in R) was used to compare treatments, the microsites and planting quality effects on RGRV. To test hypothesis (3) (causal relationships between variables), we used a path analysis (lavaan package in R) (Rosseel, 2012) to reveal the complex relationships among the explanatory variables and their effect on seedling growth and microsite availability. Also, to test hypothesis (4) (abundance of Ericaceae), a multiple correspondence analysis (package FactoMineR) was applied to evaluate the relationships among the treatments, the types of microsite exposed and the presence of Ericaceae. Where necessary, data were transformed to follow a normal distribution, using $\alpha = 0.05$ as the significance level.

2.5 Results

2.5.1 Availability of Microsites

We identified five main types of microsite (Figure 2.2): clay, organic-clay mixture, clay-humic mixture, fibric and humic [6,48]. The regression tree analysis (Figure 2.3) shows that the availability of these microsites varied with the treatment and the post-CLAAG OLT class (≤40 cm vs. >40 cm). The "treatment" variable splits along a left branch (CLAAG) and a right branch (plow-scarifier), leading to two significantly different daughter nodes. The post-CLAAG OLT node then splits into two significantly different terminal nodes: where the OLT was less than 40 cm, the distribution of microsite types varied significantly with the treatment ($p \leq 0.05$). CLAAG treatment without MSP resulted in 70% fibric microsites, followed by 20% humic microsites, while organic-clay microsites failed to exceed 10%, and clay and clay-humic microsites were hardly exposed at all (<1%). With the scarifier treatment, about 30% of the microsites exposed were clay, followed by clay-humic (about 25%) and organic-clay (about 20%). Fibric and humic microsites had the lowest percentages (about 15% and 10% respectively) on scarified plots. As for the plow, it exposed more humic microsites (40%) than other types, followed by clay-humic (20%), clay (~15%), organic-clay (~15%) and fibric (10%).

Where the OLT was greater than 40 cm, CLAAG barely exposed clay-humic microsites (<1%), but resulted in more fibric microsites (40%), followed by organic-clay (30%), clay-humic (15%) and clay (~15%). The scarifier exposed more microsites that were clay (~45%) or organic-clay (~35%) than the other types; next came fibric (~15%), humic (~5%) and clay-humic (~5%). Finally, the plow exposed more fibric microsites (~40%), followed by humic (25%), organic-clay (~15%), clay (~10%) and clay-humic (~10%).

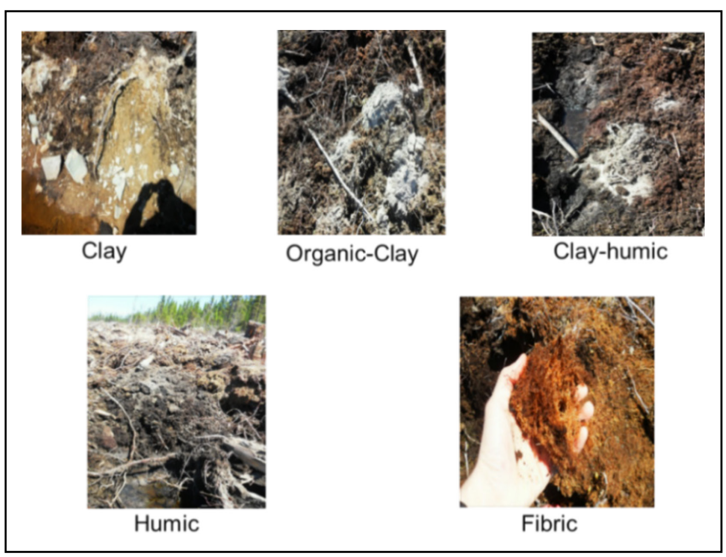

Figure 2.2 Main types of microsites found at the study site.

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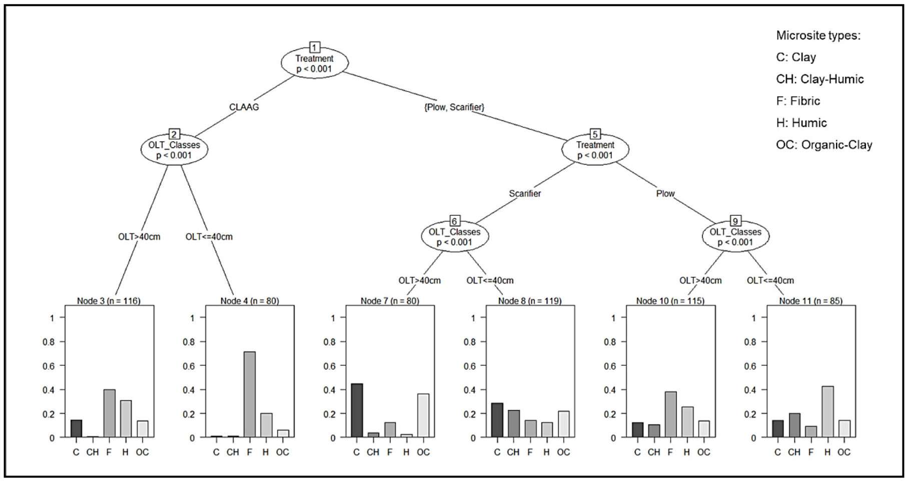


Figure 2.3 Percent microsites exposed by treatment and by post-CLAAG organic layer thickness (low to moderate OLT ≤ 40 cm and high OLT > 40 cm).

2.5.2 Seedling Growth

Overall, the stepwise selection and ANOVA results (Table 2.1) showed that seedling growth was significantly influenced by silvicultural treatments, planting position, microtopography (aspect), microsite type and planting position interaction, microsite type and planting depth interaction, percent reduction in OLT and OLT post-CLAAG interaction, planting depth and seedling verticality and the interaction among silvicultural treatments, post-CLAAG OLT and percent reduction in OLT, post-CLAAG OLT, percent reduction in the OLT and microtopography (Table 2.1). These variables and interactions were selected as part of the best mixed model (R2 = 0.497, AIC= −136.859, the worst model had an AIC = −43.965) that had more effect on seedling growth (Table 2.1). “Planting density” and “distance from Ericaceae” were not selected because of their weak influence on growth.

Where post-CLAAG OLT was low to moderate (≤40 cm), CLAAG without MSP yielded lower RGRV than the other two treatments, only if the percent reduction in OLT was under −20%. Above that threshold, growth in the CLAAG treatment decreased gradually as OLT increased (Figure 2.4). With the plow, seedling growth increased as the percent reduction in OLT increased (i.e., lower OLT). The opposite was observed with the scarifier: seedling growth increased as the percent reduction in OLT decreased (i.e., organic matter accumulation). Nevertheless, seedling growth was better with the plow than with the scarifier when OLT was reduced.

Where post-CLAAG OLT was high (>40 cm) (Figure 2.4), seedling growth was better overall with the plow and scarifier than CLAAG treatment without MSP. Indeed, with the plow and scarifier, seedling growth increased gradually as the percent reduction in OLT decreased. The opposite was observed for CLAAG treatment without MSP.

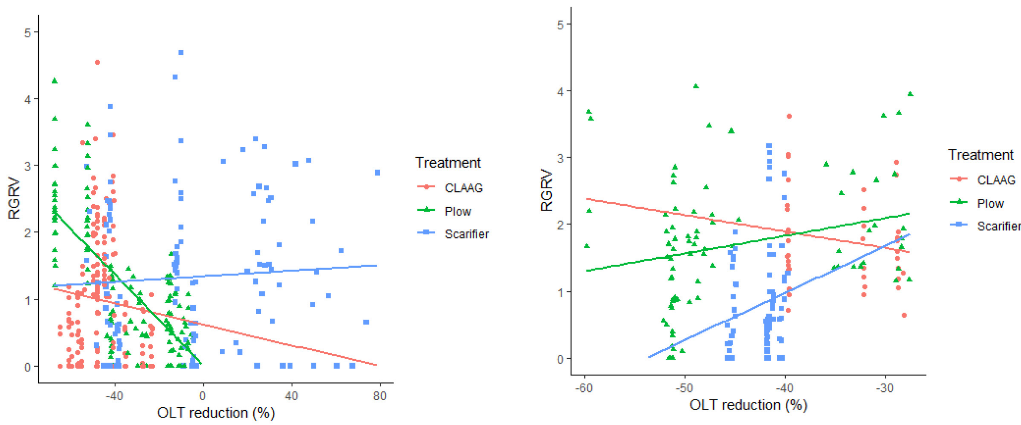
The effect of microsite type on growth was significant only in combination with the planting position and depth. RGRV was generally better on clay microsites, especially at planting positions 1, 4 and 5 (Figure 2.5a). Linear regression (Figure 2.5b) showed that when the seedling collar was at ground level (depth = 0 cm), growth was better on clay, organic-clay and fibric microsites. When the collar was above ground level, growth was better on clay microsites. As the collar approached 10 cm below ground level, clay microsites showed the lowest growth response.

ANOVA results revealed a significant effect of seedling verticality on RGRV. The effect varied with planting depth for non-vertical seedlings (Table 2.1). When planting depth was more than 3 cm below ground level, growth was better with non-vertical seedlings. Within vertically planted seedlings, growth was similar regardless of planting depth (Figure 2.5c). Finally, aspect had a significant effect on growth, which was better in N, NW and W orientations than with SE (Figure 2.5d).

Tableau 2.1 Listing of variables and interactions selected by stepwise (backward-forward selections) composing the best mixed model. Summary of ANOVA results for the effect of selected variables and interactions on seedling relative growth rate in volume index (RGRV). The mixed effect model explained 49.7% of the variation in RGRV.

Selected Variables and Variables Interactions	Df	Sum Sq	Mean Sq	*F*-Value	*p*-Value (>F)
Treatment	2	4.7219	2.3610	4.5835	0.013
Planting position	4	4.9752	1.2438	2.4147	0.048
Aspect	6	6.7586	1.1264	2.1868	0.043
Microsite type × Planting position	16	15.3619	0.9601	1.8640	0.021
Microsite type × Planting depth	4	5.0100	1.2525	2.4316	0.047
OLT reduction × OLT post-CLAAG	1	3.6261	3.6261	7.0397	0.008
Planting depth × Seedling verticality	1	2.1480	2.1480	4.1701	0.042
Treatment × OLT post-CLAAG × OLT reduction	4	15.4200	3.8550	7.4840	<0.001

OLT: organic layer thickness; CLAAG: careful logging around advance growth. Significance at $p \leq 0.05$.



ECO post-CLAAG ≤ 40 cm   ECO post-CLAAG > 40 cm

Figure 2.4 Effect of silvicultural treatments on the relative growth rate in volume index (RGRV) of the seedlings, by post-CLAAG OLT and percent reduction in OLT ($p < 0.001$). A negative value of the variable "OLT reduction" means that there was a decrease in OLT; a positive value means an increase in OLT. OLT: organic layer thickness; CLAAG: careful logging around advance growth.

2.5.3 Path Analysis and Correlations among Variables Influencing Growth

The path analysis (Figure 2.6) showed that the direct correlations between seedling growth and the following variables—post-CLAAG OLT, % OLT reduction, planting position and microsite type—did not appear to be significant. This was true for both the scarified and plowed conditions.

The effect of post-CLAAG OLT on % OLT reduction was greater in plots treated with the scarifier than in those treated with the plow (Figure 2.6). Treatment directly and significantly influenced OLT reduction, planting position, microsite type and seedling growth. We observed direct, significant correlations between planting position and types of microsites exposed. At locations treated with the scarifier, microsite type was linked with planting depth and seedling verticality. The path analysis also revealed a direct, significant link between planting depth and seedling verticality (Figure 2.6). The coefficients for these correlations were higher under the conditions created by the scarifier than under those created by the plow. Lastly, we noted a direct correlation between seedling growth, planting depth and seedling verticality. The direct influence of aspect on seedling growth was significant only in plots treated with the plow.

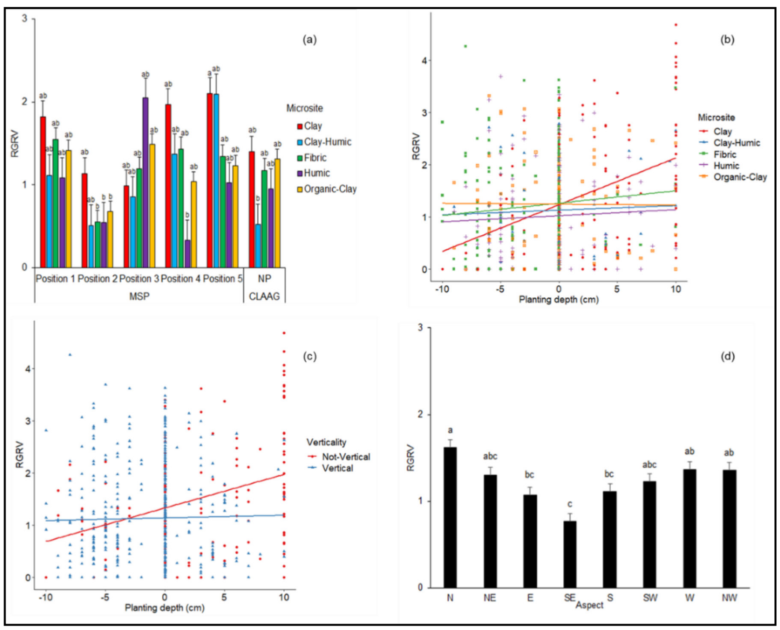


Figure 2.5 (a) Differences in relative growth rate in volume index (RGRV) by microsite type and planting position (see Figure 1.1c for a description of the planting positions). NP (No-Positions) indicates no planting position due to lack of furrow. (b) Effect of microsite type on the RGRV of seedlings by planting depth ($p = 0.047$). (c) Significant linear relationship ($p = 0.042$) among RGRV, seedling verticality and planting depth. (d) Differences in RGRV by aspect. Bars topped by the same letter are not statistically different ($p \geq 0.05$). CLAAG: careful logging around advance growth. 3.3. Path analysis and correlations among variables influencing growth.

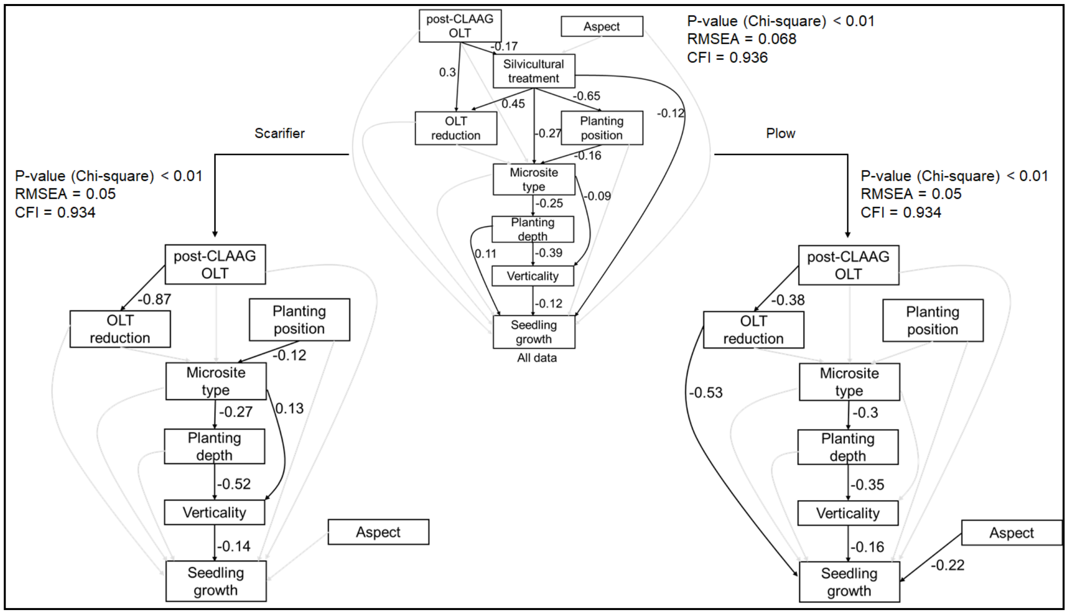


Figure 2.6 Path analysis summarizing the direct and indirect correlations influencing seedling growth, as expressed by their relative growth rate in volume index. The analysis was performed for all of the data combined and for the scarifier (left) and plow (right) separately. The variables included account for 50% of the variability. Darker arrows indicate significant correlations. The number beside each arrow is the coefficient representing the influence of each correlation. The parameters used to fit the models were the Root Mean Square Error of Approximation (RMSEA) and the Comparative Fit Index (CFI). OLT: organic layer thickness; CLAAG: careful logging around advance growth.

2.5.4 Post-Planting Ericaceae Cover

The first two axes of the multiple correspondence analysis (Figure 2.7) explained 36.9% of the variability in the data. Vaccinium species were closely associated with conditions created by the plow and humic microsites, but showed little association with clay microsites. Rhododendron was associated more with CLAAG without MSP, and with fibric microsites; they were scarce on organic-clay and clay-humic microsites. Kalmia was associated with the MSP-treated plots, in particular those that had been scarified, as well as with organic-clay and clay-humic microsites. Kalmia was less associated with CLAAG without MSP and with fibric microsites. Lastly, none of the Ericaceae species were closely associated with the clay microsites, a large proportion of which were exposed by the scarifier (Figure 2.7).

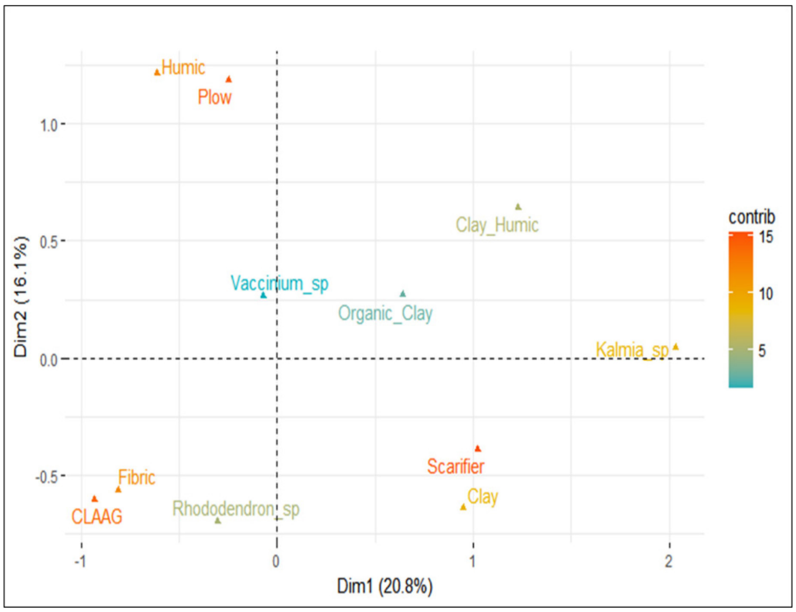


Figure 2.7 Multiple correspondence analysis summarizing the relationships among Ericaceae cover, silvicultural treatments, and types of microsites exposed. The color gradient represents the contribution of each variable on the two explanatory axes. CLAAG: careful logging around advance growth.

2.6 Discussion

2.6.1 Availability of Microsites

In general, the plow and the scarifier exposed more clay microsites, mixed (clay-humic, organic-mineral) microsites and nutrient-rich organic (humic) microsites (Prescott et al., 2000), compared with the control treatment (CLAAG with no MSP), independently of OLT. The soil disturbance resulting from MSP improves survival and growth, increases nitrogen availability, and improves tree nutrition while reducing inter-species competition (Lafleur et al., 2011; Prévost, 1992). MSP also improves soil temperature, moisture, and fertility (Örlander et al., 1990; Sutherland et Foreman, 2000; Sutton, 1993) and makes work easier for planters, because it relocates or eliminates part of the woody debris left by logging operations (Cole et al., 1999; Löf et al., 2012). In contrast, the soil disturbance caused by CLAAG without MSP is limited to the skidding trails (25% of the area of the cutovers; (Harvey et Brais, 2002) as a way of protecting soils in accordance with the Forestry Act in Quebec. Consequently, exposure of microsites favourable to seedling growth occurs only on harvesting and skid trails, while most of the cutover remains intact.

Post-CLAAG OLT directly influenced the relative effectiveness of the MSP treatments in exposing microsites. Where post-CLAAG OLT was low to moderate (≤40 cm), the scarifier exposed more clay and mixed microsites than the plow, but the plow exposed more humic microsites (>40%) than the scarifier. Humic microsites represent an important nutrient reserve (especially N) and support nutrition and growth of plantations over the medium and long term (Wershaw, 1993). Humus also helps to increase the soil's cation exchange capacity and regulates oxidation-reduction, thus improving availability of oxygen to the roots (Binkley et Fisher, 2012).

Where post-CLAAG OLT exceeded 40 cm, the scarifier was more effective than the plow in exposing microsites conducive to growth. The plow exposed more fibric microsites with a low nutrient content; its effectiveness was limited by the greater OLT. In contrast, the scarifier severely disturbed the thick organic layer, exposing more clay microsites (about 45%) and mixed organic-clay microsites (about 35%). Our results support those of earlier studies that demonstrated how scarifiers can increase the productivity of black spruce plantations in paludified environments (Fenton et al., 2005; Lecomte et al., 2006; Lecomte et Bergeron, 2005). The discs of the T26 scarifier are 1.35 m in diameter; they thus can reach the deep mineral horizons and mix them with the organic material.

2.6.2 Seedling Growth

Seedling growth depended on several variables and the interactions among them. In general, and as reported elsewhere (Lafleur et al., 2010a; Lecomte et al., 2006), CLAAG with MSP resulted in greater growth than CLAAG alone. On sites where post-CLAAG OLT was low to moderate, seedling growth was better with plowing than with the two other treatments. However, growth diminished as the percent reduction in OLT approached 0. At sites where the reductions in OLT were large, microsites favourable to seedling growth—in particular, humic, clay, and mixed microsites—were probably exposed by the plow. But at sites where the reductions in OLT were smaller (i.e., where the organic layer was less disturbed), the number of microsites favourable to seedling growth that were exposed was small, because of the plow's ineffectiveness in disturbing the thick organic layer (Lafleur et al., 2011; Prévost, 1996; Von der Gönna, 1992).

In plots treated with the scarifier, seedling growth increased gradually despite OLT accumulation. Indeed, the mounds built up on either side of the furrows by the scarifier exposes many mineral and organic-mineral microsites (Henneb et al., 2015) that may favour seedling growth in the short term (Lafleur et al., 2011). Generally, such planting conditions are not recommended on non-paludified sites, because of their instability and the high risk of drying out (Sutherland et Foreman, 2000; Sutton, 1993), which could affect seedling growth negatively in the long term (Närhi et al., 2013; Prévost et Dumais, 2003; Sutinen et al., 2006).

We found that seedling growth was better on clay microsites than on other types of microsites in almost all planting positions. At this early stage of growth, access to light and water is more critical than access to other resources. While light levels are not an issue for regeneration on recently cut areas in paludified forests, access to water is better on clay microsites that are exposed at the surface (disturbed clay), since these have a high water-retention capacity (Boivin et al., 2004; Bruand et Tessier, 2000) compared to other types of microsites. However, planting in bare, undisturbed clay soil entails a high risk of root asphyxiation caused by the stagnation of the water on the surface, especially in depressions (Bergsten et al., 2001; de Chantal et al., 2003; Lavoie et al., 2007, 2005). We also observed that seedlings planted with the collar below ground level (planting depth < 0 cm) showed poor growth on clay microsites but better growth on organic-clay microsites. In the presence of organic material or on organic-mineral microsites, deep planting provides better access to water at greater depths and stimulates the expansion of the initial roots and growth of adventitious roots (DesRochers et Gagnon, 1997; Krause et Morin, 2005; Prescott et al., 2000).

Seedlings that were planted vertically grew steadily, regardless of planting depth, whereas among the seedlings that were not planted vertically, growth increased gradually as planting depth decreased. Below the planting depth of −3 cm, a common practice in eastern Canada, the growth of the vertical seedlings was greater than that of the non-vertical seedlings. The advantage of the non-vertical seedlings above this threshold was probably the result of the growth of adventitious roots in contact with the moist soil (LeBarron, 1945; Pernot et al., 2019).

Seedlings planted on northern slopes generally grew better than those planted on southern slopes. The reason, we believe, is that northern slopes are less exposed to solar radiation and so remain wetter than southern slopes (Laamrani et al., 2014b; McCune, 2007). However, the influence of aspect on seedling growth varies from one site to another and depends on several factors, notably site topography, OLT, and the degree of disturbance of the organic layer (Henneb et al., 2015; Laamrani et al., 2014b).

2.6.3 Relationships among the Variables that Influence Seedling Growth

The path analysis showed that on paludified sites, the effectiveness of silvicultural treatments was significantly correlated with post-CLAAG OLT; this variable determines the direct (Henneb et al., 2015) and the indirect influence of treatments on other environmental variables and, ultimately, on seedling growth (Löf et al., 2012; Örlander et al., 1990; Sutton, 1993). The characteristics of the equipment and the penetration depth of the discs probably explain the observed differences between the MSP methods that we tested (Figure 2.6; (Örlander et al., 1990; Sutton, 1993)). The path analysis also revealed close relationships between the planting depth and the verticality of the seedlings, which supports the importance of planting quality. Lastly, our results show how planting location, with regard to aspect at the microtopographic scale, can be decisive for seedlings when a site is mechanically prepared with a plow (Henneb et al., 2015; Von der Gönna, 1992).

2.6.4 Abundance of Ericaceae

The presence and distribution of Ericaceae after planting are highly correlated with post-disturbance environmental conditions, and with site fertility in particular (Nguyen-Xuan et al., 2000; Økland, 1996; Thiffault et al., 2015). These relationships were clearly present on the experimental site; we found that Vaccinium was more abundant on humus-rich plowed sites; Rhododendron was more abundant in the control plots, characterized by fibric organic material; and Kalmia was closely associated with microsites having high proportions of organic-clay and clay-humic mixtures. Ericaceae were less abundant on microsites with a high clay content, which are less fertile than humic or mixed sites. Also, and contrary to what we had hypothesized, our results did not show any significant relationship between the abundance of Ericaceae and the short-term growth of the seedlings (three growing seasons). We conclude that scarification and plowing reduced the Ericaceae cover sufficiently to limit their direct and indirect interference with planted seedlings (Thiffault et al., 2004; Yamasaki et al., 2002).

2.7 Conclusion and Implications for Forest Management

Although the selected model explained a significant portion of the seedling growth variability (49.7%), other factors that we have not studied are significantly influential, as 50% of the variability remains unexplained. Nevertheless, our study confirms that the use of MSP to disturb paludified soils is effective in establishing a productive regeneration cohort in eastern Canada (Lavoie et al., 2005; Prévost et Dumais, 2003; Thiffault et al., 2004a). MSP with a plow provided the best growth in areas with low to moderate post-CLAAG OLT (≤40 cm). However, the scarifier performed better in areas with post-CLAAG OLT greater than 40 cm. To ensure successful establishment of plantations on these sites, it is therefore essential to distinguish between those that are slightly or moderately paludified and those that are highly paludified. Doing so will make it possible to choose the right MSP treatments and expose more microsites that are conducive to seedling establishment. MSP also enables adequate control over Ericaceae in the short term; reinvasion of the microsites over the medium and long terms remains to be documented. During planting operations, preference should be given to clay and mixed (organic-clay and clay-humic) microsites so as to ensure sufficient availability of water and nutrients. On clay microsites, seedlings should be planted fairly shallow, so as to stimulate the appearance of adventitious roots near the surface and thus give the seedlings better access to the resources (water and nutrients) available in the soil.

2.8 Acknowledgments

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CHAPITRE III

BLACK SPRUCE SEEDLING GROWTH RESPONSE IN CONTROLLED ORGANIC AND ORGANIC-MINERAL SUBSTRATES

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3.1 Abstract

In the boreal forest of eastern Canada, a large proportion of black spruce (*Picea mariana* [Mill.] BSP) stands are affected by paludification. Edaphic conditions that are created by paludification processes, including an abundance of microsites with high moisture and low nutrient contents, hinder forest regeneration. Disturbance of paludified sites by mechanical soil preparation (MSP) reduces organic layer thickness, while generating a range of substrates for regeneration establishment. Yet, little information is available regarding the effects of these substrates on tree growth. Our objective was to determine the effect of organic, mineral and organo-mineral substrates that are created following MSP of a paludified site on the growth and root development of black spruce seedlings in a controlled environment. We demonstrated that substrate exerted a significant effect on seedling growth and foliar concentrations of N, P and K. Increase in height and diameter were respectively greatest on clay (mineral) and mesic substrates. Substrate effects did not affect total biomass increases or final root biomass. Foliar nutrients (N, P, K) were relatively high in seedlings that were established on mesic substrates and relatively low for those established on clay substrates. To ensure successful seedling establishment, we recommend the application of MSP techniques that may expose more organic-mesic microsites on sites that are susceptible to paludification.

3.2 Résumé

Dans la forêt boréale de l'Est canadien, une grande proportion des peuplements d'épinette noire (*Picea mariana* (Mill.) B.S.P) est paludifiée. Les conditions créées par la paludification, notamment l'abondance de microsites avec une forte teneur en eau et pauvres en éléments nutritifs, nuisent à la régénération forestière. La perturbation des sites paludifiés par la préparation mécanique du sol (PMS) résulte en une réduction de l'épaisseur de la couche organique et engendre une variété de substrats d'établissement pour la régénération. Peu d'informations sont disponibles concernant l'effet de ces substrats sur la croissance des arbres mis en terre lors des opérations de reboisement. Notre objectif était de déterminer les effets des substrats organiques, minéraux et organo-minéraux exposés suite à une PMS sur un site paludifié sur la croissance et le développement racinaire des plants d'épinette noire en milieu contrôlé. Les résultats ont montré que les substrats ont eu un effet significatif sur la croissance des plants et leurs concentrations foliaires en nutriments (N, P, K). L'augmentation en hauteur et en diamètre était meilleure avec les substrats argileux (minéral) et mésique, respectivement. Nous n'avons noté aucun effet significatif des substrats sur l'augmentation en biomasse totale et sur la biomasse racinaire finale. Les concentrations foliaires en nutriments (N, P, K) étaient relativement élevées dans les plants établis sur les substrats mésiques et relativement faibles dans ceux établis sur les substrats argileux. Pour garantir le succès d'établissement des plants, nous recommandons l'application de techniques de PMS pouvant exposer davantage de microsites organiques-mésiques sur les sites susceptibles à la paludification.

3.3 Introduction

Picea mariana (Mill.) BSP (black spruce) is a common conifer that dominates the North American boreal forest (Farrar, 1995). The intrinsic characteristics of its wood make black spruce a desirable source of fiber, especially favoured by the pulp and paper industry (Koubaa et al., 2007). Black spruce can grow under conditions of low nutrient availability (Viereck et Johnston, 1990) and on a wide range of mineral and organic soils (Cauboue et Malenfant, 1988; Sims et al., 1990). The species is also tolerant of low temperatures and excess moisture in the soil (Levan et Riha, 1986; Bannister et Neuner, 2001). Yet, its survival and growth are negatively affected by soil conditions that are encountered in paludified areas (Gower et al., 1996; Prescott et al., 2000; Lavoie et al., 2005; Bergeron et al., 2007).

Under paludification, increasing moisture saturation of the surface and underlying edaphic layers contributes to soil cooling, reduces microbial activity and limits the mineralization of nutrients and their subsequent uptake by plants (Gower et al., 1996; Prescott et al., 2000). With paludification, mortality of existing trees is incurred, the survival of natural or planted regeneration is reduced and tree growth decreases (Simard et al., 2007, 2009). On such sites, microsites that are available for regeneration have few nutrients within the surface horizons that are composed of living and dead mosses. The mineral soil and humified horizon (rich in nutrients) become buried under a thick organic layer (low in nutrients), thereby rendering nutrients inaccessible to regenerating trees.

Use of mechanical soil preparation (MSP) (i.e., scarification) in paludified areas reduces the thickness and disrupts the structure of the organic matter layer (Henneb et al., 2015). MSP yields a range of substrates that are available for the establishment of natural or planted regeneration. Substrates consisting of organic soil types (fibric, mesic, humic or mixtures of the three) or mixtures with mineral soil (organo-mineral) promote or hinder the survival and growth of conifer regeneration (Sutherland et Foreman, 1995; Schmidt et al., 1996; Sutherland et Foreman, 2000; Prévost, 2004). For example, decomposed or burned *Pleurozium schreberi* (Brid.) Mitt. (red-stem feather moss) is rich in nutrients and better for black spruce growth than purely mineral substrates (Lavoie et al., 2007a, b). However, little research has documented the characteristics of substrates that are derived from MSP on paludified sites, together with their effects on the growth of black spruce plantations (Lavoie et al., 2007a).

In this context, our objective was to determine the effects of organic, mineral and organo-mineral substrates that were exposed following MSP of a paludified site on the growth and root development of black spruce seedlings under controlled environmental conditions. We conducted a six-month-long greenhouse experiment to test the following hypotheses: 1) organo-mineral mixtures promote growth and root development of black spruce seedlings relative to other types of substrates; and 2) organo-mineral mixtures offer greater nutrient availability (N, P, K, Ca, Mg) than do other types of substrates, which results in higher concentrations of foliar nutrients.

3.4 Materials and methods

3.4.1 Collection of substrates

In autumn of 2016, four substrates were collected from a paludified forest site that had been subjected to MSP. This spruce-feather moss site was located in the Clay Belt of Quebec (Canada), about 80 km north of the municipality of Villebois (49°06' N, 79°08' W). The material consisted of three organic substrates (fibric, mesic and humic) and a mineral substrate that was typical of the clayey lacustrine deposits of the proglacial lakes Barlow and Ojibway. This mineral substrate is low in carbonates (2 %) and characterized by its fine grain size (Ballivy et al., 1971; Locat et al., 1984). Physico-chemical characteristics of the substrates are summarized in Annexe A.

3.4.2 Experimental design and monitoring

A greenhouse experiment was undertaken in Rouyn-Noranda (Quebec), from late January 2017 to late July 2017. The six-month period was equivalent to one growing season (root and shoot growth) in this region (*Abitibi-Témiscamingue*). The average ambient daytime temperature was set to 25°C, while nighttime temperatures were maintained at 18°C. Light exposure was set to 15 h per day(photoperiod), without controlling relative humidity of the air. Greenhouse conditions were used to stimulate seedlings growth, in order to rapidly detect the growth response to treatments (substrates).

Tableau 3.1 Physico-chemical characteristics of organic and clay substrates used in the experiment.

Substrates	Relative degree of decomposition	pH	CEC (meq $100g^{-1}$)	N ($g\ kg^{-1}$)	P ($g\ kg^{-1}$)	K ($g\ kg^{-1}$)	Mg ($g\ kg^{-1}$)	Ca ($g\ kg^{-1}$)
Clay[a]	-	5.7	25.9	0.9	0.005	0.08	0.28	1.57
Fibric[b]	Low	3.2-4	124	5-10	0.1	0.08	1	0.9
Mesic[b]	Moderate	4-7	116	8-11	3.5	5.7	4.4	2.4
Humic[b]	High	3.5-8	160	9-19	8	12.5	4.9	6

a: sampled clay (60 samples) on the prepared site (Clay-Belt).
b: (Henneb et al. 2019a; Soil Classification Working Group 1998).

Six groups of rooting substrates (Table 3.1), which were representative of a paludified site that had been subjected to mechanical soil preparation (Henneb et al., 2019a), were prepared from the field-harvested material. The six experimental groups were: Group

1) 100 % clay substrate (control); Group 2) 100 % fibric substrate; Group 3) 100 % mesic substrate; Group 4) 100 % humic substrate; Group 5) mixed organic substrates, where fibric, mesic or humic material each dominated the mixture; and Group 6, which was organo-clay mixtures. Mixtures from Group 5) were blended in the following proportions: (2/3 volume) fibric + (1/3 volume) mesic; (1/2 volume) fibric + (1/2 volume) mesic; (1/3 volume) fibric + (2/3 volume) mesic; (2/3 volume) mesic + (1/3 volume) humic; (1/2 volume) mesic + (1/2 volume) humic; and (1/3 volume) mesic + (2/3 volume) humic. Substrates from Group 6) were composed of the following mixtures: (1/2 volume) clay + (1/2 volume) fibric; (1/2 volume) clay + (1/2 volume) mesic; and (1/2 volume) clay + (1/2 volume) humic. Each of the prepared substrates was placed in a sterilized cylindrical PVC pot (diameter, 20 cm; height, 20 cm; volume, 6.28 dm^3) and replicated 10 times, for a total of 130 pots that were distributed over the six groups. Pots were arranged randomly on the greenhouse bench (Fig. 3.1).

At the end of November 2016, we obtained 200 container-grown black spruce seedlings (2-year-old; produced in containers of 45-cavities of 110 cm^3 each) from a provincial government nursery (Pépinière forestière de Trécesson, Amos, Québec). The 2+0 seedlings were dormant at the beginning of the experiment. We stored the plants inside the greenhouse from the end of November to January 2017. The aim was to gradually acclimatize seedlings to greenhouse temperature and lift off dormancy.

Prior to planting, we randomly selected 10 seedlings to measure their initial oven-dry biomass (g, 65 °C for 48 h) and foliar concentrations of macronutrients (N, P, K, Ca, Mg). Foliar concentrations were determined on 2 g-subsamples of dried needles. The tissues were ground (Pulverisette 0, Fritsch, Idar-Oberstein, Germany) prior to analyses. Nitrogen was quantified following high-temperature dry combustion followed by thermo-conductometric detection (TruMAC, LECO Corp., St Joseph, MI).

Tissues were digested in hot H_2SO_4/H_2O_2 prior to determining P, K, Ca and Mg by plasma atomic emission spectroscopy (Thermo Jarrel-Ash-ICAP 61E, Thermo Fisher Scientific, Waltham, MA).

Figure 3.1 Randomized distribution of 130 potted black spruce seedlings on the greenhouse bench. The pots contained seedlings transplanted into the six different substrates.

At the end of January 2017, we transplanted 130 seedlings into pots containing one of the growth substrate groups (one seedling per pot) and measured their initial size (average ± SD: height, 23.29 cm ± 2.04 cm; root collar diameter, 2.45 mm ± 0.3 mm). During the experiment; to avoid the drying of the substrates, the seedlings were watered twice a day until saturation. All seedlings received the same amount of water.

We carried out weekly measurements of seedling height (cm) and root collar diameter (mm) throughout the experiment. We also measured substrate temperature (root zone temperature) hourly using miniature data loggers (iBWetland 22L, Alpha Mach iButton®, Bombardier, Ste-Julie, QC), which were buried at the centers of 28 pots that had been randomly selected and that were representative of the six substrate groups. These measurements verified whether greenhouse temperatures were sufficiently controlled (i.e., minimal temperature variation among substrates groups) during the experiment. At the end of the experiment, five seedlings were randomly selected from each substrate group for foliar nutrient analysis using the aforementioned methods. Results of foliar nutrient analysis were compared to the foliar concentrations (g kg^{-1}) that have been suggested for optimal growth of black spruce. These same diagnostic concentrations were used by Lavoie et al. (2007a, b), and were reported by Swan (1970), as critical concentrations corresponding to deficiency and sufficiency, respectively: N (12-15 g kg^{-1}); P (1.4-1.8 g kg^{-1}); K (3.0-4.0 g kg^{-1}); Ca (1.0-1.5 g kg^{-1}); Mg (0.9-1.2 g kg^{-1}). The remaining seedlings (3 to 5 per substrate, due to the disponibility after mortality) were used to determine final total shoot and root biomass after oven-drying.

3.4.3 Statistical analyses

All analyses were conducted in the R statistical environment (v. 3.5.1; R Core Team, 2018). In order to verify if the temperature was adequately controlled in the greenhouse, one-way analyses of variance (ANOVA) and multiple Tukey tests [*multcomp* library] were used to compare the average temperatures that were recorded in each substrate during the experimental period. We then subjected growth and nutrient data to one-way ANOVAs, followed by multiple means comparisons [*Ismeans* library, *emmeans*], to evaluate: 1) the effect of substrate on the relative increases in height (final height - initial height)/initial height) × 100 %), root-collar diameter (final diameter - initial diameter)/initial diameter) × 100%), total biomass (final total biomass - initial total biomass)/initial total biomass) × 100%), and final root biomass; and 2) the effect of substrate type on needle nutrient concentrations of N, P, K, Ca, and Mg. Transformations were applied to the data to respect normality and homoscedasticity assumptions. Effects were reported as significant using a threshold α of 0.05.

Finally, we used a principal component analysis (PCA) [*ade4* library] to explore the relationships and correlations among the variables that we studied, including substrate, growth and seedling nutrition.

3.5 Results

We noted no significant differences in average substrate temperatures among the groups during the experimental period (Table 3.2). Thus, substrates and seedling roots were maintained under the same temperatures, confirming that greenhouse conditions were controlled sufficiently during the experimental period.

Tableau 3.2 Mean temperatures (°C) of the greenhouse and substrates during the experimental period (6 months). The averages followed by the same letter are not statistically different ($p \geq 0.05$).

		Mean temperature (°C)
Greenhouse		22.6 (0.151) b
Substrates	Fibric	20.1 (0.151) ab
	Mesic	19.7 (0.151) a
	Humic	19.6 (0.151) a
	Clay	20.0 (0.151) a
	Organic-mix	20.0 (0.062) a
	Organic-Clay	20.0 (0.087) a

Note : The values in parentheses represent the standard deviation.

3.5.1 Seedling mortality and growth

We observed seedling mortality on most substrates (cf. fibric substrate, 0 %) over the course of the experiment (Table 3.3). Mortality was highest on the humic material (40 %) and high on clay (30 %) compared to the remaining substrates.

Substrate exerted a significant effect on seedling growth (ANOVA, Table 3.4), in terms of increases in height (P = 0.01) and collar diameter (P = 0.04). Increases in height were greater for seedlings that were planted on clay compared to those on humic substrates and organic mixtures (Table 3.5; $P < 0.05$). Differences in height increases were not observed ($P > 0.05$) among fibric, mesic, humic, and organic and organo-mineral substrates (Table 3.5). However, greater mean seedling diameter increases were observed on mesic compared to humic substrates (120 % vs 85 %, respectively; Table 3.5). We further noted no differences among substrates in total biomass or final root biomass (Table 3.4).

Tableau 3.3 Seedling mortality (mortality number of seedling and mortality rate (%)) by substrate type.

Substrates groups	Mortality (number of seedlings)	Mortality rate (%)
1) Fibric	0	0
2) Mesic	1	10
3) Humic	4	40
4) Clay	3	30
5) Organic-mix	8	13.3
6) Organic-Clay mix	1	3.3

F: Fibric, M: Mesic, H: Humic, C: Clay

3.5.2 Seedling nutrition

Substrate significantly influenced ($P < 0.05$) foliar concentrations of N, P and K (Table 3.4), but not those of Ca ($P = 0.401$) or Mg ($P = 0.339$). Foliar N was higher in seedlings that were planted on mesic substrate compared to those on fibric, clay, organic and organo-clay substrates (Table 3.5). No significant differences in foliar N were detected between seedlings planted in mesic and humic substrates. Yet, seedling growth on all substrates resulted in foliar N concentrations below the critical threshold of 12 g kg^{-1} (Swan, 1970). In contrast, foliar P (Table 3.5) exceeded the critical upper threshold of 1.4 g kg^{-1} (Swan, 1970) in most substrates, except for clay. Seedling growth on clay resulted in the lowest concentrations of foliar P, when compared with those measured in mesic, humic, organic and organo-clay substrates. No differences in foliar P concentration were observed between clay and fibric substrates (Table 3.5). All seedlings resulted in foliar K concentrations that were below the critical deficiency level of 3 g kg^{-1} (Swan, 1970). Seedlings planted in organic and organo-clay mixtures had higher foliar K concentrations than those measured in the clay substrate. No significant differences in foliar K concentration were observed among clay, fibric, mesic and humic substrates (Table 3.5). Foliar concentrations of Ca and Mg were above the critical threshold (1 g kg^{-1}, Ca; 0.9 g kg^{-1}, Mg) for all seedlings, with no difference among treatments (Table 3.5).

The first two axes of the PCA explained 53.8 % of the total variation in the data (Fig. 3.2). Fig.3.3 shows the contributions (%) of the variables in explaining the variance on the first two axes. Foliar concentrations of nutrients (N, P, Ca) were mainly associated with variation on Axis 1, while diameter growth, substrate type and foliar K were associated with Axis 2.

Tableeau 3.4 ANOVA summary of substrate effects (degrees of freedom = 5) on black spruce seedling growth, biomass, and foliar nutrient concentrations.

Response variable	*F*-Value	*P*-Value
Seedling height increase (%)	2.266	0.014
Seedling diameter increase (%)	1.894	0.044
Total biomass increase (%)	0.695	0.630
Root biomass (g)	1.189	0.330
Foliar total N (g kg^{-1})	4.525	< 0.001
Foliar P (g kg^{-1})	2.659	0.001
Foliar K (g kg^{-1})	2.227	0.021
Foliar Mg (g kg^{-1})	1.145	0.339
Foliar Ca (g kg^{-1})	1.075	0.401

Values in bold type indicate significance at $P = 0.05$

Table 3.5 Summary of multiple means comparisons concerning substrate effects on seedling growth and foliar nutrient concentrations. For each variable (column), means followed by the same letter do not differ at P = 0.05.

Substrates	Height increase (%)	Diameter increase (%)	N (g kg^{-1})	P (g kg^{-1})	K (g kg^{-1})	Ca (g kg^{-1})	Mg (g kg^{-1})
Fibric	41.8 ab	88.7 ab	8.4 ab	1.4 ab	4.3 ab	14.1 a	1.9 a
Mesic	40.8 ab	119.9 b	11.4 c	1.8 b	4.6 ab	18.7 a	2.1 a
Humic	31.8 a	85.2 a	9.9 bc	1.7 b	4.6 ab	17 a	1.9 a
Clay	50.8 b	92.6 ab	6.3 a	1.2 a	4.0 a	15 a	2.0 a
Organic-mix	39.6 a	108.4 ab	9.2 b	1.8 b	5.1 b	15.8 a	2.0 a
Organic-Clay mix	39.9 ab	94.4 ab	6.9 a	1.7 b	5.2 b	16.4 a	2.0 a

The PCA analysis further showed that foliar N and diameter growth were positively correlated, especially for seedlings that were growing in mesic substrate. Further, the highest foliar concentrations of N, Ca, and Mg were more closely associated with mesic substrate than with other substrates. Height growth was more associated with clay substrates than with other substrates, and was negatively correlated with foliar concentrations of P and K, which were higher in humic substrates than in other substrates.

3.6 Discussion

The observed mortality rates are probably due to the no- acclimatization of some seedlings to greenhouse temperature and to new substrates during transplantation at the beginning of the experiment. The same observations were reported by Lavoie et al. (2007a). However, it would be preferable to increase the number of replicas for each substrate to consider potential plant mortality that may be associated with acclimatization. The rooting substrates had a significant effect on height and diameter growth of the black spruce seedlings. Similar responses in the greenhouse (Lavoie et al., 2007a) and in field conditions (i.e., a prepared paludified site; Lavoie et al., 2007b; Henneb et al., 2019a) have been previously observed. Seedling diameter growth was greatest on the mesic substrate, which is rich in nutrients (Lavoie et al., 2007a; Lafleur et al., 2010a) (see Table 3.1).

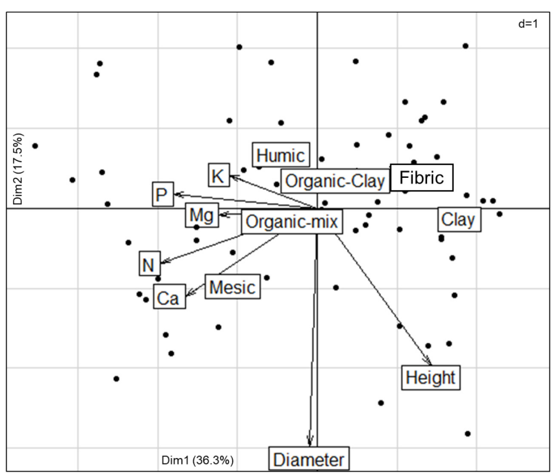

Figure 3.2 Principal component analysis (PCA) summarizing associations that exist between the substrates, seedling growth, and seedling nutrition. PCA explains about 53.8% of the variation.

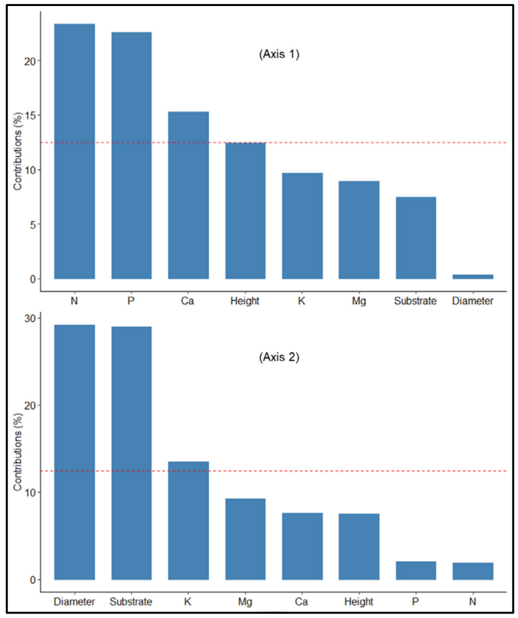

Figure 3.3 Contribution (%) of the variables to the two axes (axis 1 and 2) of the principal component analysis. The red dotted line indicates the expected average contribution for each axis. A variable whose contribution is greater than this limit can be considered important in its contribution to the variance on each axis.

This is particularly true at greenhouse temperatures that were conducive to black spruce growth (18–25 °C, Table 3.2) (Lopushinsky et Max, 1990; Lahti et al., 2005). At cold temperatures, nutrients become less limiting as plants growth and nutrient requirements are low (Pregitzer et al., 2000; Alvarez-Uria et Körner, 2007). However, provided that the establishment phase is completed and that planting shock associated with water stress has been alleviated (Grossnickle, 2005), seedling growth is promoted by increasing soil temperature and nutrient availability (Londo et Mroz, 2001; Kabrick et al., 2005; Löf et Birkedal, 2009). In the boreal forest, an increase in root zone temperature stimulates microbial activity in mesic organic soils, compared to mineral soils and other underlying organic horizons (Kähkönen et al. 2001; Dioumaeva et al., 2002; Li et al., 2012). Increased microbial activity, in turn, increases the availability of nutrients (especially N), which has a positive effect on seedling growth (Van Cleve et al., 1983a,b; Li et al., 2012).

In contrast, height growth was greatest on clay substrate. However, seedlings had relatively low foliar nutrient concentrations with clay substrate compared to the mesic substrate, especially for N and P. In response to low nutrient availability, seedlings tend to reorganize their growth patterns for more efficient use of available nutrients (Madgwick, 1971; Farmer, 1975; Immel et al., 1978; Farmer, 1980). Indeed, seedlings that were established on clay, which was nutrient-poor particularly with respect to N (Lavoie et al., 2007a, b), likely favoured height growth over root growth in response to low nutrient supplies (Boivin et al., 2002; Munson et Bernier, 1993; Rikala et al., 2004; Heiskanen, 2005). Also, these seedlings likely depleted foliar nutrient reserves to optimize height growth at the expense of root growth (Van den Driessche, 1985; Thiffault et Jobidon, 2006).

Other studies have reported that short-term seedling growth is better on clay substrates than on organic or organo-mineral substrates following mechanical soil preparation of paludified sites (Henneb et al., 2019a). In mechanically prepared paludified soils (scarified and plowed paludified soils), seedlings favor access to light and water over other resources (e.g., nutrients) in order to maximize growth (Haase et Rose, 1993; Lamhamedi et Bernier, 1994; Johnstone et Chapin, 2006). Under these conditions, access to water is more reliable on clay substrates that were exposed by disturbance of the surface soil, characterized by high water-retention capacity (Bruand et Tessier, 2000; Boivin et al., 2004). During our short experiment under controlled conditions, all seedlings had unlimited access to water. The nutrient availability on the substrates has thus emerged as the principal factor limiting seedling nutrition and growth.

3.7 Conclusion

The objective of this study was to determine the effects of organic, mineral and organo-mineral substrates on the growth and root development of black spruce seedlings in a controlled environment. Temperature, soil moisture and light conditions were controlled to highlight effects of substrate on growth and nutrition of black spruce. In opposite of our initial hypotheses, mesic substrates exhibited the best results, both in terms of diameter growth (119.9 % increase) and nutrient foliar concentrations (N, P, K). Clay promoted the greatest height growth (50.8 % increase) with low nutrient contents. In mechanically prepared paludified soil, Henneb et al. (2019a) also found that seedling growth in clay substrates was better than those planted in organic or organo-mineral substrates because of high water retention that is maintained in the former during dry summer periods. To ensure the success of seedling establishment in the short-term, we recommend the use of MSP techniques that can expose more clay and organic-mesic microsites on sites with limited and unlimited access to water, respectively, to guide silviculturists in planning effective actions for regenerating paludified forest stands. Longer term monitoring will be necessary to understand nutrition and growth impacts of mechanical soil preparation on paludified soils.

3.8 Acknowledgements

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CHAPITRE IV

REGIONAL CLIMATE, EDAPHIC CONDITIONS AND ESTABLISHMENT SUBSTRATES INTERACT TO INFLUENCE INITIAL GROWTH OF BLACK SPRUCE AND JACK PINE PLANTED IN THE BOREAL FOREST

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4.1 Abstract

In eastern Canada, spruces (*Picea* spp.) and pines (*Pinus* spp.) are among the main commercial species being logged for their lumber or wood fiber. Annually, about 175 million seedlings are planted in areas totaling ~100 000 ha. Appropriate microsite selection is essential during reforestation operations, given that it can improve chances of survival and initial growth of seedlings. In fir (*Abies* spp.) and spruce forests of eastern Canada, optimal characteristics of establishment microsites have yet to be identified; these would be determined by different physical and climatic variables operating at several scales. Our study determined the influence of climatic (regional-scale), edaphic (stand-scale), local (microsite-scale) and planting conditions on the establishment substrate and initial growth of black spruce (*Picea mariana* Britton, Sterns & Poggenb) and jack pine (*Pinus banksiana* Lamb.). Substrate characterization and growth monitoring (3 growing seasons) for the two species were conducted on 29 planted cutblocks that were distributed over an east-west climatic gradient (precipitation and temperature) in the balsam fir and black spruce-feather moss forests of Quebec (Canada). Linear mixed models and multivariate analyses (PCAs) determined the effects of climatic, edaphic, micro-environmental variables and their interactions on the establishment substrate and seedling initial growth. The predictive models explained respectively 61 % and 75 % of growth variability of black spruce and jack pine. Successful establishment of black spruce and jack pine depended upon regional conditions of precipitations and temperature, as well as on their interactions with stand-scale edaphic variables (surface deposit, drainage, slope) and local variables (micro-environmental) at the microsite-scale (establishment substrate types, substrate temperature). Mineral, organo- mineral and organic establishment substrates exerted mixed effects on seedling growth according to regional precipitations and temperature

conditions and their interactions with edaphic and local variables at the stand and microsite-scales, respectively.

4.2 Résumé

Dans la forêt boréale de l'est canadien, les épinettes (*Picea* spp.) et les pins (*Pinus* spp.) sont parmi les principales essences commerciales exploitées pour le bois d'œuvre ou les fibres. Environ 175 millions de plants sont mis en terre annuellement sur des superficies totalisant près de 100 000 ha. Le choix de microsite d'établissement est primordial lors des opérations de reboisement, puisque celui-ci est censé améliorer la chance de survie et la croissance initiale des plants mis en terre. Dans les domaines de la sapinière et de la pessière de l'est canadien, les caractéristiques du microsite d'établissement restent à être identifiées, et cela selon différentes variables physiques et climatiques à plusieurs échelles, incluant le climat régional, les caractéristiques édaphiques à l'échelle du peuplement, et le microenvironnement (variables locales) des plants à l'échelle du microsite (incluant les conditions de plantation). L'objectif de cette étude était de déterminer l'influence des variables climatiques (échelle régionale), édaphiques (échelle du peuplement), locales (échelle du microsite) et les conditions de plantations sur le substrat d'établissement et la croissance initiale de plants d'épinette noire (*Picea mariana* Britton, Sterns & Poggenb) et de pin gris (*Pinus banksiana* Lamb.). La caractérisation des substrats et le suivi de croissance (3 saisons de croissance) pour les deux espèces plantées ont été réalisés sur 29 parterres de coupe répartis sur un gradient climatique (précipitations et température) d'est en ouest, notamment dans le domaine de la sapinière et de la pessière à mousse de l'est canadien. Des modèles mixtes et des analyses multivariées (ACP) ont été utilisés pour déterminer l'influence des variables physiques, climatiques et leur interaction sur le substrat d'établissement et la croissance initiale de plants d'épinette noire et de pin gris. Les

modèles mixtes prédictifs expliquaient respectivement 61% et 75% de la variabilité de croissance des plans d'épinette noire et de pin gris. L'établissement des plants d'épinette noire et de pin gris dans l'est canadien dépendait du climat régional (température, précipitations), des caractéristiques édaphiques à l'échelle du peuplement (types de dépôt de surface, drainage, pente) et des variables locales (micro-environnementaux) à l'échelle du microsites (types de microsite d'établissement, température du substrat). Les substrats d'établissements minéraux, organo-minéraux et organiques ont exercé des effets mixtes sur la croissance des plants selon les précipitations régionales, les conditions de température et leurs interactions avec les variables édaphiques et locales aux échelles du peuplement et du microsite, respectivement.

4.3 Introduction

The boreal forest of Eastern Canada remains a strong supplier of wood for both domestic and export markets. Indeed, the forest products industry is engaged in extensive harvesting and forest management activities across the region (De Grandpré et al., 2003). Softwoods, most notably spruces (*Picea* spp.) and pines (*Pinus* spp.), are among the main commercial species being logged for their lumber or wood fiber (Zhang et al., 2009). In Eastern Canada, reforestation operations complement natural regeneration to restore or maintain forest productivity, so to ensure continuous wood production that meets local and global demands (Ressources Naturelles Canada, 2016). Annually, about 175 million trees are planted in eastern Canada, across an area totaling about 100 000 ha (National Forestry Database, 2017). In Quebec (Canada), black spruce (*Picea mariana* Britton, Sterns & Poggenb) and jack pine (*Pinus banksiana* Lamb.) represent 77% of the ~130 million seedlings planted in this province each year (Salmon, 2018). Although they can be found on similar sites in the boreal forest, jack pine is a shade-intolerant species with high potential rates of resource capture relative to black spruce, which is a shade tolerant species adapted to low-resource environments (Reich et al., 1998).

In the boreal forest, reforestation is generally preceded by mechanical soil preparation (MSP) to create favourable conditions for seedling establishment on suitable microsites (Henneb et al., 2019a, 2019b; Prévost, 2004, 1992; Schmidt et al., 1996). Following site preparation, seedlings are to be planted in microsites that maximize their survival and initial growth. Suitable conditions are determined by climatic and physical variables at several scales (Margolis et Brand, 1990). These variables include regional climate (temperature, total precipitation, and relative humidity), soil characteristics at the stand-scale (drainage, surface deposits, slope), and seedling microenvironment at the microsite-scale (establishment or rooting substrate, substrate temperature, planting position, and humus thickness) (Spittlehouse and Stathers, 1990). Yet, microsites that promote seedling growth are likely to differ, depending upon geomorphological characteristics at the stand-scale, regional climatic conditions, and the characteristics of the species being planted (Barras and Kellman, 1998; Bergeron et al., 2007; Henneb et al., 2015; Lafleur et al., 2011; Lavoie et al., 2007; Simon et al., 2011; Sutherland et Foreman, 1995).

It is important to identify the interactions between regional climate variables, stand characteristics, and local planting conditions so that practitioners can adapt reforestation practices to reflect their respective regional situations. Incorporating these interactions into site planning would further ensure successful plantation establishment in the context of ongoing global change that will have significant effects on temperature and precipitation patterns and consequently, on the conditions for tree establishment (Boucher et al., 2019; Goldblum et Rigg, 2005; Hansen et al., 2001; Shafer et al., 2001; Walker et al., 2002). The subsequent application of this knowledge would have immediate effects on silvicultural practices and the productivity of managed forest stands. Therefore, the overall objective of our study was to identify the role that environmental variables play at regional, stand and microsite scales in the growth of black spruce and jack pine plantations. More specifically, we determined the influence of climatic (regional scale), edaphic (stand scale), local (microsite scale) and planting conditions, both on the establishment substrate and on the initial growth of black spruce and jack pine. These plantations were established in the balsam fir (*Abies balsamea* (L.) Mill.) and spruce-moss bioclimatic domains of boreal Quebec (Canada). We tested the hypothesis that the effects of the establishment substrate leading to the highest growth rate depended on interactions between regional climate, edaphic and planting conditions across boreal Quebec.

4.4 Materials and Methods

4.4.1 Study area and data collection

We used data that were collected from 29 operational cutblocks (average area: 8.5 ha) that had been submitted to mechanical site preparation and planted. The selected planted cutblocks covered a wide moisture and temperature gradient from eastern to western Quebec; the plots were located in the balsam fir and black spruce-feather moss bioclimatic domains (Figure 4.1). The balsam fir domain is dominated by mixed stands of yellow birch (*Betula alleghaniensis* Britton), paper or white birch (*Betula papyrifera* Marshall), and softwoods such as balsam fir, white spruce (*Picea glauca* (Moench) Voss) and white cedar (*Thuja occidentalis* L.) (Saucier et al., 2009). The black spruce-feather moss domain is dominated by closed canopy black spruce stands (Saucier et al., 2009).

Twenty-one cutblocks were reforested with black spruce between 2010 and 2016; eight cutblocks were reforested with jack pine between 2011 and 2016 (Figure 4.1). In all cases, containerized seedlings were derived from local seed sources and produced in governmental or contracted private nurseries over two years in 45-cavity containers (each with a volume of 110 cm3). One to four weeks after cutblock reforestation, we established a 130 m transect and installed permanent sampling plots (8 m radius; 200 m2, or about 40 seedlings per plot) every 50 m along the transect, to a maximum of five plots per cutblock. The transect was oriented east-west and located in the middle of the block. A total of 105 plots were established in sites that had been planted with black spruce and 40 plots in sites that were planted with jack pine. All seedlings were identified with a numbered metal tag to allow long-term monitoring at the seedling level. In each plot, we measured stem diameter at ground-level and seedling height at the end of three consecutive growing seasons following planting. A total of N = 4492 seedlings (2996 black spruce and 1496 jack pine) were identified and monitored.

During the first three growing seasons on each site, data were collected at the microsite-scale for each seedling (≤ 1 m2): 1) planting substrate, which was classified into one of five types (fibric organic matter, humic organic matter, intact forest litter, exposed mineral soil, organo-mineral mixture (MFFP, 2016); 2) relative planting position (mound, shoulder of the scarifying furrow, scarifying furrow depression); and 3) humus thickness (cm). We measured soil temperature on an hourly basis using iButton probes (Alpha Mach iButton®, Bombardier, Ste-Julie, Quebec). Loggers were buried at 10 cm depth next to a seedling that was located at each plot centre. The logged data were subsequently used to calculate monthly averages.

At the stand-level, we extracted surface deposit data, slope classes and drainage classes from the most recent ecoforestry map that was produced by the Government of Quebec (MFFP (Ministère des Forêts, de la Faune et des Parcs), 2019). Site slope was categorized as zero to low (< 8 %), gentle (< 15 %), moderate (< 30 %), strong (< 40 %) or steep (> 41 %). Soil drainage was rated as rapid, good, moderate, imperfect, or poor. The inventoried cutblocks are found on one of five types of surface deposits: thick till, thin till, rock deposits, glaciolacustrine deposits, or fluvio-glacial deposits.

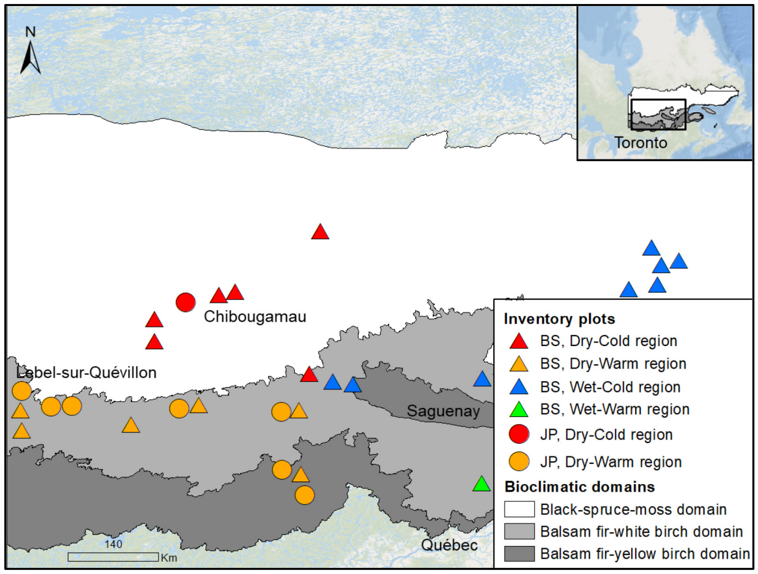

Figure 4.1 Distribution of permanent inventory plots distributed in cutblocks planted with black spruce (BS, filled triangles) and jack pine (JP, filled circles) in the balsam fir (grey areas) and spruce-moss (white area) bioclimatic domains of boreal Quebec, Canada (Saucier et al., 2009). Plots are located in four regions that were delineated based on their precipitation and temperature regimes (different coloured symbols). The regions are Dry-Cold, Dry-Warm, Wet-Cold and Wet-Warm.

At the regional level, extrapolated monthly data were extracted for temperature, total precipitation and relative humidity from NASA's Global Climate Data Platform (2-metre resolution) (https://power.larc.nasa.gov/data-access-viewer/). The climatic data were collected from May to September (growing season) during the first three growing seasons for each cutblocks; i.e. climate data we used as explaining variables corresponded to the 3-year growth periods specific to each plantation included in our dataset.

4.4.2 Statistical analyses

We conducted all statistical analyses in R version 3.5.1 (R Core Team, 2018). We used seedling height and ground collar diameter data to calculate a volume index (V), based upon the volume of a cone (Avery and Burkhart, 2015), which was computed as follows:

$$V = \pi \times (D/2)2 \text{ x } (H/3) \qquad (1)$$

where V is volume in cm3, D is stem diameter at ground level (cm), and H is height (cm). We then calculated relative volume growth (RGRV), following (Margolis and Brand, 1990), according to the following formula:

$$RGRV= [\text{In } (V_3) \text{ -In } (V_0)] /[t_3\text{-}t_0] \qquad (2)$$

where V_3 and V_0 represent tree volumes at time t_3 (i.e., after three growing seasons) and t_0 (at planting).

Ten environmental variables, together with their interactions, were incorporated into a linear mixed model as fixed effects explaining volume growth. The geographical distribution (longitude and latitude) of the plots were considered random effects in the model, which was fitted using the lme4 library (Bates et al., 2015). Also, ANOVA analysis was used to evaluate the effect of explanatory variables on volume growth. Explanatory variables were categorized into three groups: 1) the microsite scale, which included humus thickness, planting position, substrate type, and monthly average substrate temperature; 2) the stand scale, which included surface deposition, slope class, and drainage class; and 3) the regional scale, which was represented by the seasonal climate data (i.e., average monthly temperature, monthly total precipitation, and average relative humidity). We considered effects to be significant at $\alpha = 0.05$.

Last, we used medians of mean monthly temperature (13.5 °C) and total monthly precipitation (95.9 mm) as boundaries to delineate four regional groups: dry and cold region; wet and cold region; dry and warm region; and wet and warm region. The use of the median values of temperature and precipitation was more relevant than the mean values to delimit the four regions. Unlike mean value, the median value is relatively insensitive to outliers and detects the break point that can subdivide the data into several groups (Kim et Wessel, 2008; Leys et al., 2013; Werner et al., 2003). This subdivision method of data has already been successfully applied in ecology in previous studies (Diaci, 2002; Wickham et al., 2000). Table 4.1 summarizes the number of black spruce and jack pine seedlings in each delineated regions.

Table 4.1 Number of jack pine and black spruce seedlings in the four regions, with their corresponding height and ground collar diameter at the end of their third growing season.

Species	Region	Number of seedlings	Ground collar diameter (mm)	Height (cm)
Black spruce	Wet-Warm	1120	18.0 (±6.3)	89.7 (±26.8)
	Wet-Cold	1289	12.9 (±5.2)	61.8 (±27.0)
	Dry-Warm	239	9.6 (±4.6)	51.4 (±18.2)
	Dry-Cold	348	9.6 (±6.6)	47.1 (±21.9)
Jack pine	Dry-Warm	1034	15.2 (±6.7)	69.3 (±25.1)
	Dry-Cold	462	10.2 (±2.5)	44.1 (±9.6)

Note: Data are presented as mean (±standard deviations).

We assigned the cutblocks and their plots to these distinct groups according to their temperature and precipitation regimes (Figure 4.1). Principal component analyses (PCAs) were then used for each group to assess the correlations among seedling growth, establishment substrates and environmental variables at the regional, stand and microsite levels. PCAs were produced using CANOCO version 5 (Braak and Smilauer, 2012; Šmilauer and Lepš, 2014).

4.5 Results

Our dataset comprised 4,492 seedlings distributed across the two species and over the four regions (Table 4.1). After three growing seasons, blacks spruce seedling ground collar diameter and height ranged from 9.6 to 18 mm and from 47 to 90 cm, respectively, with the larger sizes observed in the wetter regions. Jack pine seedlings, which were only found in the dry regions, respectively ranged from 10.2 to 15.2 mm in ground collar diameter and from 44 to 69 cm in height.

4.5.1 Black spruce

Our predictive model explained 61 % of variation in the data (Table 4.2). Several individual environmental variables affected seedlings growth at the stand and regional levels, including slope and monthly mean temperature. Significant interactions also were observed among environmental variables at microsite, stand, and regional scales. These included two-way interactions between substrate type and total monthly precipitation, substrate type and surface deposit, soil temperature and surface deposit, and drainage and surface deposit; significant three-way interactions were observed for substrate type, surface deposit and drainage, and for substrate type, drainage and slope (Table 2). No effects on seedlings growth were reported for relative humidity, humus thickness, and planting position (Table 4.2).

Table 4.2 ANOVA summary of explanatory variable effects and their interactions at three spatial scales on relative volume growth of black spruce and jack pine seedlings in the boreal forest of Quebec.

Explanatory variables		Black spruce (Model R^2 = 0.61)		Jack pine (Model R^2 = 0.75)	
		F-value	P-value*	F-value	P-value*
Microsite scale	Humus thickness	0.944	0.331	0.790	0.374
	Planting position	1.055	0.384	0.357	0.840
	Substrate temperature (°C)	0.649	0.420	2.775	0.096
	Substrate type	1.429	0.199	1.661	0.127
Stand scale	Surface deposit	0.598	0.621	5.627	0.001
	Drainage class	1.608	0.206	0.291	0.884
	Slope class	3.928	0.007	2.773	0.040
Regional scale	Precipitation (mm)	0.103	0.748	1.953	0.162
	Temperature (°C)	8.067	0.009	1.425	0.233
	Relative humidity (%)	0.067	0.796	1.030	0.310
Interactions	Substrate type x Substrate temperature	1.399	0.211	2.713	0.008
	Substrate type x Precipitation	3.742	0.001	4.385	0.002
	Substrate type x Relative humidity	1.604	0.142	1.954	0.070
	Substrate type x Planting position	0.889	0.633	1.544	0.055
	Substrate type x Surface deposit	2.031	0.018	3.205	0.001
	Substrate type x Drainage class	1.050	0.399	2.069	0.006
	Humus thickness x Surface deposit	1.170	0.320	0.414	0.661
	Planting position x Substrate temperature	1.307	0.258	0.968	0.436
	Planting position x Surface deposit	0.859	0.603	1.309	0.219
	Planting position x Drainage class	1.443	0.139	0.807	0.671

Tableau 4.2 (suite)

Surface deposit x Substrate temperature	2.781	0.043	0.300	0.825
Surface deposit x Drainage class	2.329	0.034	1.039	0.385
Surface deposit x Slope class	0.580	0.679	1.355	0.255
Drainage class x Slope class	1.977	0.101	2.334	0.072
Substrate type x Substrate temperature x Surface deposit	0.750	0.690	2.222	0.030
Substrate type x Planting position x Drainage class	1.169	0.241	1.241	0.206
Substrate type x Surface deposit x Drainage class	2.134	0.008	0.934	0.505
Substrate type x Drainage class x Slope class	2.522	0.002	0.827	0.578
Planting position x Substrate type x Substrate temperature	1.402	0.096	0.810	0.676
Planting position x Drainage class x Surface deposit	0.920	0.565	0.926	0.508
Surface deposit x Drainage class x Slope class	0.563	0.573	0.042	0.839

In the dry-cold region (Figure 4.2a), seedlings growth was favoured by mineral-type substrates and moderate slopes. However, seedlings growth was negatively influenced by litter, organo-mineral, fibric and humic substrates, together with zero slopes. In the wet-cold region (Figure 4.2b), seedlings growth was favoured by an increase in substrate temperature. Increased seedling growth also has been associated with the presence of litter and organo-mineral substrates, and sites with poor to imperfect drainage on rocky surface deposits. Seedlings growth was negatively influenced by fibrous substrates, especially at sites with thick surface deposits (thick tills). In the dry-warm region (Figure 4.2c), seedlings growth was favoured by fibrous substrates, but negatively affected by mineral substrates. Also, thick surface deposits, imperfect drainage, and gentle slopes appeared to favour seedlings growth. In the wet-warm region (Figure 4.2d), seedling growth was higher for seedlings that were planted in humic (poorly drained sites) and fibric (well-drained sites) substrates. Sites on thick surface deposits (thick tills), with moderate and extreme slope classes, favoured seedling growth. In addition, organo-mineral substrates, glaciolacustrine surface deposits and shallow slopes negatively affected seedling growth in this region.

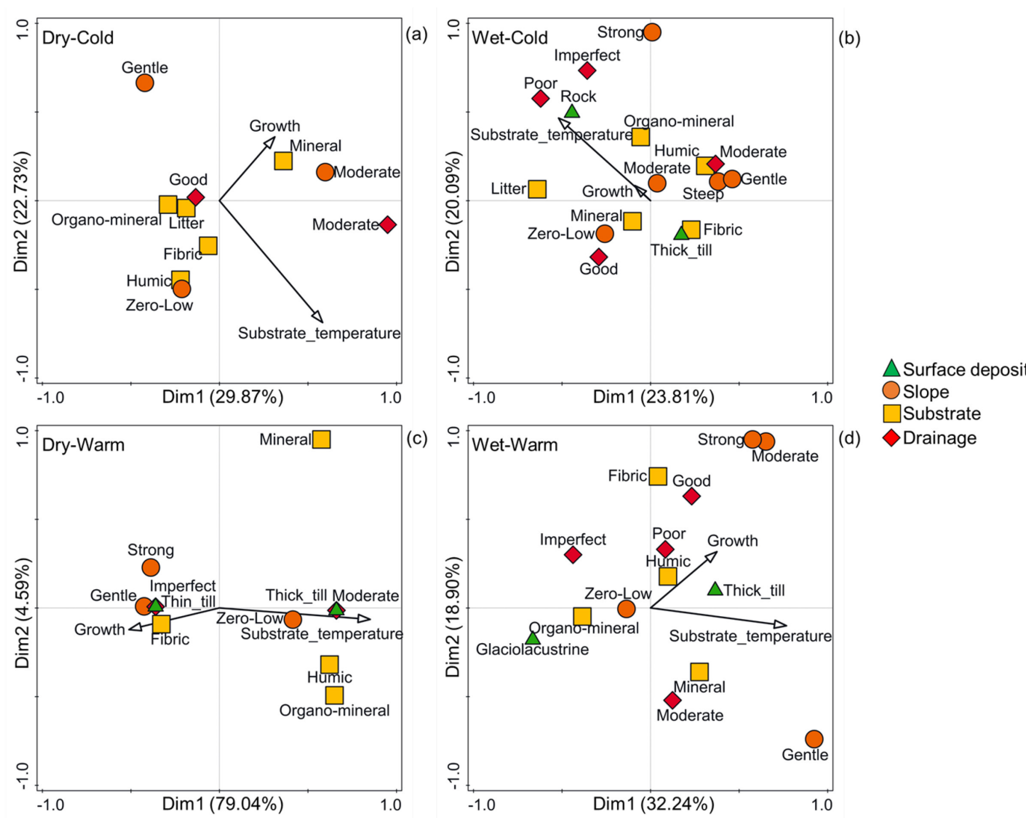

Figure 4.2 Principal component analysis (PCA) summary of black spruce growth responses to local variables at the microsite level and soil variables at the stand level, within four regions that are delineated by annual precipitation and average temperature: (a) dry-cold.; (b) wet-cold; (c) dry-warm; and (d) wet-warm.

4.5.2 Jack pine

The predictive model explained 75 % of variation in the jack pine data (Table 4.2). There was a significant effect of slope (stand level) on seedling growth. Further, significant two- and three-way interactions were observed among environmental variables at microsite-, stand- and regional-scales. Interactions involved substrate type and ground temperature, substrate type and total monthly precipitation, substrate type and surface deposition, and substrate type and drainage. As was the case with black spruce, we encountered no significant effects of relative humidity, humus thickness, and planting position on jack pine seedling growth (Table 4.2).

The representative jack pine plots were located in the western portion of the study area, i.e., the driest areas of the gradient. In the dry-cold region (Figure 4.3a), seedling growth was favoured by humic substrates and sites with thin till and glaciolacustrine surface deposits, which has been characterized by imperfect to moderate drainage. Lower jack pine seedling growth was associated with well-drained sites. Slope classes did not influence jack pine seedling growth in these two regions. In the dry-warm region (Figure 4.3b), jack pine seedling growth was favoured by increased substrate temperature, together with fibrous, litter, humic (sites with till deposits), and organo-mineral substrates. In addition, seedling growth was negatively affected by mineral-type substrates, particularly on sites with thin surface deposits (thin tills) and rapid drainage.

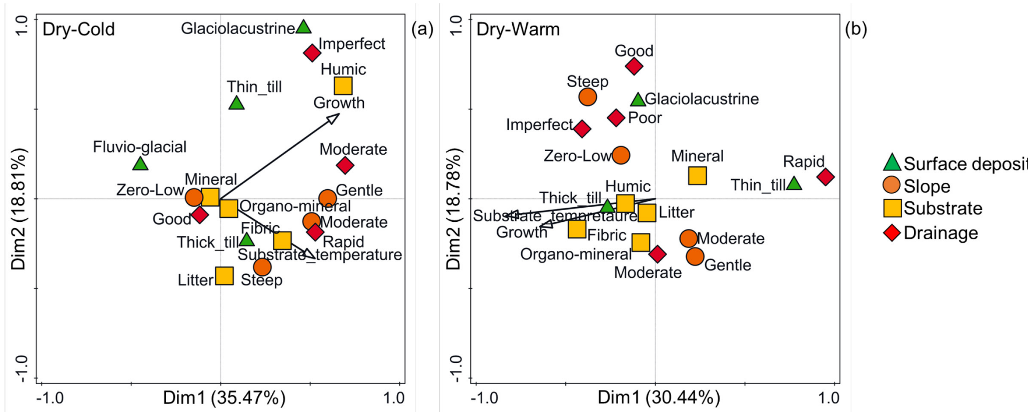

Figure 4.3 Principal component analysis (PCA) summary of jack pine growth responses to local variables at the microsite level and soil variables at the stand level, within four regions that are delineated by annual precipitation and average temperature: (a) dry-cold; and (b) dry-warm.

4.6 Discussion

We found that growth responses of black spruce and jack pine seedlings were closely associated with regional climate variables (temperature, precipitation), which allows better understanding of both stand scale soil conditions effects (surface deposit types, drainage, slope) and local conditions effects at the microsite scale (types of establishment substrate, soil temperature) (Table 4.2). These responses are consistent with several previous studies (Hamilton et Krause, 1985; Herr et Duchesne, 1995; Walker et Johnstone, 2014).

4.6.1 Black spruce

In the boreal forest, black spruce can establish on many types of surface deposits, with a preference for deep forest soils and deposits (e.g., thick tills) (Hamel et al., 2004) due to high nutrient availability (Steele et al., 1997; Strong et Roi, 1983). Nevertheless, growth of black spruce is sensitive to water availability in surface deposits and the overlaying soil. Indeed, the species is adversely affected by extreme water levels in the soil, including those causing water stress (Barber et al., 2000; D'Arrigo et al., 2008) or chronic flooding conditions (Gower et al., 1996; Grossnickle, 2000; Prescott et al., 2000). Thus, moderately to well-drained sites are to be preferred for reforestation activities to increase the success of black spruce establishment (Hamel et al., 2004). At the microsite scale, reforestation on north-facing slopes should also be preferred, given that these locations are characterized by relatively favourable moisture conditions for seedling establishment (Henneb et al., 2019a; Viereck et al., 1983).

In the dry regions (Figure 4.2a, 4.2c) of our study area, regardless of whether they are warm or cold, access to water is a limiting factor for conifer growth, especially during the establishment and juvenile stages (Thiffault et al., 2003). Water availability in establishment substrates substantially influences seedling growth during these period (Boivin et al., 2004; Bruand etTessier, 2000). Organic and mineral substrates offer the best conditions for seedling growth, under conditions of both excess moisture (e.g., paludified sites) and moisture deficiency (e.g., clay substrates are characterized by their high moisture retention capacity, even during dry periods) (Boivin et al., 2004; Bruand and Tessier, 2000; Henneb et al., 2019a, b). In wet-cold regions (Figure 4.2b), substrate temperature is considered an important factor limiting seedling growth (Körner, 2003; Rossi et al., 2008), particularly when decomposition processes are slowed by low temperatures (Pregitzer et al., 2000).

The growth of black spruce seedlings is positively related to increasing temperature (Kabrick et al., 2005; Löf et Birkedal, 2009; Londo et Mroz, 2001), but only up to a certain limit above which physiological processes are negatively affected (Dang et Cheng, 2004; Way et Sage, 2008). In wet-cold regions, organo-mineral substrates are the best substrates for establishing seedlings (Prévost et Dumais, 2003; Sutherland et Foreman, 2000, 1995). When an optimal balance is attained between mineral and organic fractions, organo-mineral substrates are good thermal insulators (soil temperature conservation) (Satoh, 1984) and are characterized by high moisture retention and natural drainage in the case of excess water (Moskal et al., 2001). In addition, organo-mineral substrates provide seedlings with direct access to nutrients, thereby stimulating expansion of initial roots and the appearance of adventitious roots (Anderson et Paul, 1984; DesRochers et Gagnon, 1997; Krause et Morin, 2005; Prescott et al., 2000).

In the wet-warm regions (Figure 4.2d), seedling growth was favoured by fibrous and humic organic substrates, yet constrained on mineral and organo-mineral substrates. Excess water naturally drains from organic substrates, owing to their porous texture, thereby reducing the risk of anaerobiosis when compared to fine-textured mineral substrates (e.g., predominantly clay). The latter pose high risks for root asphyxiation due to surface water stagnation and reduced gas exchange, particularly in depressions (Bergsten et al., 2001; de Chantal et al., 2003; Lavoie et al., 2007, 2005). In addition, elevated temperature and moisture conditions can contribute to increased microbial activity in organic substrates. Increased microbial activity, in turn, increases the availability of nutrients, especially N, which has a positive effect on seedling growth (Li et al., 2012; Van Cleve et al., 1983).

4.6.2 Pin gris

Jack pine is less sensitive to temperature variation than black spruce (Dang et Cheng, 2004; Peng et Dang, 2003; Zhang et Dang, 2007). While moderate temperature increases favour the growth of jack pine seedlings, higher temperatures lead to slower growth (Dang et Cheng, 2004; Peng et Dang, 2003; Reich et al., 2015; Zhang et Dang, 2007). Several studies have confirmed the influence of precipitation regime and soil conditions on jack pine establishment in the boreal forest (Bell et al., 2000; Day et al., 2005; Strimbu et al., 2017). Jack pine generally performs better than black spruce in dry conditions (Blake et Li, 2003; Boucher et al., 2019; Hébert et al., 2006; Sirois, 1993). Well-drained surface deposits, including till, fluvio-glacial expanses, and lacustrine and sandy deposits, promote jack pine growth (Béland et Bergeron, 1996; Chesick et Bergmann, 1991; Little et Garrett, 1990; Rudolph et Laidly, 1990). Further, jack pine performance is better on dry, well-drained mineral and organic substrates, particularly sand, silty sand and humus, compared to poorly drained wet substrates (Béland et al., 1999; Chesick et Bergmann, 1991; Rudolph et Laidly, 1990). In the dry regions of our study area (Figure 4.3a, 4.3b), we found that jack pine seedling growth was favoured by organic (fibric, humic, and litter) and organo-mineral substrates. Organic microsites are characterized by high porosity, which permits very rapid drainage of water, thereby providing a relatively dry and favourable environment for seedling growth (Boiffin et Munson, 2013; Chrosciewicz, 1990, 1988; Little et Garrett, 1990). In well-drained dry environments, organo-mineral substrates allow natural moisture drainage and thus promote the establishment of jack pine seedlings (Kenkel, 1986).

4.7 Conclusion and implications for forest management

Future climate change will directly affect tree growing conditions in the boreal forest zone (Amiro et al., 2001). In eastern Canada, tree species will be particularly vulnerable to temperature increases (Boucher et al., 2019). Our analyses allowed us to identify regional, stand and microsite variables that affect the growth of recently planted black spruce and jack pine seedlings. Our results thus make it possible to consider how plantation silviculture will have to be adapted to promote the success of seedling establishment in the face of climate change.

We demonstrated that black spruce and jack pine establishment in boreal Quebec depends upon regional climatic conditions. In turn, regional climate interacts with soil conditions at the stand level and local conditions at the microsite level. In the dry regions of our study area, black spruce seedling growth was favoured on microsites that were dominated by fibric and mineral substrate on moderate slopes. In the wet-cold regions under study, growth of black spruce seedlings was favoured by the increase in substrate temperature, the presence of microsites that are dominated by a litter and organo-mineral substrate, and on rocky surface deposits with poor drainage. In the wet-warm regions of our study, the growth of black spruce seedlings was favoured by microsites that are dominated by humic substrate on poorly drained sites and fibric on well-drained sites. Sites with thick till deposits, with moderate and extreme slope classes, appeared to favour the growth of black spruce seedlings. Growth of jack pine seedlings in the dry regions of our study area (the only sites that were sampled for this species) was favoured by microsites that were dominated by organic and organo-mineral substrates.

Some regions had fewer plots than others did, as distribution of the plots was dependent on operational management planning and reforestation activities during the corresponding years, combined with constraints related to plot establishment in remote areas. Our study is ongoing, with new plots being added in new plantations across the entire study area to better balance the design. Further measurements and analyses that will include a larger set of plots will thus allow confirming the robustness of our first conclusions.

4.8 Acknowledgements

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CHAPITRE V

CONCLUSION GÉNÉRALE

5.1 Remise en production des sites paludifiés

5.1.1 Efficacité des traitements sylvicoles

Les résultats du chapitre II ont confirmé que l'utilisation des perturbations mécaniques sur le sol paludifié par la préparation mécanique du sol (PMS) permet la remise en production des forêts de l'Est canadien (Prévost et Dumais, 2003; Thiffault et al., 2004a, b; Lavoie et al., 2005), du moins à court terme. La herse forestière a présenté les meilleures croissances dans les sites faiblement à modérément paludifés (ECO $\leq$ 40 cm). En revanche, le scarificateur a mieux performé dans les sites fortement paludifés (ECO > 40 cm). Pour assurer un établissement réussi des plants dans ces sites, il est important d'identifier et délimiter les sites faiblement-modérément paludifés des sites fortement paludifés. Ceci permettra d'appliquer les traitements de PMS adéquats et d'exposer davantage de microsites propices à l'établissement des plants. La PMS permet par ailleurs une maîtrise efficace du recouvrement des espèces éricacées à court terme (chapitre II). Cependant, dans les peuplements de pins et d'épinettes coupés de l'ouest du Québec, l'étude de Thiffault et al. (2012) a montré que les microsites créés par le scarifiage mécanique ont été rapidement réenvahis par des éricacées (*Kalmia angustifolia)*. Également, Bock et Van Rees (2002) ont trouvé que plus le traitement de PMS était sévère, plus la présence de la végétation concurrente était accentuée après le traitement (à court terme). La présence de la végétation concurrente a augmenté en réponse à la disponibilité des éléments nutritifs dans le sol après traitement. L'augmentation de présence de la végétation concurrente était dans cet ordre : forêt non coupée, récolte sans PMS, broyeur (Meri), PMS avec cultivateur (Grizz R-ex), déblaiement d'hiver et utilisation du broyeur (Meri), déblaiement avec le cultivateur (Grizz R-ex), déblaiement d'hiver seul. Ce constat a été partagé par Haeussler et al. (1999), qui ont enregistré une augmentation de 22% en regard du recouvrement d'espèces envahissantes dans les traitements sévères de PMS dans des sites en forêt boréale. De ce fait, il est très recommandé de planter immédiatement après une perturbation par la préparation mécanique du sol pour assurer un établissement réussi des plants (Thiffault et al., 2012).

Sur le long terme, l'effet de la PMS sur la productivité forestière en forêt boréale, reste très mitigé et semble dépendant de plusieurs facteurs tels que la sévérité de la perturbation et le choix de la technique de PMS. En effet, Hébert et al. (2014) ont constaté que le scarifiage léger du sol (peu profond) a maintenu une croissance et une survie optimale des plants d'épinette noire par rapport aux parterres non scarifiés, à court et moyen termes. Tandis qu'à moyen terme (après 10 ans), le scarifiage léger ne semblait pas maintenir cet effet, car les taux de survie étaient trop faibles. Les quelques plants qui ont survécu n'ont pas présenté de différences significatives en regard de leur croissance comparés à ceux des parterres non scarifiés. Ces auteurs recommandent d'utiliser une PMS sévère pour la remise en production des sites boréaux improductifs. Également, dans le même type de sites, Wallertz et Malmqvist (2013) proposent des perturbations plus sévères (que le scarifiage léger) en profondeur telles que la PMS par inversion ou PMS par monticules pour maintenir l'effet positif de la PMS sur la productivité des sites forestiers à long terme. Le même constat a été confirmé par Thiffault et al. (2004b), Löf et al. (2012) et Thiffault et Roy (2011). Les auteurs ont confirmé l'effet positif à long terme de la PMS sévère sur la structure du sol et la disponibilité des éléments nutritifs dans le sol, qui permettent d'améliorer à leur tour la survie et la croissance des plants dans les sites boréaux. Ces auteurs considèrent que la PMS par scarifiage est une approche efficace dans différents environnements et contextes sylvicoles, notamment dans le maintien de la croissance. Par ailleurs, le choix d'une technique de PMS appropriée aux conditions du site pourrait influencer positivement la survie et la croissance des plants dans les sites boréaux reboisés (Gradowski et al., 2008; Van Cleve et al., 1983).

Le réenvahissement des microsites par la végétation concurrente post-perturbation à moyen et long termes demeure à documenter (chapitre II). Haeussler et al. (2004) ont constaté qu'après 15-16 ans de suivi des communautés végétales de la forêt boréale mixte, l'intensité et le type de perturbations peuvent influencer la croissance de l'espèce à régénérer et les interactions compétitives avec la végétation du sous-bois. Les mêmes auteurs ont trouvé que la PMS légère (perturbation surfacique) ne semble avoir aucun effet significatif sur le recouvrement de la végétation concurrente sur des sites humides comparée aux traitements sévères de scarifiage (plusieurs passages) et modérés par monticules. Plusieurs études recommandent l'utilisation de perturbations sévères telles que le scarifiage pour l'élimination (déchiquetage, enfouissement, déracinement) de la végétation concurrentee avant le reboisement (Haeussler et al., 2004; Jobidon et al., 2003; Thiffault et al., 2003). Néanmoins, le risque du retour de la végétation concurrente est assez probable suite aux perturbations sévères du sol forestier. Face à cette contrainte, en Scandinavie, on recommande d'utiliser la PMS par monticules (perturbation sévère), car cette technique permet de drainer l'excès d'eau et de minimiser la compétition végétale (Löf et al., 2012).

5.1.2 Choix des substrats (microsites) d'établissement pour la remise en production des sites paludifés

Le choix de substrat approprié pour l'établissement de la régénération artificielle est primordial lors de la mise en terre des plants, puisque le substrat est censé améliorer la chance de survie et la croissance initiale des plants. L'utilisation de substrats inappropriés aux espèces mises en terre peut diminuer la productivité en affectant la croissance, ou entrainer une mortalité des plants lors du reboisement (Spittlehouse et Stathers, 1990). Dans les sites paludifiés, la disponibilité des substrats d'établissement dépend de l'efficacité de la technique de PMS appliquée et de l'épaisseur de la couche organique se référant aux deux classes de paludification (faible à modérée, forte) (chapitre II). Par ailleurs, le choix des substrats d'établissement dépend du statut hydrique du site (chapitre II et III). Dans les sites présentant un accès limité en eau, nous avons constaté que la disponibilité de l'eau dans les substrats d'établissement est le facteur limitant de la croissance des jeunes plants (chapitre II). Dans ce cas, il est nécessaire de privilégier les substrats argileux et mélangés (organo-argileux et argileux-humiques) lors des opérations de reboisement afin d'assurer une disponibilité suffisante en eau (chapitre II). En effet, l'accès à l'eau est plus avorisé par les substrats argileux exposés en surface (argile perturbée), caractérisés par leur grande capacité de rétention hydrique (Boivin et al., 2004; Bruand et Tessier, 2000), que dans les substrats organiques. Cependant, la mise en terre sur un substrat argileux nu, non perturbé, n'est pas recommandée (chapitre II). Ceci entraîne un risque d'asphyxie élevé des racines causée par la stagnation de l'eau en surface, surtout dans les dépressions (Bergsten et al., 2001; de Chantal et al., 2003; Lavoie et al., 2007b, 2007a, 2005). Dans les sites présentant un accès illimité en eau, nous avons constaté que la disponibilité des éléments nutritifs dans les substrats s'est manifestée comme le facteur limitant de la croissance des plants. Dans ce cas, selon nos résultats (chapitre III), il a été recommandé de privilégier les substrats organiques de type mésique (chapitre III). Il a été démontré que les substrats organiques moyennement décomposés étaient riches en éléments nutritifs (N, P, K) (Lavoie et al., 2007a; Lafleur et al., 2010a) (voir Annexe A) et favorisent la croissance des plants dans les sites paludifiés, surtout en présence de températures du sol favorables (18-25 °C) à l'établissement des plants (Lahti et al., 2005; Lopushinsky et Max, 1990).

Afin de garantir le succès d'établissement des plants à court terme, nous recommandons l'utilisation de techniques de PMS aptes à exposer davantage de substrats argileux et organiques-mésiques sur les sites présentant un accès limité et illimité en eau, respectivement. Ces recommandations permettront d'orienter les sylviculteurs dans la mise en place d'actions efficaces pour la remise en production des forêts paludifiées.

5.1.3 Impacts des facteurs environnementaux multi-échelles sur le substrat d'établissement et la croissance initiale des plants

Nous avons constaté que les réponses de croissance initiale des plants (épinette noire et de pin gris) étaient étroitement associées aux variables climatiques régionales (température, précipitations) et à leur interaction avec les conditions édaphiques à l'échelle du peuplement (types de dépôt de surface, drainage, pente) et les conditions locales à l'échelle du microsites (types de substrat d'établissement, température du sol) (Chapitre IV).

En forêt boréale, l'épinette noire peut s'établir sur tous les types de dépôts de surface. Cette dernière présente une croissance maximale sur les dépôts et sols forestiers profonds (p. ex. les dépôts de till épais) (Hamel et al., 2004) en raison de la disponibilité élevée des éléments nutritifs (Strong et La Roi, 1983; Steele et al., 1997).

Néanmoins, la croissance des plants d'épinette noire est sensible à la teneur en eau dans le sol. En effet, l'établissement des plants d'épinette noire est négativement influencé par le manque d'eau dans le sol (causant des stress hydriques) (Barber et al., 2000; D'Arrigo et al., 2008) ou les conditions d'inondations chroniques (Gower et al., 1996; Grossnickle, 2000; Prescott et al., 2000). Ainsi, les sites modérément à bien drainés seraient à privilégier pour le reboisement afin d'augmenter le succès d'établissement de l'épinette noire (Hamel et al., 2004). À l'échelle du microsite, le reboisement sur les pentes orientées vers les versants nord, caractérisés par des conditions d'humidité relativement favorables à l'établissement des plants (Henneb et al., 2019a; Viereck et al., 1983), seraient également à privilégier.

Dans les régions sèches, la croissance des plants d'épinette noire était favorisée par les substrats d'établissement de type fibrique et minéral sur les pentes modérées. Dans ces régions, l'accès à l'eau est un facteur limitant pour la croissance des plants, surtout durant le stade de croissance juvénile de ces derniers (Thiffault et al. 2003). La disponibilité en eau dans les substrats d'établissement influence significativement la croissance des plants durant cette période (Boivin et al., 2004; Bruand et Tessier, 2000). Les substrats organiques et minéraux favorisent l'établissement et la croissance des plants à la fois en conditions d'excès d'eau (p. ex. sites paludifiés) et de manque d'eau (p. ex. les substrats argileux sont caractérisés par leur grande capacité de rétention en eau, même en période sèche), respectivement (Boivin et al., 2004; Bruand et Tessier, 2000; Henneb et al., 2019a, b).

Dans les régions humides et froides, la croissance des plants d'épinette noire était favorisée par l'augmentation de la température du substrat, la présence de substrats d'établissement de type organo-minéral, et les dépôts de surface rocheux. Avec une texture équilibrée en fraction minérale et organique, les substrats organo-minéraux sont thermiquement isolants (Satoh, 2012) et caractérisés par une bonne rétention de l'eau et un drainage naturel en cas d'excès d'eau (Moskal et al., 2001). De plus, les substrats organo-minéraux permettent un accès privilégié aux éléments nutritifs stimulant ainsi l'expansion des racines initiales et l'apparition de racines adventives (Anderson et Paul, 1984; DesRochers et Gagnon, 1997; Krause et Morin, 2005; Prescott et al., 2000).

Dans les régions humides et chaudes, la croissance des plants d'épinette noire était favorisée par les substrats d'établissement de type humique (exposés dans les sites faiblement drainés) et fibrique (exposés dans les sites bien drainés). Les sites à dépôts de surface épais (de type tills épais), avec des classes de pentes modérées et extrêmes semblent favoriser la croissance des plants d'épinette noire à l'échelle du peuplement. La texture poreuse des substrats organiques permet de drainer naturellement l'excès d'eau et ainsi réduire le risque de conditions anaérobiques, lorsque comparée aux substrats minéraux à texture fine (p. ex. à dominance d'argile), lesquels entrainent un risque d'asphyxie élevé des racines en raison de la stagnation de l'eau en surface, surtout dans les dépressions (Bergsten et al., 2001; de Chantal et al., 2003; Lavoie et al., 2007, 2005). De plus, les conditions élevées d'humidité et de température contribuent à l'augmentation de l'activité microbienne dans les substrats organiques; ceci augmente à son tour la disponibilité des éléments nutritifs, surtout l'azote, ce qui a un effet positif sur la croissance des plants (Li et al., 2012; Van Cleve et al. 1983).

Les plants de pin gris sont moins sensibles aux variations de température que les plants d'épinette noire (Peng et Dang, 2003; Dang et Cheng, 2004; Zhang et Dang, 2007). Les augmentations modérées de température favorisent la croissance des plants de pin gris, mais les températures plus élevées entraînent une croissance ralentie de ces plants (Peng et Dang, 2003; Dang et Cheng, 2004; Zhang et Dang, 2007; Reich et al., 2015).

Plusieurs études ont confirmé l'influence du régime de précipitation et les conditions édaphiques du site sur l'établissement du pin gris en forêt boréale (Bell et al., 2000; Day et al., 2005; Strimbu et al., 2017). Généralement, le pin gris performe mieux que l'épinette noire dans des conditions sèches (Blake et Li 2003; Boucher et al. 2019; Hébert et al. 2006; Sirois 1993). Les dépôts de surface présentant un bon drainage, notamment les tills, les épandages fluvial-glaciaires, les dépôts lacustres et sableux favorisent la croissance du pin gris (Béland et Bergeron, 1996; Chesick et Bergmann, 1991; Little et Garrett, 1990; Rudolph et Laidly, 1990). Le suivi de croissance des plants de pin gris s'est effectué exclusivement dans les régions sèches de l'Est canadien (chapitre IV). La croissance des plants de pin gris était favorisée par les substrats organiques (fibrique, humique et litière) et organo-minéraux. Les substrats organiques sont caractérisés par une porosité élevée, permettant un drainage rapide de l'eau, offrant ainsi un milieu assez sec et favorable pour la croissance des plants (Boiffin et Munson, 2013; Chrosciewicz, 1990, 1988; Littleet Garrett, 1990). Dans les milieux secs bien drainés, les substrats organo-minéraux permettent un drainage relativement rapide de l'eau favorisant ainsi l'établissement des plants de pins gris (Kenkel, 1986).

Néanmoins, l'étude réalisée dans le chapitre IV comporte certaines limites d'ordre expérimental. En effet, certaines régions comptaient moins de placettes d'inventaires que d'autres, car la distribution des placettes dépendait de la planification opérationnelle et des activités de reboisement au cours des années correspondantes, combinées aux contraintes liées à l'établissement des placettes dans les zones reculées. Un suivi des plants à moyen et long termes est prévu suite aux résultats de cette étude (chapitre IV). De nouvelles placettes seront ajoutées dans de nouveaux parterres reboisés sur toute la zone d'étude pour mieux équilibrer le design expérimental. De nouvelles mesures et analyses qui incluront un nombre important de placettes permettront ainsi de confirmer la robustesse de nos premières conclusions.

5.1.4 Implications pour l'aménagement et recommandations

Ce travail a permis de mieux comprendre les conditions d'établissement de la régénération en forêt paludifiée. La préparation mécanique du sol (PMS) est un traitement sylvicole que les sylviculteurs pourraient considérer dans l'aménagement des sites paludifiés. La PMS permet la réduction de l'épaisseur de la couche organique (ÉCO) accumulée (Henneb et al., 2015). Également, la PMS semble favoriser la création de microsites et de substrats propices à la régénération artificielle des sites paludifiés (chapitres II, III et IV). Le choix des microsites et des substrats propices à l'établissement lors des opérations de reboisement est indispensable (chapitre III et IV) pour garantir une meilleure croissance et survie des plants dans les sites paludifiés. Suite aux résultats du chapitre II et III, pour un aménagement efficace des sites paludifiés avant une opération de reboisement, nous recommandons d'appliquer les actions suivantes :

- À l'échelle du peuplement, il est essentiel de délimiter les zones faiblement-modérément paludifées des zones fortement paludifées.
- Avant une opération de reboisement, il est nécessaire d'appliquer des perturbations (issues des traitements de PMS) adéquates aux niveaux de paludification présents dans le site, notamment des perturbations sévères (p. ex. scarifiage) dans les sites fortement paludifiés et des perturbations intermédiaires (p. ex. herse forestière) dans les sites faiblement-modérément paludifés. Ceci permettrait la réduction de l'épaisseur de la couche organique (ÉCO) accumulée et favoriser l'exposition des microsites propices.

- Lors des opérations de reboisement, pour garantir une meilleure croissance et un meilleur taux de survie des plants, il est nécessaire de bien choisir le microsite d'établissement. Le choix des microsites d'établissement dépend du statut hydrique du site paludifié aménagé. Dans les sites présentant un accès limité en eau, il est nécessaire de privilégier les substrats argileux et organo-argileux afin d'assurer une disponibilité suffisante en eau (éviter le stress hydrique) et en éléments nutritifs. Dans les sites présentant un accès illimité en eau, il est recommandé de privilégier les microsites organiques de type mésique lors des opérations de reboisement, vu leur richesse en éléments nutritifs.

Suite aux résultats du chapitre IV, les recommandations sylvicoles ont été synthétisées dans le Tableau 5.1 sous forme d'un guide pratique d'aménagement des sites reboisés dans les différentes régions bioclimatiques de l'Est canadien, selon leurs caractéristiques édaphiques à l'échelle du peuplement et locales (types de substrats d'établissement ou de mise en terre) à l'échelle du microsite. Ce guide pratique vise à proposer les meilleures conditions d'établissements des plants d'épinette noire et de pin gris le long du gradient climatique dans l'Est canadien.

5.2 Potentiel sylvico-économique des sites paludifés et perspectives de recherche

Les forêts dominées par l'épinette noire occupent une grande partie du biome boréal canadien du nord et sont considérées comme une importante source de bois pour les entreprises forestières (Koubaa et al., 2007; Robitaille et Saucier, 1998). Cependant, ces forêts boréales nordiques, notamment les pessières à mousses, sont caractérisées par de vastes zones paludifées avec une faible productivité forestière (Harper et al., 2003; Munson et Timmer, 1989). La productivité forestière se réfère à la quantité de bois qu'un site est capable de produire dans une période de temps donnée (Skovsgaard and Vanclay, 2008) et dépend principalement d'une combinaison de variables climatiques et environnementales (Laamrani et al., 2014a, b, c). Des études antérieures ont déjà estimé le volume de bois marchand dans les sites paludifiés occupés par l'épinette noire, de 262 m^3/ha (IQS (50 ans) = 17.1 m) et 26 m^3/ha (IQS (50 ans) = 9.8 m) dans les sites faiblement-modérément paludifiés (ECO $\leq$ 40 cm) et fortement paludifiés respectivement (ECO> 40 cm) (Nappi, 2013; Laamrani et al., 2014a). De ce fait, la remise en production des sites paludifiés est nécessaire pour augmenter la productivité des peuplements paludifiés et les volumes de bois marchants. Les résultats du chapitre II ont prouvé l'efficacité de la PMS sévère (via le scarificateur) dans la remise en production des zones fortement paludifiées à faible productivité (Henneb et al., 2015). En effet, les travaux menés par le MFFP confirment la nécessité d'appliquer un scénario sylvicole intensif (coupe totale + scarifiage + reboisement) dans les sites fortement paludifiés (Nappi, 2013). Le scénario intensif s'avère plus adapté à ces conditions, puisqu'il assure un rendement supérieur à un scénario sylvicole extensif de base (CPRS seulement). Néanmoins, on recommande d'orienter les interventions sylvicoles vers les peuplements faiblement-modérément paludifiés (Simard et al., 2009; Nappi, 2013), puisque dans les sites fortement paludifiés, la remise en production pourrait être difficile, coûteuse et moins rentable (Nappi, 2013).

Bien qu'elle soit très peu documentée, la rentabilité économique de la remise en production des sites faiblement-modérément paludifiés est aussi problématique (Stöd et al., 2006). En effet, la récolte d'un peuplement paludifé en place (non aménagé) reste un meilleur investissement en regard de la rentabilité économique qu'une remise en production de ce dernier (Farrell et Boyle, 1990). Ces mêmes auteurs ont noté que le retour sur les investissements sylvicoles des peuplements paludifiés reste très marginal et recommandent d'exploiter uniquement leur potentiel écologique, notamment pour leur valeur de séquestration de carbone. Néanmoins, il serait nécessaire d'améliorer nos connaissances sur la rentabilité économique de la remise en production des sites paludifiés; ceci permettra d'orienter efficacement l'aménagement forestier de ces sites.

Tableau 5.1 Recommandations sylvicoles visant à favoriser l'établissement des plants d'épinette noire et du pin gris. Les recommandations sont présentées sous forme d'un guide pratique d'aménagement des sites reboisés selon les régions bioclimatiques incluant l'influence des variables édaphiques à l'échelle du peuplement et locales (types de substrats) à l'échelle du microsite. Les recommandations sont issues des résultats des ACPs réalisées dans le Chapitre IV.

Espèce plantée	Régions bioclimatiques							
	Sèches-Froides		Humides-Froides		Sèches-Chaudes		Humides-Chaudes	
	Échelle du peuplement	Échelle du microsite	Échelle du peuplement	Échelle du microsite	Échelle du peuplement	Échelle du microsite	Échelle du peuplement	Échelle du microsite
Épinette noire	- Dépôts de surface : Pas d'effet - Drainage : éviter le drainage rapide - Pente : modérée	Substrats minéraux	- Dépôts de surface : rocheux - Drainage : mauvais à imparfait - Pente : absence d'effet	Substrats organo-minéraux et litière	- Dépôts de surface : épais - Drainage : imparfait - Pente : douce	Substrats organiques	- Dépôts de surface : épais (p. ex. tills épais 1A) - Drainage : bon - Pente : modérée à forte	Substrats organiques
Pin gris	- Dépôts de surface : épais et glacio-lacustres (4GA) - Drainage : imparfait à modéré - Pente : absence d'effet	Substrats organiques (humiques)	-		- Dépôts de surface : épais (p. ex. tills épais 1A) - Drainage : éviter le drainage rapide - Pente : absence d'effet	Substrats organiques et organo-minéraux	-	

5.3 Changements climatiques et perspectives de recherche

Les changements climatiques globaux devraient influencer les écosystèmes forestiers, notamment l'écosystème boréal, à travers des mécanismes complexes, y compris des changements dans la quantité de précipitations, les fréquences de retour du feu, dans la température des sols et la minéralisation de l'azote (Lavoie et al., 2005; Lupi et al., 2013). L'augmentation de la température peut favoriser la croissance des arbres en raison d'une période de photosynthèse plus longue, d'une période de croissance quotidienne et saisonnière plus longue et d'une disponibilité accrue des éléments nutritifs du sol (Saxe et al., 2001). Dans les régions chaudes et sèches de la forêt boréale, les précipitations ne seront pas en mesure de compenser l'augmentation de l'évaporation induite par l'augmentation de la température, entraînant une baisse de l'humidité du sol ainsi que des périodes de stress hydrique prolongées, notamment durant la saison de croissance (Way et Sage, 2008). Dans les régions froides, la température est considérée comme le facteur limitant de la croissance (Körner, 2003; Rossi et al., 2008), et un réchauffement modéré conduit généralement à une augmentation de croissance et de survie des plants, principalement par des effets directs sur la photosynthèse (Dang et Cheng, 2004; Wilmking et al., 2004). Le réchauffement climatique prévu pourrait augmenter la durée de la saison de croissance dans les régions froides, ce qui pourrait à son tour favoriser la croissance des plants (Rossi et al., 2011). De plus, les températures élevées du sol entraînent une décomposition accrue de la matière organique et une minéralisation des éléments nutritifs, avec des effets positifs potentiels sur la croissance des plants (Viereck, 1983). Cependant, les effets bénéfiques du réchauffement climatique sur la croissance en zone boréale peuvent être de courte durée, compte tenu des baisses concomitantes de l'humidité du sol (D'Orangeville et al., 2018). D'une part, les températures élevées peuvent induire un stress hydrique estival qui atténue ou empêche les augmentations de croissance (Lloyd et Fastie, 2002; Wilmking et al., 2004). En revanche, une augmentation des températures hivernales pourrait avoir des effets différents de ceux de l'augmentation estivale (Vitasse et al., 2018). Par exemple, au Québec, des températures hivernales plus élevées et une durée de couverture neigeuse raccourcie ont entraîné une diminution de la survie des semis grâce à une sortie précoce de la dormance, ce qui a exposé les plants aux gels dus aux températures glaciales (Renard et al., 2016).

Dans la forêt boréale de l’Est canadien, selon les projections futures des modèles (Boucher et al., 2019), l’épinette noire semble être particulièrement vulnérable aux conditions climatiques futures. La température moyenne annuelle devrait être supérieure à l'enveloppe climatique de l'épinette noire, avec de fortes augmentations projetées de la fréquence des feux et de la sécheresse. Par ailleurs, le pin gris devrait être vulnérable aux augmentations de température. Néanmoins, les espèces d'arbres peuvent éventuellement s'adapter à des conditions plus sèches et plus chaudes. En effet, les arbres des latitudes nordiques présentent des tolérances à la température qui diffèrent de celles des génotypes spécifiques du sud (Thomson et al., 2009; Pedlar et McKenney, 2017). On peut donc se demander si les changements climatiques laisseront aux arbres suffisamment de temps pour s'adapter ou s'acclimater à de nouvelles conditions (Boucher et al., 2019).

Dans les forêts boréales paludifiées, une augmentation de la température devrait augmenter l'évapotranspiration et l'évaporation et diminuera donc le niveau de la nappe phréatique. En conséquence, cela peut entraîner une augmentation de la décomposition de la matière organique et une réduction de la croissance des sphaignes qui sont à l’origine du phénomène de la paludification (Lavoie et al., 2005). La décomposition de la matière organique entraine une augmentation de la disponibilité de l’azote pour la régénération et les arbres en place (Kirschbaum, 1995;

MacDonald et al., 1995; Verburg, 2005). Ceci aura des incidences sur la croissance des plants, la productivité primaire des forêts (augmentation de la productivité) et sur l'équilibre entre l'azote stocké dans les sols et la biomasse stockée dans les végétaux (Kirschbaum, 2000; Price et al., 1999).

La régénération (artificielle et naturelle) en forêt boréale sera probablement impactée par les changements climatiques, notamment par les conditions chaudes et sèches, au moins d'ici la fin de ce siècle (Boucher et al., 2019). De plus, les changements climatiques pourraient avoir des répercussions importantes sur l'approvisionnement en bois. Les forêts dominées par les conifères peuvent devenir moins productives qu'elles ne le sont actuellement, et l'approvisionnement en bois provenant des forêts feuillues pourrait également diminuer (Boucher et al., 2019). En effet, les recherches futures devraient identifier les zones où les espèces commerciales pourraient être les plus vulnérables aux futures conditions climatiques, où les peuplements forestiers pourraient être les plus à risque d'échec de régénération et où les efforts de surveillance de la régénération devraient être prioritaires. Également, les recherches futures devraient améliorer notre compréhension de l'effet des changements climatiques sur la dynamique des éléments nutritifs et sur le stockage de l'azote dans les sols forestiers boréaux et paludifiés, car ce dernier est considéré comme le facteur limitant de la croissance des arbres en forêt boréale. Ceci nous permettra de mettre en place de nouvelles stratégies d'aménagements forestiers qui visent à adapter nos pratiques sylvicoles aux changements climatiques.

ANNEXE A

Physico-chemical characteristics of organic and clay substrates used in the experiment.

Substrates	Decomposition degree	pH	CEC (meq/ 100g)	N (%)	P (%)	K (%)	Mg (%)	Ca (%)
Argile[a]	-	5.7	25.9	0.09	0.0005	0.008	0.028	0.157
Fibrique[b]	Low	3.2-4	124	0.5-1	0.01	0.008	0.1	0.09
Mésique[b]	Moderate	4-7	116	0.8-1.1	0.35	0.57	0.44	0.24
Humique[b]	High	3.5-8	160	0.9-1.9	0.8	1.25	0.49	0.6

a: sampled clay (60 samples) on the prepared site (Clay-Belt).
b: (Soil Classification Working Group 1998).

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