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CROISSANCE ET PROPRIÉTÉS DU BOIS DE LA TIGE ET DES RACINES DE
L'ÉPINETTE NOIRE ET DU SAPIN BAUMIER APRÈS UNE COUPE PARTIELLE EN
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LISTE DES ABRÉVIATIONS ET ACRONYMES

CLASS: Careful logging around small merchantable stems

CPPTM: Coupe avec protection des petites tiges marchandes

DBH: Diameter at breast height

DOY: Day of the year

EWD: Earlywood density

LWD: Latewood density

MaxD: Maximum latewood density

MinD: Minimum earlywood density

MOE: Modulus of elasticity

MOR: Modulus of rupture

PAR: Photosynthetically active radiation

PPFD: Photosynthetic photon flux density

RÉSUMÉ

Les coupes partielles sont de plus en plus utilisées au Québec. Elles consistent à prélever une partie seulement des arbres d'un peuplement forestier, ce qui permet de maintenir un certain couvert forestier. Les coupes partielles permettent généralement une augmentation de la croissance des tiges résiduelles et une récolte plus hâtive des secteurs traités (temps de révolution plus court). La croissance plus rapide pourrait toutefois causer des changements indésirables dans les propriétés du bois qui pourraient éventuellement réduire l'aptitude du bois à être utilisé pour un usage précis. Plus précisément, une augmentation de croissance se traduit généralement au niveau du cerne par une augmentation du nombre de cellules de bois initial, mais souvent sans grand changement au niveau du bois final, ce qui résulte en une diminution du pourcentage de bois final et de la masse volumique chez plusieurs espèces.

Toutes les propriétés du bois sont liées de près avec les structures anatomiques des cellules du xylème, de sorte que la quantité et la qualité du bois produit ont toutes deux leur origine dans la région cambiale. Ainsi, tous les facteurs ayant une influence sur l'activité cambiale, comme par exemple les traitements sylvicoles, auront donc également une influence sur la quantité et la qualité du bois qui sera produit par l'arbre. Cependant, bien que les connaissances soient essentielles pour l'utilisation du bois transformé, il existe encore peu d'informations sur les effets des pratiques sylvicoles sur les propriétés du bois de l'épinette noire et du sapin baumier. De plus, l'ouverture du milieu suite à des coupes partielles peut rendre les peuplements forestiers plus susceptibles aux chablis. La stabilité des arbres, qui dépend fortement du développement adéquat du système racinaire, doit être maintenue afin de pouvoir soutenir la croissance améliorée attendue après la coupe partielle. Les racines doivent également être en mesure de puiser et transporter une quantité plus importante d'eau en raison de la transpiration plus élevée après l'ouverture du peuplement. Malgré son importance dans le succès des coupes partielles, le système racinaire des arbres matures reçoit moins beaucoup d'attention que la tige dans les études scientifiques. L'objectif général de la thèse est donc d'évaluer l'effet de différents types de coupes partielles sur la croissance et sur les propriétés du bois produit dans la tige et les racines de l'épinette noire et du sapin baumier. Pour ce faire, trois différents types de coupe partielle ont été étudiés.

Tout d'abord, pour évaluer l'effet d'une coupe partielle sur la xylogénèse, une éclaircie expérimentale a été réalisée à la forêt d'enseignement et de recherche Simoncouche, dans la réserve faunique des Laurentides. Les résultats ont montré

qu'une augmentation du taux de trachéides produites après la coupe partielle était responsable de l'augmentation de croissance observée dans les années après la coupe et non un changement dans le *timing* ou la durée des phases de la xylogénèse. Puisque la saison de croissance n'est pas décalée ou étendue sur une plus longue période de temps, cela laisse supposer qu'une coupe partielle ne place pas les arbres dans une situation de risques accrus de dommages dus aux gels au moment de l'initiation de la croissance ou plus tard en fin saison.

Par la suite, une coupe avec protection des petites tiges marchandes (CPPTM) a été étudiée pour évaluer la réaction des tiges résiduelles après une coupe partielle. Quatre sites répartis entre le Saguenay-Lac-Saint-Jean et la Côte-Nord ont été utilisés. Les tiges résiduelles d'épinette noire et de sapin baumier ont augmenté leur croissance radiale après l'application de la CPPTM. Cette augmentation de croissance n'a toutefois pas entraîné de changement majeur dans les propriétés du bois mesurées chez l'épinette noire. Dans le cas du sapin baumier, des diminutions ont été observées, mais globalement, le bois produit avant la coupe partielle n'est pas significativement différent de celui produit après la coupe. Cela suggère que la CPPTM peut augmenter la croissance des tiges sans trop affecter les propriétés du bois à court terme.

Finalement, un traitement d'éclaircie commerciale a permis de comparer la réaction entre les racines et la tige. Quatre sites répartis dans entre l'Abitibi et la Côte-Nord ont été étudiés. Les résultats ont montré que la masse volumique est plus élevée dans les racines que dans la tige, en particulier dans le bois initial. La majorité du transport d'eau ayant lieu dans cette partie du cerne de croissance, la masse volumique plus élevée rend le réseau hydraulique des racines sécuritaire et confère une protection accrue contre les embolies dues à la cavitation. Cette protection supérieure est nécessaire puisque les racines sont généralement considérées comme étant plus vulnérables à la cavitation que la tige. Les résultats offrent une meilleure compréhension de la fonction des racines chez l'épinette noire et portent à croire que le système racinaire de l'épinette noire est peut-être moins vulnérable à la cavitation que l'on suppose.

En somme, l'étude de la formation du bois, de la croissance et des propriétés du bois dans la tige et les racines de l'épinette noire et du sapin baumier après une coupe partielle apporte de précieuses informations sur la structure du xylème et sur la variation des propriétés du bois dans les arbres, en particulier dans les racines, qui sont souvent négligées. Ces résultats, qui confirment le maintien à court terme des propriétés du bois à un niveau satisfaisant chez les deux espèces, intéresseront certainement les gestionnaires de la forêt.

Mots-clés: *Picea mariana*, *Abies balsamea*, xylogénèse, éclaircie commerciale, CPPTM, coupe partielle expérimentale, croissance radiale, masse volumique du bois, longueur des trachéides, MOE, MOR

CHAPITRE I

INTRODUCTION

INTRODUCTION

1.1 PROBLÉMATIQUE

Dans sa démarche de gestion orientée vers le développement durable, le gouvernement du Québec s'est engagé à protéger ses forêts. Désormais, en plus d'avoir comme objectif la récolte de bois, la régénération des forêts et l'éducation des peuplements, la sylviculture vise également à façonner les peuplements forestiers pour remplir diverses fonctions écologiques et sociales. Les considérations d'aménagement durable des forêts, en particulier l'orientation vers l'aménagement écosystémique, demandent de nouvelles options sylvicoles qui permettront de réaliser ces objectifs.

Il est bien connu que la plupart des écosystèmes forestiers sont fortement influencés par les perturbations naturelles (Attiwill, 1994) et la forêt boréale ne fait pas exception, celle-ci étant affectée périodiquement par des perturbations telles que le feu (Bergeron *et al.*, 2001), les épidémies d'insectes (Morin, 1998) et les chablis (Ruel, 2000). Puisque la forêt boréale est bien adaptée à se régénérer suite à ces perturbations, il devient intéressant de se baser sur les effets de ces perturbations pour aménager les peuplements forestiers de façon à préserver l'intégrité des écosystèmes (Gauthier *et al.*, 2008). À l'échelle du peuplement, on tente donc de respecter ce principe en appliquant des interventions sylvicoles qui peuvent s'apparenter aux perturbations naturelles. Les coupes partielles s'inscrivent dans cette optique (Fenton *et al.*, 2008; Grenon *et al.*, 2010; Fenton *et al.*, 2013).

Les coupes partielles consistent à prélever une partie seulement des arbres d'un peuplement forestier (Côté, 2000), sans seuil minimum de rétention, ce qui permet de maintenir un certain couvert forestier. Ces coupes visent également la récolte partielle d'un peuplement, tout en maintenant de manière éparsée ou regroupée des arbres vivants de différents diamètres, des chicots, des débris ligneux, des espèces de sous-bois et des portions de litière forestière intacte, et ce, pour au moins la durée de vie du prochain peuplement (MRNF, 2008; Doucet *et al.*, 2009). Ces traitements permettent donc, comme le font les perturbations naturelles, de conserver certains éléments (par exemple du bois mort) qui agiront comme legs biologiques dans le futur peuplement.

Des coupes partielles d'éducation, où une partie des compétiteurs sont retirés pour favoriser la croissance des arbres résiduels, sont pratiquées couramment en Scandinavie, en Europe centrale et au Japon depuis plusieurs années déjà (Kimmins, 1997). Les coupes partielles avec rétention de groupes d'arbres ou de bois morts sont quant à elles appliquées aux États-Unis et en Europe depuis les années 1980 (Santaniello *et al.*, 2016). Au Québec, les coupes partielles sont aussi de plus en plus utilisées. En effet, au cours des dernières années, la récolte avec maintien de couvert a représenté en moyenne de 15% à 25% des superficies de récolte en forêt publique (Doucet *et al.*, 2009; MFFP, 2016). Les coupes partielles représentent des interventions intéressantes à préconiser puisqu'elles permettent une récolte plus hâtive des secteurs traités (temps de révolution plus court) et une augmentation de la disponibilité du bois de sciage (Cameron, 2002). Il est d'ailleurs bien établi que la réduction de la densité d'un peuplement forestier par l'intermédiaire de coupes partielles augmente la croissance des tiges résiduelles en forêt boréale (Thorpe *et al.*, 2007; Vincent *et al.*, 2009; Goudiaby *et al.*, 2012; Pamerleau-Couture *et al.*, 2015; Montoro Girona *et al.*, 2016), en raison de l'ouverture de la canopée qui entraîne une augmentation des ressources disponibles pour les arbres (lumière, eau, éléments

nutritifs) (Tang *et al.*, 1999; Thibodeau *et al.*, 2000). La croissance plus rapide et les révolutions raccourcies pourraient toutefois causer des changements dans les propriétés du bois qui pourraient éventuellement réduire l'aptitude du bois à être utilisé pour un usage précis (Saranpää, 2003). Il est donc essentiel de mieux comprendre les effets des pratiques sylvicoles telles que les coupes partielles sur les variations dans les propriétés du bois pour s'assurer du maintien des usages que l'on peut faire du bois. Pourtant, peu d'informations sont disponibles jusqu'à maintenant sur la réaction des arbres résiduels après une coupe partielle, en particulier en ce qui concerne la formation du cerne de croissance et les propriétés du bois. De plus, l'ouverture du milieu suite à des coupes partielles rend les peuplements forestiers plus susceptibles aux chablis (Riopel *et al.*, 2010; Lavoie *et al.*, 2012), en raison de la pénétration plus importante du vent dans le peuplement résiduel après coupe (Ruel, 1995; Achim *et al.*, 2005). La stabilité des individus, qui dépend fortement du développement adéquat du système racinaire, doit être maintenue pour être en mesure de soutenir la croissance améliorée attendue après la coupe partielle. Le système racinaire doit donc être résistant et adapté aux nouvelles conditions du milieu. Pour ce faire, les racines peuvent modifier leur forme et augmenter leur diamètre (Nicoll et Ray, 1996; Ruel *et al.*, 2003), mais en plus de cela, le bois des racines formé dans la période suivant la coupe partielle doit posséder des propriétés équivalentes ou supérieures à celui formé dans la période précédant l'intervention. Les racines doivent également être en mesure de puiser et transporter une quantité plus importante d'eau en raison de la transpiration plus élevée après l'ouverture du peuplement (Gebhardt *et al.*, 2014; Boczoń *et al.*, 2016). Les racines jouent donc un rôle important dans le succès des coupes partielles. Malgré cela, seules quelques recherches ont été réalisées sur la réaction du système racinaire après des interventions sylvicoles (Ruel *et al.*, 2003; Vincent *et al.*, 2009), et aucune ne s'est intéressée aux propriétés du bois des racines comme la masse volumique et la dimension des trachéides, qui ont un rôle physiologique et biomécanique fondamental et sont partiellement responsables de la résistance du système racinaire face aux stress

environnementaux.

Puisque la détermination de la qualité du bois présente plusieurs facettes et dépend de l'usage prévu, il n'existe pas de mesure absolue de la qualité. Parmi les propriétés les plus importantes permettant de définir la qualité du bois chez les conifères, on retrouve le diamètre et la forme de la tige, la masse volumique du bois, le contenu en bois juvénile, la longueur des trachéides, l'angle des microfibrilles dans la paroi cellulaire, le nombre et la taille des nœuds et les propriétés mécaniques (Willcocks et Bell, 1995; MacDonald et Hubert, 2002). Toutes ces propriétés du bois sont liées de près avec les structures anatomiques de sorte que la quantité et la qualité du bois produit ont toutes deux leur origine dans la région cambiale (Savidge, 2003).

1.2 ÉTAT DES CONNAISSANCES

La formation du bois résulte de l'accumulation de nouvelles cellules formées par le cambium vasculaire (Deslauriers *et al.*, 2010). Lors de la formation du bois, les nouvelles cellules de xylème produites par le cambium passent par quatre phases successives de différenciation qui leur permettent de remplir leurs fonctions (Cuny et Rathgeber, 2014; Rathgeber *et al.*, 2016): (1) la division d'une cellule mère cambiale qui crée une nouvelle cellule; (2) l'élargissement et l'élongation de cette cellule nouvellement formée; (3) le dépôt et la lignification de la paroi cellulaire; (4) la mort cellulaire programmée. Au début de la saison de croissance, le cambium sort de sa dormance et reprend son activité, produisant alors de nouvelles cellules de xylème (Prislan *et al.*, 2013). Pendant la première partie de la saison de croissance, la division cellulaire est intense, la durée d'élargissement cellulaire est longue et l'épaississement des parois est relativement court, produisant ainsi plusieurs grandes cellules de bois

initial à paroi mince; lors de la deuxième partie de la saison de croissance, la division cellulaire ralentit, la durée de l'élargissement est plus courte et la durée de l'épaississement des parois augmente, produisant alors un nombre relativement faible de cellules étroites et épaisses de bois final (Cuny *et al.*, 2014).

La formation du bois peut être influencée par le climat ou encore par des facteurs physiologiques ou environnementaux. Ceux-ci peuvent avoir un effet sur la dynamique et les mécanismes de formation du cerne de croissance, sur le moment de la production et de la différenciation des cellules du xylème et, de ce fait, sur la croissance radiale et les propriétés du bois (Deslauriers *et al.*, 2010; Cuny *et al.*, 2012; Cuny et Rathgeber, 2016; Rathgeber, 2017). Tous les facteurs ayant une influence sur l'activité cambiale auront donc également une influence sur la quantité et la qualité du bois qui sera produit par l'arbre. Un de ces facteurs pouvant modifier la dynamique de la formation du bois est l'aménagement forestier, car celui-ci entraîne généralement un changement dans les conditions de croissance des arbres (Doucet *et al.*, 2009). En effet, des manipulations sylvicoles telles que les coupes partielles entraînent des changements du microclimat des arbres, notamment une augmentation de la disponibilité de la lumière (Tang *et al.*, 1999), une augmentation de la température du sol et une disponibilité accrue d'éléments nutritifs en raison de la décomposition plus importante de la matière organique (Thibodeau *et al.*, 2000). Ces ressources supplémentaires peuvent ainsi profiter aux différentes espèces présentes, qui réagissent plus ou moins fortement en fonction de leur plasticité morphologique et physiologique.

Les changements de l'environnement découlant d'une coupe partielle résultent généralement en une augmentation de la croissance, ce qui peut entraîner une

diminution de la masse volumique (ou densité du bois) et de la résistance mécanique chez plusieurs espèces (Saranpää, 2003). En effet, les cernes annuels de croissance affectent les propriétés du bois des conifères par leur largeur et par le ratio de bois initial et de bois final à l'intérieur de chaque cerne (Butterfield, 2003). L'augmentation de croissance se traduit au niveau du cerne par une augmentation du nombre de cellules de bois initial, mais souvent sans grand changement au niveau du bois final (Barbour *et al.*, 1994; Mäkinen *et al.*, 2002b). Cette modification dans les proportions de bois initial et de bois final résulte en une diminution du pourcentage de bois final dans le cerne (Zhang, 1995; Koga et Zhang, 2002; Mäkinen *et al.*, 2002b). Puisque la masse volumique du bois dépend en partie du pourcentage de bois final (Lindström, 1997; Mäkinen *et al.*, 2002b), une diminution de ce dernier a comme conséquence une masse volumique inférieure dans le cerne (Jaakkola *et al.*, 2005a; Jyske *et al.*, 2010) et une diminution de la masse volumique globale du bois produit par l'arbre. Koga et Zhang (2002) ont également relevé que la masse volumique moyenne du cerne était fortement liée à ses composants, soit la masse volumique du bois initial et celle du bois final, et au pourcentage de bois final. Ainsi, des modifications dans la masse volumique intra-cerne, et donc des modifications dans l'uniformité du bois après traitement, sont susceptibles de causer des changements indésirables des propriétés du bois (Peltola *et al.*, 2007). Quant aux propriétés mécaniques du bois, celles-ci sont fortement corrélées à la masse volumique, de telle façon que le module d'élasticité et le module de rupture, soit la rigidité et la résistance du bois, augmentent de façon presque linéaire avec la masse volumique (Shmulsky et Jones, 2011). D'autres facteurs qui peuvent être observés de façon plus importante après une coupe partielle sont aussi susceptibles d'affecter les propriétés mécaniques du bois, comme la proportion de bois juvénile, la présence de bois de compression et la taille des nœuds (Zhang et Koubaa, 2009). Des études ont aussi montré une diminution de la longueur des trachéides avec l'augmentation du taux de croissance chez des espèces d'épinettes (Herman *et al.*, 1998; Mäkinen *et al.*, 2002a; Jaakkola *et al.*, 2005b).

Bien que les connaissances soient essentielles pour l'utilisation du bois transformé, il existe encore peu d'informations sur les effets des pratiques sylvicoles sur les propriétés du bois. L'effet des coupes partielles sur la croissance des tiges résiduelles commence cependant à être mieux connu. Quelques études récentes ont montré qu'une augmentation de croissance est observable à la suite de coupes partielles en forêt boréale, généralement avec un délai de trois à quatre ans suivant l'intervention (Thorpe *et al.*, 2007; Vincent *et al.*, 2009; Goudiaby *et al.*, 2012; Pamerleau-Couture *et al.*, 2015; Montoro Girona *et al.*, 2016). Par contre, l'effet de tels traitements sur la croissance et les propriétés du bois des racines est beaucoup moins documenté. Une réaction plus rapide et plus importante de la croissance des racines par rapport à la tige a été observée chez différentes espèces après des coupes partielles (Kneeshaw *et al.*, 2002; Ruel *et al.*, 2003; Vincent *et al.*, 2009). Toutefois, les informations portant sur les propriétés du bois des racines, telles que la masse volumique ou la dimension des trachéides, sont plutôt rares, voire même inexistantes pour les espèces de la forêt boréale de l'Est de l'Amérique du Nord.

Par ailleurs, on commence à mieux connaître la phénologie de la formation du cerne de croissance. Les études sur la xylogénèse produites jusqu'à maintenant ont permis d'obtenir des informations sur la dynamique de l'activité cambiale, les processus de différenciation cellulaire et les effets du climat (Deslauriers *et al.*, 2003; Gričar *et al.*, 2006; Rossi *et al.*, 2007; Thibeault-Martel *et al.*, 2008; Lupi *et al.*, 2012; Balducci *et al.*, 2013). De nouvelles informations commencent également à apparaître concernant la mécanique de la formation du bois en lien avec l'anatomie du bois (Cuny *et al.*, 2014; Balducci, 2015). On sait toutefois peu de choses sur l'effet d'une coupe partielle sur la formation du bois et le développement intra-annuel du cerne, si ce n'est que la coupe modifie les conditions de croissance des arbres résiduels, et donc,

les propriétés du bois produit (Da Silva Perez et Fauchon, 2003). La quantité et la qualité du bois produit ayant toutes deux leur origine dans la région cambiale (Savidge, 2003), il importe d'avoir une compréhension la plus précise possible (jusqu'à l'échelle de la cellule) pour obtenir de meilleures connaissances sur la structure du xylème et ainsi avoir une meilleure compréhension des propriétés anatomiques et mécaniques du bois au niveau microscopique.

1.3 OBJECTIFS ET HYPOTHÈSES

Cette étude vise à répondre aux interrogations concernant la réaction de l'épinette noire et du sapin baumier après une coupe partielle en forêt boréale. L'objectif général est d'évaluer l'effet de différents types de coupes partielles sur la croissance et sur les propriétés du bois produit dans la tige et les racines d'arbres résiduels des deux espèces. Plus spécifiquement, le travail de la thèse peut être séparé en trois objectifs spécifiques, traités dans trois chapitres:

1. Évaluer l'effet d'une coupe partielle sur le développement intra-annuel du cerne de croissance dans la tige et les racines de l'épinette noire et du sapin baumier (Chapitre II);
2. Évaluer l'effet d'une coupe partielle sur l'accroissement radial et les propriétés du bois (pourcentage de bois final, masse volumique, propriétés mécaniques en flexion, longueur des trachéides) de tiges résiduelles d'épinette noire et de sapin baumier (Chapitre III);

3. Comparer la croissance et les propriétés du bois des racines et de la tige de l'épinette noire ayant subi une coupe partielle (Chapitre IV).

L'hypothèse principale était que la croissance serait augmentée après la coupe partielle et que le bois produit après l'intervention pourrait présenter des propriétés inférieures. Plus spécifiquement, nous avons émis l'hypothèse que dans les années suivant une coupe partielle, le début de la formation du bois pourrait être devancé de quelques jours dans la tige et les racines en raison du réchauffement du sol et de l'air plus important par les rayons solaires au printemps chez les arbres résiduels. La coupe partielle devrait également entraîner une augmentation du nombre de cellules produites chez les arbres résiduels après la coupe partielle. Ces deux effets pourraient être plus marqués dans les racines.

En ce qui concerne la croissance et les propriétés du bois, les hypothèses étaient que la croissance radiale serait plus élevée 3-4 ans après la coupe pour l'épinette noire, mais serait plus rapide (2-3 ans) et plus forte pour le sapin baumier (Youngblood, 1991; Thorpe *et al.*, 2007; Vincent *et al.*, 2009; Pamerleau-Couture *et al.*, 2015; Montoro Girona *et al.*, 2016). Cette augmentation de croissance devrait se traduire par une diminution de la proportion de bois final dans le cerne (Barbour *et al.*, 1994; Zhang, 1995; Koga et Zhang, 2002), causant une diminution des propriétés du bois (masse volumique, propriétés mécaniques en flexion, dimensions des trachéides).

Au niveau des racines, l'augmentation de croissance après la coupe partielle devrait être supérieure à celle de la tige et devrait être perceptible une ou deux années plus tôt que la tige, soit vers la deuxième ou la troisième année après la coupe (Kneeshaw *et al.*, 2002; Ruel *et al.*, 2003; Vincent *et al.*, 2009). Les propriétés du bois des racines

pourraient être inférieures à celles de la tige. En effet, le pourcentage de bois final légèrement inférieur dans les racines par rapport à la tige et le plus grand lumen observé dans le bois final des racines (Krause *et al.*, 2010) pourrait donner une masse volumique et des propriétés mécaniques inférieures aux racines. La longueur des trachéides pourrait toutefois être supérieure dans le bois des racines, tel qu'observé par Bannan (1965).

1.4 APPROCHE MÉTHODOLOGIQUE

La thèse s'intéresse à deux espèces de la forêt boréale présentant un grand intérêt commercial, l'épinette noire et le sapin baumier. L'épinette noire couvre tout le territoire forestier québécois et est l'essence commerciale la plus importante dans l'Est du Canada. C'est une espèce à croissance lente, bien adaptée à la vie sous-étage et capable de croître dans une vaste gamme de conditions (Viereck et Johnston, 1990). Sa croissance lente et son bois dense en font une espèce très recherchée pour la qualité de son bois et de sa fibre (Zhang et Koubaa, 2009). Le système racinaire de l'épinette noire est étendu et superficiel, ce qui la rend toutefois plus susceptible au chablis (Ministère des ressources naturelles, 2013). Elle est classée comme tolérante à l'ombre (Viereck et Johnston, 1990).

Le sapin baumier est aussi largement répandu en Amérique du Nord. Il est plutôt reconnu pour la faible qualité de son bois (Zhang et Koubaa, 2009). Le sapin baumier a une forte capacité à s'établir et à croître à l'ombre de grands arbres; il est classé comme très tolérant à l'ombre, plus tolérant que l'épinette noire (Frank, 1990). Le sapin baumier est connu pour réagir vigoureusement après l'ouverture du couvert car il s'adapte plus rapidement que l'épinette noire à de nouvelles conditions

environnementales (Sullivan et Peterson, 1994; Ministère des ressources naturelles, 2013).

Trois différents types de coupe partielle ont permis de répondre aux objectifs de la thèse. Tout d'abord, pour étudier l'effet d'une coupe partielle sur la xylogénèse (Chapitre II), une éclaircie expérimentale a été réalisée à la forêt d'enseignement et de recherche Simoncouche, dans la réserve faunique des Laurentides. L'éclaircie a été effectuée à l'échelle de l'arbre, où tous les compétiteurs de diamètre commercial ont été retirés dans un rayon de quatre mètres autour des arbres expérimentaux sélectionnés.

La coupe avec protection des petites tiges marchandes (CPPTM) a été étudiée pour évaluer la réaction des tiges résiduelles après une coupe partielle (Chapitre III). La CPPTM est une récolte variant entre 70 et 90% du volume marchand d'un peuplement et au cours de laquelle la régénération, les gaules des classes de diamètre de 2 à 8 cm ainsi que les petites tiges marchandes de classes de 10 à 14 cm sont soigneusement protégées (MRNFP, 2003). Il s'agit d'un traitement conçu pour les peuplements de structure inéquienne ou irrégulière où l'on trouve un sous-étage de gaules et de petites tiges marchandes de sapin baumier ou d'épinette noire, ayant la capacité de profiter de l'apport de lumière consécutif à l'élimination de l'étage dominant (Doucet *et al.*, 2009). Les quatre sites utilisés pour ce chapitre font partie des dispositifs permanents d'un projet plus large mené par l'équipe de Jean Bégin à l'Université Laval (Riopel *et al.*, 2010, 2011; Riopel, 2012).

Finalement, un traitement d'éclaircie commerciale a permis de comparer la réaction entre les racines et la tige (Chapitre IV). L'éclaircie commerciale consiste à récolter une partie des tiges (25 à 35% de la surface terrière) dans des peuplements de structure régulière n'ayant pas atteint l'âge d'exploitabilité (Ministère des Ressources Naturelles, 2003). Elle est destinée à accélérer l'accroissement en diamètre des arbres résiduels et aussi, par une sélection convenable, à améliorer la qualité du peuplement et augmenter la valeur des tiges (Cameron, 2002; MRNFP, 2003).

1.5 STRUCTURE DE LA THÈSE

Cette thèse de doctorat est divisée en cinq chapitres, dont trois qui exposent les résultats obtenus sous forme d'articles scientifiques.

Chapitre II: Xylogénèse de la tige et des racines de l'épinette noire et du sapin baumier après une éclaircie expérimentale

Ce chapitre porte sur la formation du bois, à l'échelle intra-annuelle, de la tige et des racines après une éclaircie expérimentale. Des microcarottes de bois ont été récoltées hebdomadairement à la forêt d'enseignement et de recherche Simoncouche, dans une pessière et une sapinière. La différenciation cellulaire (élongation et élargissement cellulaire, épaissement et lignification des parois, maturation) a été observée tout au long de la saison de croissance, et ce, pendant quatre ans. Les résultats ont montré que l'éclaircie n'a pas eu d'effet sur le début, la fin ou la durée des phases de différenciations cellulaires. Par contre, une augmentation du taux de production

cellulaire a été observée, ce qui a mené à une augmentation du nombre total de cellules produites à la fin de la saison de croissance.

Chapitre III: Croissance et propriétés du bois de la tige de l'épinette noire et du sapin baumier après une coupe avec protection des petites tiges marchandes (CPPTM)

Le second chapitre s'intéresse à l'effet que peut avoir une coupe partielle sur la croissance et les propriétés du bois de tiges résiduelles d'épinette noire et de sapin baumier. Quatre sites ayant subi une CPPTM ont été échantillonnés et différents paramètres de croissance et de qualité du bois ont été mesurés. Les résultats ont montré que la CPPTM avait augmenté la croissance de façon significative chez les deux espèces, mais que l'augmentation était plus forte et plus rapide chez le sapin baumier. L'épinette noire n'a présenté aucun changement significatif au niveau des propriétés du bois, alors qu'une diminution du pourcentage de bois final et de la masse volumique a été observée pour le sapin baumier. Cependant, en prenant en compte l'ensemble des propriétés du bois mesurées, une analyse canonique discriminante n'a révélé aucune différence significative entre les propriétés du bois avant et après la CPPTM pour l'une ou l'autre espèce. Cela suggère que la CPPTM peut augmenter la croissance radiale des tiges résiduelles sans entraîner d'effets majeurs à court terme sur la qualité du bois.

Chapitre IV: Comparaison de la croissance et des propriétés du bois des racines et de la tige de l'épinette noire après une éclaircie commerciale

Le chapitre IV aborde la comparaison entre la croissance et les propriétés du bois des racines et de la tige de l'épinette noire avant et après une éclaircie commerciale. La tige et le système racinaire de 24 arbres répartis dans quatre sites ont été récoltés. La croissance, la masse volumique et la dimension des trachéides ont été analysées sur une période de 20 ans. Avant l'éclaircie, la croissance était légèrement supérieure dans la tige alors qu'après l'éclaircie, la croissance était significativement plus élevée dans les racines éloignées. Sur toute la période étudiée, la masse volumique moyenne du cerne et la masse volumique du bois initial étaient plus élevées dans les racines que dans la tige. Ce résultat confère aux racines une résistance possiblement supérieure contre la cavitation et les embolies, ce qui leur permet de pouvoir tenir leur rôle de transport d'eau de façon sécuritaire. L'éclaircie commerciale a entraîné une légère diminution de la masse volumique moyenne dans les racines éloignées, et une légère diminution de la masse volumique du bois initial et de la masse volumique minimale observée dans le bois initial dans les deux parties de l'arbre. Ces résultats ne devraient pas rendre les racines plus vulnérables à la cavitation; cependant, des études supplémentaires sont nécessaires pour le mesurer.

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CHAPITRE III

XYLOGENESIS IN STEMS AND ROOTS AFTER THINNING IN THE BOREAL FOREST OF QUEBEC, CANADA

PUBLISHED RESEARCH PAPER

Title: Xylogenesis in stems and roots after thinning in the boreal forest of Quebec, Canada

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2.1 ABSTRACT

The reduction of competition through thinning increases radial growth in the stem and roots of many conifer species. However, not much is known about the effect of thinning on the dynamics of wood formation and intra-annual development of the growth ring, especially in the roots, which are an essential part of the tree for stability and resource acquisition. The aim of the study was to evaluate the effect of an experimental thinning on the dynamics and phenology of xylogenesis in the stem and roots of black spruce and balsam fir. Experimental and control trees were selected in two mature even-aged stands, one black spruce (*Picea mariana* (Mill.) BSP) and one balsam fir (*Abies balsamea* (L.) Mill.). Wood microcores were collected weekly in the stem and roots from May to October for a period of 4 years. The onset and ending of each cell differentiation phase were computed, as well as growth rate and total cell production. Results show that thinning increased the cell production rate of stem and roots of black spruce and balsam fir. This higher daily growth rate caused an increase in the total number of cells produced by the cambium. The intensity of the treatment was sufficient to significantly increase light availability for residual trees, but insufficient to modify soil temperature and water content to a point at which a significant change in the timing or duration of xylogenesis would be induced. Thus, thinning increased cell production rate and total number of cells produced in both stem and roots, but did not result in a change in the phenology of wood formation that could lead to increased risks of frost damage in the spring or autumn.

2.2 INTRODUCTION

Traditionally, clearcuts have been the most common silvicultural treatments in Quebec's boreal forest. However, the transition to ecosystem-based forest management requires silvicultural options that maintain or enhance the long-term health and functions of forest ecosystems. Thinning, which involves removing only a selected part of the trees in a stand (Côté, 2000), can be used to either maintain or modify stand structure and composition, or increase the resistance of some stands to spruce budworm (*Choristoneura fumiferana* Clem.) (Bauce, 1996; Ministère des Ressources Naturelles, 2003).

Conifers are very important for the wood industry in eastern Canada, particularly black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir (*Abies balsamea* (L.) Mill.), two species of great commercial interest. Black spruce has the capacity to grow in a broad range of conditions but is slow-growing (Viereck and Johnston, 1990), while balsam fir is more shade-tolerant (Frank, 1990) and can react more vigorously than black spruce to a canopy opening (Lemay *et al.*, 2016). The effect of thinning on the growth of residual stems of both species typically results in increased radial growth, usually within 2 to 4 years following the intervention (Ruel *et al.*, 2003; Vincent *et al.*, 2009; Goudiaby *et al.*, 2012; Pamerleau-Couture *et al.*, 2015; Lemay *et al.*, 2016). However, the effect of such treatment on root growth is less

documented. Growth increases in roots have been observed to occur 1 to 2 years earlier and be more marked than in the stem (Kneeshaw *et al.*, 2002; Ruel *et al.*, 2003; Vincent *et al.*, 2009; Krause *et al.*, 2014). This has been interpreted as a response to the increased availability of resources in the soil and to the mechanically induced forces resulting from increased wind penetration in the stand (Ruel, 1995; Thibodeau *et al.*, 2000).

Xylogenesis, or wood formation, is a complex process of cambium division and differentiation, where cambial cells divide and generate derivatives that differentiate physiologically and morphologically until their final maturity (Rossi *et al.*, 2006b). Cell morphology is the result of processes occurring in two successive differentiation phases: duration and rate of cell enlargement determine the final cell radial diameter, while the duration and rate of wall deposition determine the amount of secondary cell wall (Cuny *et al.*, 2014). Environmental conditions have an influence on the dynamics of xylogenesis, timing of production and differentiation of xylem cells and, thus, on radial growth (Linares *et al.*, 2009; Cuny and Rathgeber, 2016; Rossi *et al.*, 2016). Lupi *et al.* (2012b) found that an increase in soil temperature resulted in earlier onsets of xylogenesis and that the effect of warming was especially marked in the phenology of the roots. It has also been shown that a reduction of competition through thinning prolongs xylem cell production (Linares *et al.*, 2009), and that dominant trees, which are subject to low competition for resources, have longer

periods of cambial activity than suppressed trees (Rathgeber *et al.*, 2011). Thus, the changes in environmental conditions following thinning, such as increased soil temperature and light availability, could influence xylogenesis, especially in the roots through soil warming. However, an earlier or longer growth period might expose trees to unfavourable conditions, for instance a late frost in spring, at the onset of cell division, or in autumn, before the beginning of winter dormancy. Despite this, little attention has been dedicated to understanding the effect of a partial canopy removal on the phenology and dynamics of wood formation. Most previous studies on xylogenesis have yielded information on the dynamics of cambial activity and the effects of climate, and the majority of those studies have concentrated on the stem. Very little information is available on the roots, an essential component for resource acquisition and tree stability. Better knowledge of the dynamics of wood formation after thinning could help identify how critical factors affect development and production of wood.

The aim of the study was to evaluate the effect of an experimental thinning on the intra-annual growth dynamics of the stem and roots of black spruce and balsam fir in the boreal forest. Our hypotheses were that: 1) more cells are produced in residual trees following treatment; 2) thinning induces an earlier onset and longer duration of wood formation; 3) both of these effects should be more marked in the roots.

2.3 MATERIAL AND METHODS

2.3.1 Study sites and experimental design

The study site is located within the Simoncouche research station (48°12'N, 71°14'W, 350 m a.s.l.), in the Laurentides Wildlife Reserve of Quebec, Canada. Two mature, even-aged and homogenous stands originating from a forest fire in the 1920s (Gagnon, 1989) were selected. One was dominated by black spruce and the other by balsam fir, and they were located about 400 m apart. The area is included in the balsam fir-white birch bioclimatic domain of Quebec (Saucier *et al.*, 1998). The mean annual temperature and total precipitation recorded at the sites during the 4 years of the study were 3.0 °C and 760 mm, respectively. Because of the cold climate and long snow cover, the period of cell differentiation at the sites generally occurs between the end of May and end of September (Thibeault-Martel *et al.*, 2008).

At each site, three experimental trees and three control trees were selected randomly. The study trees were dominant or codominant individuals, healthy-looking and free of visible injury or defect, with a diameter at breast height (DBH) between 14 and 22 cm (Table 2.1). Trees had at least four main lateral roots with a horizontal diameter larger than 10 cm. An experimental thinning was conducted in early spring 2012, which consisted of removing all neighbouring trees with a DBH greater than 10 cm

within a 4 m radius around the experimental trees. To quantify thinning intensity, Hegyi's competition index (Hegyi, 1974) was calculated before and after treatment according to the following formula:

$$CI = \sum_{j=1}^n \left(\frac{DBH_j}{DBH_i} \times \frac{1}{Dist_{ij}} \right) \quad (2.1)$$

where DBH_i and DBH_j are the diameter at breast height of the subject tree i and competitor tree j , respectively, $Dist_{ij}$ is the distance between subject tree i and competitor j and n is the number of competitors within a 4 m radius around the subject tree i (Mailly *et al.*, 2003). The treatment reduced the Hegyi's competition index by 60 and 45% for black spruce and balsam fir, respectively.

Table 2.1 Mean experimental trees characteristics (\pm standard deviation), measured at the beginning of the study in 2011, and number of competitors removed during the thinning in 2012.

Black spruce				
Trees	DBH (cm)	Height (m)	Number of competitors	Competitors removed
Treated	18.6 \pm 2.0	17.1 \pm 2.7	9.3 \pm 1.1	4.0 \pm 1.0
Control	20.8 \pm 2.0	19.0 \pm 1.9	4.0 \pm 1.7	-
Balsam fir				
Trees	DBH (cm)	Height (m)	Number of competitors	Competitors removed
Treated	17.5 \pm 1.2	16.4 \pm 0.7	12.7 \pm 4.7	3.7 \pm 1.1
Control	20.0 \pm 1.1	18.6 \pm 2.5	8.7 \pm 3.0	-

2.3.2 Microclimatic measurements

Soil temperature sensors were installed in November 2011 near one of the main lateral roots of each tree, in the northwest direction about 50 cm from the stem, between the organic and mineral layers. Measurements were taken every 15 min and data were stored as hourly averages in two CR10X dataloggers (Campbell Scientific Corporation, Edmonton, Canada). The soil volumetric water content was measured weekly with a Field Scout TDR 200 soil moisture metre (Spectrum Technologies Inc., Plainfield, IL, USA) at a distance of 1 m from the stem of each tree, in four orthogonal directions and at a depth of 20 cm. Understory light conditions were measured once in July 2014, 2 years after thinning, using measurements of the percentage of above-canopy photosynthetic photon flux density (PPFD) acquired under overcast sky conditions (Gendron *et al.*, 1998). Measurements were taken at 30 cm above ground, in four orthogonal directions and every 50 cm from the stem up to 4 m using a quantum sensor for photosynthetically active radiation (PAR), connected to a LI-1400 datalogger (sensor LI-190SA, Li-Cor Inc., Lincoln, NE, USA). To obtain the percentage of above canopy PPFD, each measurement was divided by the total available light, recorded at the same time by another PAR sensor installed in a nearby open area and connected to a datalogger.

2.3.3 Sample collection and preparation

From 2011 to 2014, wood microcores (2 mm in diameter, 25 mm long) were sampled weekly with a Trephor (Rossi *et al.*, 2006a) from May to October. The microcores were collected on the stem and on one main lateral root of each tree. On the stem, samples were taken every 10 cm following a counter-clockwise rising spiral, starting 1 m from soil level. On the roots, samples were taken every 3 cm following a zigzag pattern on the upper part of the root, starting 25 cm from the collar (Thibeault-Martel *et al.*, 2008) and ending when root diameter became less than 4 cm, which in all cases remained within a distance of 60 cm from the stem base. This sampling method avoids the eccentric growth pattern often observed in roots (Fayle, 1968; Krause and Eckstein, 1993). The repetitive sampling can generate a stress leading to the formation of traumatic resin ducts (Deslauriers *et al.*, 2003). Root sampling was thus limited to a single year, and different roots of the same tree were sampled for each year of the study. Microcores contained phloem tissues, the cambium and xylem tissues consisting of the developing annual ring and about five rings from the previous years. After collection, samples were stored in a water:ethanol solution (1:1) to avoid tissue deterioration during transport.

The microcores were dehydrated using successive immersions in ethanol and D-limonene, and embedded in paraffin. Samples were cut into 7 μm thick sections with

a rotary microtome, fixed on slides, and stained with cresyl violet acetate (0.16% in water) (Thibeault-Martel *et al.*, 2008). The sections were observed under visible and polarized light at magnifications of 400-500 \times . Xylem formation was assessed by counting the number of developing cells in the cambial zone, in radial enlargement, in wall thickening and lignification, and the number of mature cells, each along three radial files (Deslauriers *et al.*, 2003; Rossi *et al.*, 2006c). Cells in the cambial zone had thin walls and a small radial diameter, while enlarging cells had a radial diameter at least twice that of cambial cells, with thin walls that did not shine under polarized light. Cells in the wall thickening and lignification phase had walls that changed from light violet (at the start of lignification) to blue (when maturation was complete) and shone under polarized light. Xylem tracheids were considered mature when walls were completely blue (Rossi *et al.*, 2006c).

Xylem formation was considered to have begun when the average of number of cells in enlargement was greater than one. At the end of the growing season, xylem formation was considered complete when the average of number of cells in wall thickening and lignification was less than one. Onset and ending of enlargement and wall thickening and lignification and first mature cell were computed in days of the year (DOY).

2.3.4 Data analyses and statistics

In 2012, one thinned black spruce root did not produce a tree ring so that year was eliminated from analyses. This is not unusual; it is well known that missing rings are found more frequently in roots than stem (Fayle, 1968; Krause and Eckstein, 1993; Schweingruber, 1996) and that a root can temporarily stop secondary growth for some years.

To analyse the differences in xylem phenology, a multifactor analysis of variance (ANOVA) with repeated measures was performed using PROC MIXED of the SAS 9.1 statistical package (SAS Institute, Cary, NC, USA). The tree was designated as a random factor and year was the repeated measure on each tree. The dates of onset and ending of the different phenological phases were modelled using DOY as dependent variable.

A multifactor ANOVA was also used to assess the treatment effect on soil temperature and volumetric water content. For these two variables, an average per month was calculated and used as the dependent variable. Once again, the tree around which measurements were taken was considered a random factor, while month was the repeated measure. The PPF was analysed in a similar way, but in this case using

the distance from the stem as the repeated measurement.

The total number of tracheids produced over time was described with the Gompertz function defined as:

$$y = A \exp[-e^{(\beta - \kappa t)}] \quad (2.2)$$

where y is the weekly cumulative sum of tracheids, t is DOY, A is the function asymptote (maximum number of tracheids) and β and κ are the x-axis placement parameter and rate of change (Rossi *et al.*, 2003). Using proc NLIN (SAS Institute, Cary, NC), the parameters of the function were estimated by minimizing the sum of squared differences between the total number of tracheids observed and number of tracheids predicted by the model. A multifactor ANOVA with repeated measures was performed to compare the Gompertz parameters between species, treatments, tree parts and years. Before the analyses, data were examined to verify the normality of the distributions and homogeneity of the variances (Quinn and Keough, 2002).

2.4 RESULTS

2.4.1 Xylem cell production

The amount of tracheids produced by the cambium, summarized by the Gompertz function asymptote (Figure 2.1) was significantly different over time between control and thinned trees and this effect differed between species (parameter A , Table 2.2). Indeed, there was an increase in cell production after thinning in treated trees compared to the controls. This change was noticeable in the stem of both species, and in the roots of balsam fir. Black spruce roots did not respond the same way in the year 2013. In general, stem and roots of thinned trees produced more cells than controls in the third year after thinning, except for balsam fir stems in which this difference occurred 1 year earlier. The average number of cells produced by the stem cambium in a growing season was higher in balsam fir than black spruce, with a mean difference of about 20 cells. Root cambium produced fewer cells than stem, with the difference averaging 14 less cells for black spruce and 37 for balsam fir. The β parameter of the Gompertz function differed by species and tree part, but was unaffected by the treatment (Table 2.2). The κ parameter was different between species, between tree parts and the treatment effect differed over time between the tree parts (Table 2.2).

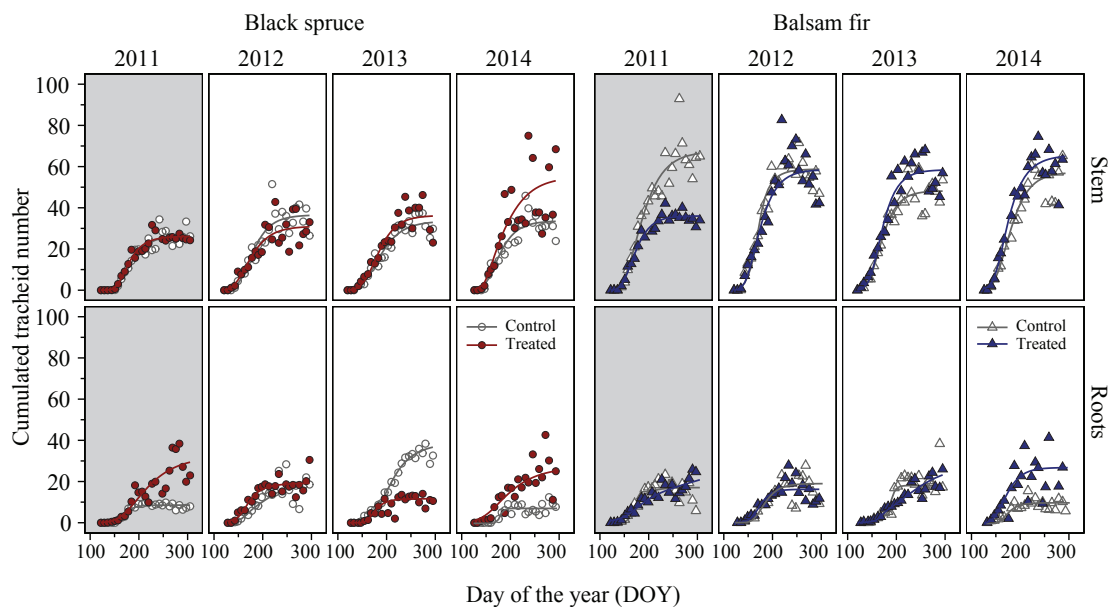


Figure 2.1 Number of xylem cells over time (circles and triangles) and Gompertz function (lines) for stem and roots of black spruce and balsam fir during the 4 years of the study. Shaded areas mark the year before treatment.

Table 2.2 ANOVA results of the Gompertz parameters tested in the stem and roots of black spruce and balsam fir during the 4 years of the study (2011-2014). Part refers to the tree part where the measurements were taken, i.e. stem or roots. Significant effects ($P < 0.05$) are highlighted in bold.

Source	A		β		κ	
	F	P	F	P	F	P
Treatment	0.00	0.9556	2.74	0.1031	3.41	0.0695
Part	75.47	<.0001	14.33	0.0004	13.46	0.0005
Treatment×Part	0.50	0.4842	3.13	0.0819	4.27	0.0430
Species	0.56	0.4583	4.58	0.0364	5.47	0.0226
Species×Treatment	0.02	0.8955	0.33	0.5665	0.79	0.3768
Species×Part	15.54	0.0002	3.06	0.0855	2.95	0.0910
Species×Treatment×Part	1.12	0.2937	0.06	0.8003	0.28	0.5988
Year	0.97	0.4112	0.20	0.8985	0.11	0.9529
Year×Treatment	2.83	0.0458	1.15	0.3366	1.25	0.2991
Year×Part	1.40	0.2507	0.40	0.7556	0.31	0.8159
Year×Treatment×Part	2.66	0.0562	1.73	0.1710	2.78	0.0486
Year×Species	0.08	0.9714	0.80	0.5008	0.90	0.4478
Year×Species×Treatment	3.08	0.0340	2.08	0.1115	2.09	0.1110
Year×Species×Part	0.29	0.8349	0.84	0.4757	0.98	0.4097
Year×Species×Treatment×Part	0.38	0.7657	1.98	0.1266	1.95	0.1303

2.4.2 Cambial activity, cell differentiation and xylem phenology

The date of onset of cell differentiation was significantly different between control and thinned trees, and between parts, species, years, and the interaction between parts and years (Figure 2.2, Table 2.3). Differences between years were not due to thinning. In balsam fir, cell enlargement in both stem and roots was observed to occur about 10 days earlier than in black spruce. On average, differentiation in stems also

started 10 days before that of roots, in both species. The start of xylem differentiation occurred at the earliest in the stem on DOY 122 (2 May) and at the latest on DOY 169 (18 June) in roots, with averages of DOY 144 for black spruce stems and DOY 136 for balsam fir stems, and delays of 10 days in roots for both species. Results varied substantially among the 4 years studied for both thinned and control trees. In the stem, the 2011 onset occurred later than in the other 3 years. For roots, the onset of cell enlargement was highly variable between years in black spruce, while a more regular pattern was observed in balsam fir.

The end of wall thickening and lignification occurred in the roots about 8 days prior to the stem. On average, xylem differentiation was completed on DOY 261 (18 September) in the roots, and on DOY 269 (26 September) in the stem. There was no significant treatment effect on these values.

For both species, the duration of xylogenesis was 18 days shorter in roots than in the stem, but this difference varied significantly between species and years. Xylogenesis was about 7 days shorter in spruce than fir. No influence of the treatment was detected.

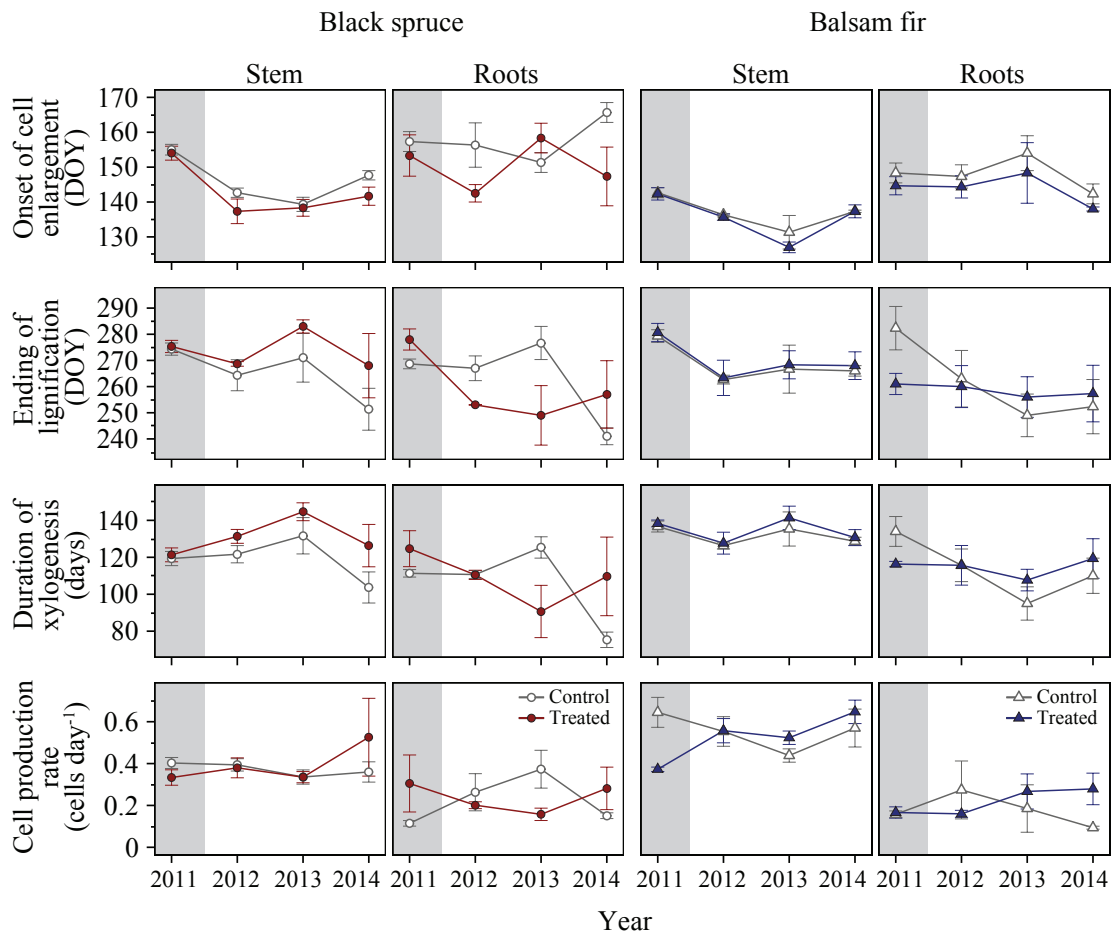


Figure 2.2 Xylem phenology and cell production rate in stem and roots of black spruce and balsam fir during the 4 years of the study. Shaded areas mark the year before thinning.

Table 2.3 ANOVA results of the onset, ending, duration and rate of the wood formation process tested in the stem and roots of black spruce and balsam fir during the 4 years of the study (2011-2014). Significant effects ($P<0.05$) are highlighted in bold.

Source	Onset of cell enlargement		Ending of wall thickening and lignification		Duration of xylogenesis		Cell production rate	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Treatment	9.84	0.0026	0.07	0.7856	2.79	0.0998	0.61	0.4371
Part	55.70	<.0001	12.03	0.0010	42.09	<.0001	95.48	<.0001
Treatment×Part	1.74	0.1914	2.88	0.0947	0.83	0.3658	0.31	0.5785
Species	40.47	<.0001	0.07	0.7983	7.11	0.0098	1.58	0.2128
Species×Treatment	0.99	0.3228	0.37	0.5478	0.98	0.3250	0.01	0.9373
Species×Part	0.00	0.9549	0.04	0.8367	0.04	0.8342	13.82	0.0004
Species×Treatment×Part	0.05	0.8275	0.64	0.4250	0.38	0.5402	0.58	0.4474
Year	5.91	0.0013	8.46	<.0001	3.36	0.0242	0.81	0.4933
Year×Treatment	1.27	0.2917	1.52	0.2188	2.23	0.0932	2.99	0.0377
Year×Part	7.43	0.0002	1.03	0.3856	3.97	0.0118	1.75	0.1664
Year×Treatment×Part	0.94	0.4259	0.59	0.6246	1.20	0.3179	2.97	0.0387
Year×Species	1.98	0.1255	1.93	0.1347	2.94	0.0399	0.08	0.9727
Year×Species×Treatment	2.52	0.0664	1.73	0.1709	2.79	0.0997	2.45	0.0717
Year×Species×Part	1.63	0.1920	0.23	0.8768	0.57	0.6344	0.00	0.9997
Year×Species×Treatment×Part	0.58	0.6272	2.46	0.0706	2.51	0.0666	0.37	0.7714

The cell production rate was significantly affected by the interaction between treatment, year and tree parts (Figure 2.2, Table 2.3). The cell production rate was generally lower in treated trees prior to treatment (i.e. 2011), except in the roots of black spruce. By the second or third year after thinning, rates became significantly

higher in treated trees. In the third year after treatment, more cells per day were produced in the stem (0.52 for black spruce, 0.64 for balsam fir) than in the roots (0.27 for both species).

2.4.3 Effect of thinning on microclimate

A significant treatment effect was observed in the percentage of above-canopy PPFD. The canopy opening created by the thinning was favourable for treated trees, which benefited from significantly more light after treatment than control trees (Figure 2.3, Table 2.4). On average, about 30% of the total PPFD reached the soil around the treated spruces, compared to 16% in the control. In balsam fir, most of the total available light was intercepted by the canopy, as only 8% of the PPFD reached the ground in treated stands compared to 4.5% for control. Close to the stem, black spruce and balsam fir trees had up to 22% and 6.5% more light available, respectively, than the control.

Soil temperature varied from -6 °C to 17 °C, being mostly around 0 °C between December and April, and close to 15 °C in July and August. After the removal of competitors around the treated trees, soil temperature was significantly affected over time, but also differed according to the species that dominated the forest cover (Table

2.4, Figure 2.3). The biggest differences in the monthly averages of soil temperature between treated and control trees occurred in the months of May and June for balsam fir (up to 2 °C warmer for treated trees), and later for black spruce, in July and August (up to 1 °C warmer for treated trees). From May to October, soil volumetric water content varied considerably (Figure 2.3). This variable showed differences between species, which were growing in two different sites, but was not significantly affected by the thinning (Table 2.4).

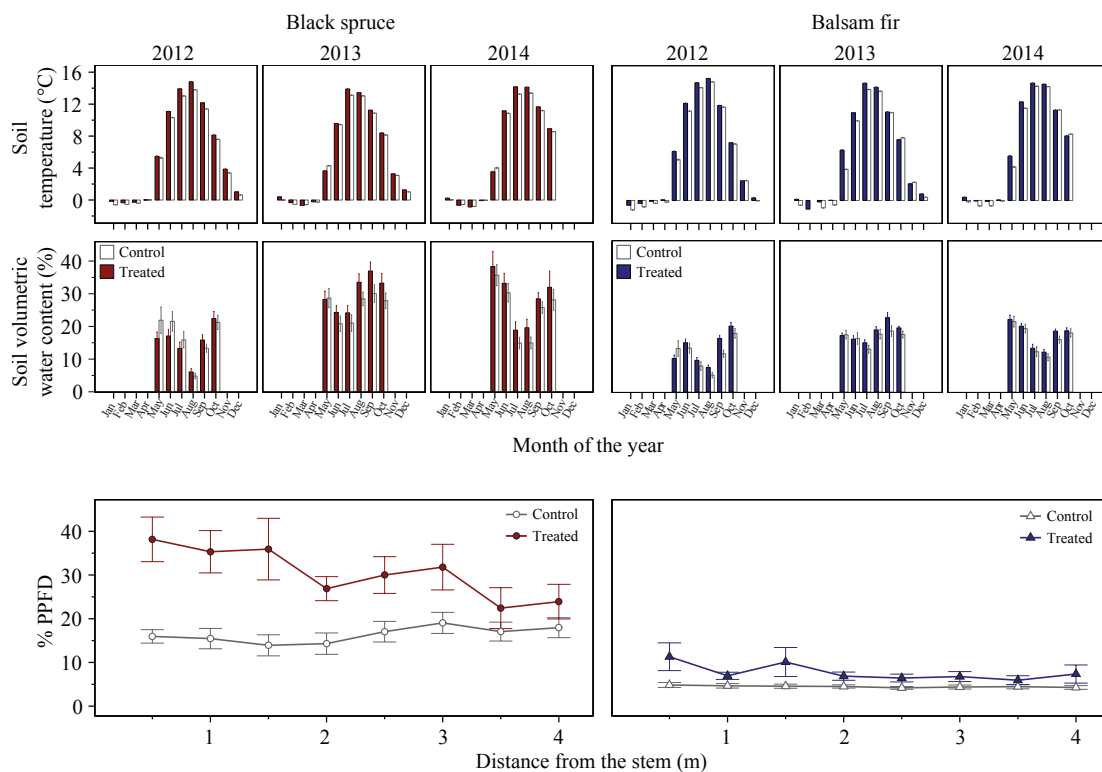


Figure 2.3 Soil temperature and volumetric water content monthly averages in the 3 years following the experimental thinning, and percentage of above-canopy photosynthetic photon flux density (PPFD) measured once in 2014.

Table 2.4 ANOVA results of the environmental variables tested in black spruce and balsam fir during the 4 years of the study (2011-2014). Distance refers to the distance from the stem where the measurements of the percentage of above-canopy photosynthetic photon flux density (PPFD) were taken. Significant effects ($P < 0.05$) are highlighted in bold.

Source	Soil temperature (°C)		Soil volumetric water content (%)		% PPFD	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Treatment	67.33	<.0001	3.59	0.0596	51.54	<.0001
Species	33.71	<.0001	15.46	0.0001	203.72	<.0001
Treatment×Species	0.03	0.8731	0.19	0.6610	20.49	<.0001
Month	1404.64	<.0001	8.19	<.0001		
Month×Treatment	1.44	0.2125	0.45	0.8108		
Month×Species	10.58	<.0001	0.57	0.7210		
Month×Species×Treatment	5.96	<.0001	0.04	0.9992		
Distance					1.26	0.2847
Distance×Treatment					1.62	0.1464
Distance×Species					0.53	0.8110
Distance×Species×Treatment					0.79	0.5957

2.5 DISCUSSION

2.5.1 Xylem cell production

Several authors working with different species have studied the growth response of residual trees to thinning, with the most common result being a radial growth increase in the stem (Peltola *et al.*, 2007; Olivar *et al.*, 2014; Pamerleau-Couture *et al.*, 2015; Montoro Girona *et al.*, 2016) and roots (Ruel *et al.*, 2003; Vincent *et al.*, 2009;

Krause *et al.*, 2014). The results in this study confirmed these patterns, with thinning inducing a significant increase over time on the number of cells produced by the cambium. Stem and roots of trees subjected to thinning produced more cells by the third year after treatment, or the second year in the stem of balsam fir. This faster reaction of balsam fir has also been observed in other studies (Doucet and Blais, 2000; Lemay *et al.*, 2016). However, contrarily to what was previously shown by Vincent *et al.* (2009) for black spruce and by Ruel *et al.* (2003) for balsam fir, roots did not react more rapidly or more strongly than stems. One of the reasons for this difference may be that the root sampling in our study was conducted on only one root per tree. The variation in the response of roots from the same tree to thinning could therefore not be distinguished from the tree-to-tree variation, which probably affected the sensitivity of our analysis. Indeed, black spruce and balsam fir stems produced more cells in general, with all trees presenting a similar response, whereas in the roots, more variability in the growth response was observed between the different trees. This large variation might explain the higher number of cells observed in control roots of black spruce in 2013. A high variability in root growth is common (Fayle, 1968; Krause and Eckstein, 1993; Drexhage *et al.*, 1999), as root radial growth is more irregular than in the stem, mainly because of the differences in soil conditions and the many functions of the different root parts (Fayle, 1968). Furthermore, the experimental thinning applied in this study was of relatively low intensity. Unlike thinnings conducted in commercial conditions, our treatment created only small gaps in the forest cover due to the removal of competitors only around the

sample trees. Carlson and Groot (1997) showed that small 9-m diameter circular openings and intact forest have the same microclimate conditions. Our observations are similar with slightly smaller canopy openings. This suggests that our experimental trees were subjected to conditions comparable to those of the control trees, and were probably not exposed to as much wind stress as in a high intensity thinning. Thus, it seems that the thinned trees may not have needed to invest more in root growth to improve their ground anchorage, as Krause *et al.* (2014) observed after commercial thinning.

2.5.2 Cambial activity, cell differentiation and xylem phenology

Conflicting results emerge when looking at the effects of thinning on xylogenesis. Some studies observed a prolonged growing season after thinning (Linares *et al.*, 2009; van der Maaten, 2013), while another found that the beginning, ending and duration of cambial activity were little affected (Wodzicki, 2001). In our study, the dates of onset and ending and the duration of wood formation remained unaffected by thinning. There was also no change observed in the timing of cell enlargement or wall thickening and lignification. Instead, a significant treatment effect was observed over time on the cell production rate. Studying the effects of thinning in *Pinus sylvestris*, Wodzicki (2001) also observed that the daily rate of tracheid production had increased after treatment. Similarly, the maximum radial increment rates and the final

tree-ring width were affected after thinning treatments in *Abies pinsapo* (Linares *et al.*, 2009). Boivin-Dompierre *et al.* (2017) showed that after thinning in spruce-fir stands in eastern Canada, trees increased their wood production per unit leaf area in response to higher light availability. Our findings suggest that thinning in this forest type affects wood formation mostly by acting on the efficiency of cambial cell division, as treatment affected the number of cells produced mainly by an acceleration in the accumulation rate of new cells, and not by a change in the duration of cell production. As a result, this increase of the cell production rate in treated trees was responsible for the increase in the total number of tracheids produced by the cambium at the end of the growing season.

2.5.3 Effect of thinning on microclimate

In this part of the eastern boreal forest of Canada, precipitation events are frequent, and the low temperatures limit evaporation, which implies that water availability is not an important limiting factor for growth. We can deduce that the thinning in our study did not lead to a sufficient change in the environmental conditions around the sample trees to modify the soil water availability. Goudiaby *et al.* (2011) also noticed that soil water content was not affected by thinning, and that light availability increased according to the basal area removed. The significantly higher light available after treatment in our study supports the hypothesis that an increase in light

intensity as a consequence of thinning is more important for plant growth than a potential increase in air or soil temperature (MacDonald, 2000). In our study, soil temperature was statistically higher for treated trees between June and September, but the differences remained marginal. Previous studies on mature trees showed no change in xylem phenology and cell production after a 4 °C soil warming for 6 years (Lupi *et al.*, 2012a; Dao *et al.*, 2015) and no change in bud burst after a 5 °C soil warming (Bergh and Linder, 1999).

2.5.4 Comparison between species and tree parts

Wood formation was initiated in black spruce about a week later than balsam fir while the end of cell differentiation occurred at about the same time. The fact that bud break occurs earlier in fir than spruce could explain why balsam fir had an earlier xylem differentiation onset because these events have been found to be synchronous in both black spruce and balsam fir (Antonucci *et al.*, 2015).

In the 4 years of the study, the onset of cell enlargement in the roots was synchronized with the stem or occurred a few days later. This result is similar to what Thibeault-Martel *et al.* (2008) observed with the same species. The onset of wall thickening also occurred earlier in the stem than in roots, and the ending of xylem

differentiation happened earlier in the roots or was similar. Accordingly, total duration of xylogenesis and duration of wall thickening and lignification were shorter in the roots, with no difference between treatments. The warming of the soil in spring, which occurs later than air temperature warming, could explain the different dynamics between the stem and roots (Thibeault-Martel *et al.*, 2008). Our experimental thinning did induce changes in soil temperatures but the magnitude of the effect was likely insufficient to lead to a measurable effect on xylogenesis in roots during the short monitoring period of the study.

Lupi *et al.* (2010) showed that a higher number of cells produced by the cambium was related to an earlier onset of cell differentiation, which in turn could have influenced the ending of cell differentiation. The synchronized or delayed onset that we observed in the roots can thus explain the fewer cells produced in the roots compared to the stem. This result contradicts other studies that observed larger ring widths in roots than stem after thinning (Ruel *et al.*, 2003; Krause *et al.*, 2014). However, these previous studies did not measure the number of cells constituting the rings. It is possible that the growth rings in our study were in fact similar or wider than in the stem, as observed in other studies. We observed that fewer cells were produced by the root cambium after thinning, but the duration of the cell enlargement and wall thickening and lignification phases were the same as in the stem. Therefore, individual root cells may have on average spent a little more time in these phases

compared to a cell produced in the stem. A longer differentiation period for roots cells could in turn result in larger cross-sectional areas, wider cell walls and higher lignin content after thinning. Indeed, cell wall thickness of a mature tracheid was observed to be correlated with the duration of its maturation phase (Wodzicki, 2001). Larger lumen and thicker walls in the roots cells produced after thinning would allow a more efficient water transport to counterbalance the higher transpiration rate of the trees (Gebhardt *et al.*, 2014; Boczoń *et al.*, 2016). Further analyses should be conducted, especially on the roots, to understand the effect of thinning on water transport, and thus improve our understanding of the below ground part of the trees.

2.6 CONCLUSIONS

The experimental thinning applied in this study had an effect on the cell production rate of the stem and roots, which was significantly increased over time after the treatment. This higher growth rate triggered an increase in the total number of cells produced by the cambium, confirming our first hypothesis. However, no influence of thinning was observed on the timing or duration of xylogenesis, which rejects our second hypothesis. And contrary to our third hypothesis, roots were not more affected by the treatment than the stem as roots produced fewer cells than the stem. Thinning applied in such conditions can be considered a useful treatment to increase wood production in stem and roots, without exposing trees to drastic changes in

environmental conditions. It is therefore unlikely that thinning would lead to increased risks of frost damage in the spring or autumn with a longer or shifted growing season. To our knowledge, this is the first study in which xylogenesis was monitored weekly after thinning. It is also one of the rare studies on root xylogenesis. Our results provide a better understanding of the effect of this silvicultural treatment on the process of xylem formation, and thus a better understanding of tree physiology and its potential effects on wood properties.

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CHAPITRE III

GROWTH AND WOOD QUALITY OF BLACK SPRUCE AND BALSAM FIR
FOLLOWING CAREFUL LOGGING AROUND SMALL MERCHANTABLE
STEMS (CLASS) IN THE BOREAL FOREST OF QUEBEC, CANADA

PUBLISHED RESEARCH PAPER

Title: Growth and wood quality of black spruce and balsam fir following careful logging around small merchantable stems (CLASS) in the boreal forest of Quebec, Canada

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3.1 ABSTRACT

Careful logging around small merchantable stems (CLASS) is a partial cutting treatment in which 70 to 90% of the merchantable volume of uneven-aged, irregular or multi-layered conifer stands is harvested. The decrease in stand density by means of partial cutting is known to induce an increase in residual stem growth, which could also influence the wood properties. This research aims to evaluate the effect of CLASS on the growth and some wood quality parameters of black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir (*Abies balsamea* (L.) Mill.) in the boreal forest of Quebec, Canada. Four uneven-aged black spruce-balsam fir stands were selected for the study and 15 black spruce and 15 balsam fir trees were sampled in each stand, distributed between a treated and a control area. Radial growth, latewood proportion, ring density, tracheid length and the moduli of elasticity and rupture were measured in each tree. A high proportion of residual stems significantly increased their radial growth after CLASS. No significant change was obtained for latewood proportion, average ring density, tracheid length or mechanical properties for black spruce. However, latewood proportion and ring density were significantly reduced in balsam fir after treatment, with no effect on MOE or MOR. When looking at the wood properties comprehensively, a canonical discriminant analysis did not detect any significant difference between the wood properties before and after treatment for either species. This suggests that CLASS can stimulate the radial growth of residual stems with limited short-term effects on wood quality.

3.2 INTRODUCTION

New silvicultural practices are increasingly being proposed in the boreal forest to pursue different aims, including a higher volume growth of individual trees, favouring the establishment of natural regeneration or emulating natural disturbances (Thorpe and Thomas, 2007; Bose *et al.*, 2013). Careful logging around small merchantable stems (CLASS, known as CPPTM in Québec) is a partial cutting treatment in which a large proportion of the forest cover (70 to 90% of the merchantable volume of a stand) is harvested (Riopel *et al.*, 2010). The residual stand consists of a minimum of 900 stems per hectare within a diameter range from 2 to 14 cm at breast height (1.3 m), including at least 125 small merchantable stems of 10 to 14 cm in diameter (Ministère des Ressources Naturelles, 2002; MRNFP, 2003). Harvesting trees with a diameter below 14 cm is generally unprofitable and generates less yield due to the small dimensions and greater handling required (Auty *et al.*, 2014). CLASS therefore allows these small stems more time to grow so that they can eventually constitute the dominant stratum of the future stand, which could decrease rotation length by about 10 years before the next scheduled harvest i.e. when the new stand will have reached maturity (Pothier *et al.*, 1995; Ministère des Ressources Naturelles, 2002; Riopel *et al.*, 2010). Currently, the CLASS treatment is not necessarily viewed as system of recurring interventions over several rotations, and may thus only be applied as punctual intervention in time (MRNFP, 2003). This type of partial harvesting is suitable for uneven-aged, irregular or multi-layered softwood

stands (Ministère des Ressources Naturelles, 2002; Riopel *et al.*, 2010) and aims to perpetuate the internal structure of a forest stand by maintaining some of its structural attributes (Groot, 2002).

The decrease in stand density by means of partial cutting is known to induce an increase in individual stem growth (Youngblood, 1991; Latham and Tappeiner, 2002; Thorpe *et al.*, 2007). An accelerated growth is reflected in the ring by an increased number of earlywood cells, with little change in the latewood width, resulting in a lower mean ring density (Barbour *et al.*, 1994; Koga *et al.*, 2002; Mäkinen *et al.*, 2002b; Jaakkola *et al.*, 2005a). Koga and Zhang (2002) explained that the average ring density is determined by its components, i.e. the earlywood and latewood density, and by the proportion of latewood. Therefore, changes in the intra-ring density, and thus in the uniformity of the wood after treatment, are likely to cause undesirable changes in wood properties (Peltola *et al.*, 2007).

Average ring density at breast height is also a good predictor of mechanical properties (Zink-Sharp, 2003) and bending strength has been shown to increase linearly with increasing wood density (Shmulsky and Jones, 2011; Todaro and Macchioni, 2011). The relationship between wood density and tracheid length has rarely been considered (Dutilleul *et al.*, 1998), but an accelerated growth caused by intensive

silvicultural treatments can result in the production of shorter tracheids (Mäkinen *et al.*, 2002a; Jaakkola *et al.*, 2005b). Since longer tracheids lead to better bonding by increasing cell to cell contact (Via *et al.*, 2004), a reduced tracheid length might also lead to a decrease in mechanical properties.

Because CLASS is still a relatively new silvicultural treatment, only a limited number of studies have investigated its effects on the tree- and stand-level responses (Liu *et al.*, 2007; Yelle *et al.*, 2008; Cimon-Morin *et al.*, 2010; Riopel *et al.*, 2010; Légaré *et al.*, 2011; Riopel *et al.*, 2011; Ruel *et al.*, 2013). A few studies have focused on the growth response of residual trees after treatment (Thorpe *et al.*, 2007; Pamerleau-Couture *et al.*, 2015), but little attention has been given to understanding the effects of the treatment on the wood quality of black spruce (*Picea mariana* (Mill.) B.S.P.) or balsam fir (*Abies balsamea* (L.) Mill.). Black spruce is a slow-growing species, well adapted to life in the understory (Viereck and Johnston, 1990) while balsam fir can survive for many years under cover (Frank, 1990). Balsam fir is known to react vigorously after canopy opening as it adapts more rapidly than black spruce to new environmental conditions (Sullivan and Peterson, 1994; Ministère des ressources naturelles, 2013). Both species are known to increase their growth after canopy removal (Solomon and Frank, 1983; Ministère des ressources naturelles, 2013), but acclimation to the new environmental condition requires a few years because the majority of resources are first allocated to root growth (Kneeshaw *et al.*, 2002; Ruel

et al., 2003), which causes a delay in the response to the treatment in other parts of the tree. Once the acclimation period is over, the growth response can differ between the two species given that balsam fir has a higher capacity for horizontal crown expansion (Messier *et al.*, 1999; Claveau *et al.*, 2002), a better capacity for morphological adjustments (like a reduced specific leaf area after canopy removal) and physiological characteristics (such as lower transpirational losses) better adapted to canopy opening (Dumais and Prévost, 2008). These two species are important commercial species in the eastern boreal forest of Canada. It is thus important to verify and quantify their growth response following CLASS, and ensure that any consequence on the wood properties of residual stems will not affect the suitability for the most important end-uses (i.e. construction lumber and pulp).

This study aims to evaluate the effect of CLASS on the radial growth of individual trees, as well as on several wood quality parameters (latewood proportion, ring density, tracheid length, moduli of elasticity and rupture) of black spruce and balsam fir in the boreal forest of Quebec, Canada. We compared growth and wood quality parameters of treated and control trees over a period of 30 years i.e. the 20 years prior to the partial cutting treatment and the 10 years that followed. The hypotheses were that: 1) a significant radial growth increase would occur three to four years after CLASS for black spruce, but the increase would occur faster (after two to three years) and be greater in balsam fir; 2) the increased radial growth of the stem following

treatment would occur in the earlywood part of the annual ring, thus causing a decrease in latewood proportion and ring density; 3) mechanical properties would decrease following CLASS since they are highly correlated with wood density.

3.3 MATERIAL AND METHODS

3.3.1 Experiment design and sampling

Four uneven-aged black spruce-balsam fir stands were sampled in the Saguenay-Lac-Saint-Jean and Côte-Nord regions, Quebec, Canada, between 48° 41' and 50° 30' N and 68° 47' and 70° 22' W. These stands are part of a project for which permanent plots were established between 1997 and 2002 in 27 experimental blocks in the balsam fir-yellow birch, balsam fir-white birch and spruce moss bioclimatic zones (Riopel *et al.*, 2010, 2011). In each selected block, one part of the stand was treated with a CLASS at least 10 years prior to sampling and another part of the stand was left untreated to be used as a control. All four blocks presented similar characteristics in terms of composition, density, diameter and age of the stands (Table 3.1).

Table 3.1 Description of sampling sites.

Stand	Merchantable volume before CLASS (m ³ ha ⁻¹)	GPS Coordinates	Treatment	Merchantable volume harvested (%)	Residual basal area (m ² ha ⁻¹)
B3	145	N 48° 41' 00.7" W 70° 21' 50.9"	CLASS	79.0	10.6
		N 48° 41' 10.0" W 70° 21' 50.0"	Control	-	
B4	157	N 50° 30' 03.7" W 68° 47' 41.0"	CLASS	84.5	8.2
		N 50° 29' 59.2" W 68° 48' 10.0"	Control	-	
B10	147	N 48° 41' 33.3" W 70° 21' 32.1"	CLASS	80.0	13.0
		N 48° 41' 36.3" W 70° 22' 07.6"	Control	-	
B20	132	N 48° 42' 58.1" W 70° 13' 15.1"	CLASS	72.0	16.6
		N 48° 43' 02.3" W 70° 13' 27.4"	Control	-	

Three 150 m² plots were established in each treated stand and two plots of the same dimensions in each control stand to characterise the variability inside each treated and control stand. A higher number of plots were used in treated stands to obtain a better representation of the variability induced by the treatment. Three black spruce and three balsam fir trees were sampled in each plot, for a total of 120 trees. Sample trees were chosen randomly from the dominant or codominant stems in the control plots and from the dominant and codominant residual stems in the treated plots, with a DBH between 8 and 15 cm, free of visible injuries or defects and located at least two meters from a logging trail. Diameter at breast height (DBH), height and age were recorded for each sample tree (Table 3.2). Due to the nature of the CLASS treatment,

where all stems with a DBH over 14 cm were harvested, the selected treated trees were slightly smaller and younger than the controls. Our general approach was to compare the resource being currently harvested (the control trees), to the trees that will eventually dominate the stands at the end of the rotation that will follow the CLASS treatment (treated trees). It was impossible to select mature trees in the latter case because the CLASS treatment has only been applied for about a decade in the province of Quebec.

Table 3.2 Characteristics of sampled trees.

Stand	Treatment	Black spruce			Balsam fir		
		Mean age (years)	Mean DBH (cm)	Mean height (m)	Mean age (years)	Mean DBH (cm)	Mean height (m)
B3	CLASS	85.0	12.7	9.5	104.7	12.3	7.8
	Control	122.3	17.5	13.8	141.7	15.4	12.3
B4	CLASS	171.8	13.7	10.2	116.4	14.3	8.7
	Control	183.5	15.0	12.4	130.8	13.6	10.3
B10	CLASS	87.2	12.9	9.0	97.9	13.3	9.5
	Control	99.8	16.1	11.7	108.0	13.6	10.6
B20	CLASS	126.2	13.6	10.4	123.3	11.8	8.1
	Control	133.3	15.1	11.4	109.0	13.5	10.7
Mean	CLASS	117.6	13.2	9.8	110.6	12.9	8.5
	Control	134.7	15.9	12.3	122.1	14.0	11.0

3.3.2 Growth and wood quality analyses

Discs were collected at every meter along the stem and at breast height. Tree-ring widths and latewood proportion were measured to the nearest 0.01 mm along four radii (up to a height of 2 m) or two radii (3 m to the top of the tree), using the WinDENDRO software (Guay *et al.*, 1992) (Régent Instruments Inc, 2009). The data were visually cross-dated (Stokes and Smiley, 1968; Fritts, 1976) and statistically verified by the COFECHA program (Holmes, 1983).

To assess the response to treatment, a radial growth percentage was calculated for each stem at breast height. The mean increase was calculated as the ratio of the average annual ring width of the 10 years following the CLASS to the average annual ring width of the 20 years preceding the treatment (Vincent *et al.*, 2009):

$$\gamma = \frac{(\sum_{t=(TY+1)}^{t=TY+10} \alpha_t) / 10}{(\sum_{t=(TY-20)}^{t=TY-1} \alpha_t) / 20} \times 100 \quad (3.1)$$

where γ = radial growth increment (%), TY = treatment year, t = time (year), and α = ring width (mm).

Wood density profile measurements were taken on radial segments from a stem

sample collected at breast height. Strips 1.63 mm thick (longitudinal) and 25 mm wide (tangential) were dried under restraint to 12% moisture content in a conditioning room at 20 °C and 65% relative humidity (Alteyrac *et al.*, 2006). Measurements were taken from bark to pith on unextracted samples at intervals of 4 µm, using a QTRS-01X Tree Ring Scanner and X-ray densitometer (Quintek Measurement System, Knoxville, TN, USA). Working from the raw data from the wood density profiles and using an algorithm developed by Genet *et al.* (2013) using the *tcltk* library in the R statistical software (R Development Core Team, 2014), the boundary between consecutive growth rings and the transition from earlywood to latewood within a ring were defined as the point where the maximum change in density was reached (Mothe *et al.*, 1998). Earlywood, latewood and average ring density were measured for every annual ring of each sample. Only the data from the 20 years prior to the CLASS until 10 years after were kept for further analyses.

A 20 mm thick (longitudinal) and 15 mm wide (tangential) piece of wood from the breast height disc was used to determine tracheid length of the 6 growth rings prior to CLASS and of years 3 to 8 after treatment. Because the process of separating each growth ring is very time consuming, the two years after treatment were not taken into account to reflect the results of several studies reporting a delay in response to the treatment (Youngblood, 1991; Latham and Tappeiner, 2002; Bebber *et al.*, 2004; Thorpe *et al.*, 2007; Vincent *et al.*, 2009). In this way, only the years when the most

important response was expected were used (Thorpe *et al.*, 2007; Pamerleau-Couture *et al.*, 2015). Earlywood and latewood portions of each ring were separated manually using a razor blade. All samples were macerated in a solution of glacial acetic acid and hydrogen peroxide (1:1, v/v) at 75 °C for 15 h (Franklin, 1945). The macerated samples were carefully rinsed with distilled water and gently shaken to obtain a uniform suspension to be measured with a L&W FiberTester (Lorentzen & Wettre, Kista, Sweden). For each sample, a length-weighted mean tracheid length (TL_w) was calculated from the measurements of 5000 tracheids:

$$TL_w = \frac{\sum n_i L_i^2}{\sum n_i L_i} \quad (3.2)$$

where $i = 1, 2, 3, \dots, n$ are categories, n is the fiber count in the « i^{th} » category and L is the contour length. Using this method, the bias caused by the large number of fines generated during preparation is reduced (Herman *et al.*, 1998; Mäkinen and Hynynen, 2014; Mäkinen *et al.*, 2015). An average tracheid length for the whole ring was computed by weighting the tracheid length for each wood zone by the relative width of each zone (Mvolo *et al.*, 2015).

Small clear specimens of 10 mm x 10 mm x 150 mm (R x T x L) were prepared from a 50 cm stem bolt collected between 0.5 and 1.0 m from the ground to measure bending strength and stiffness in static bending. Because wood is a non-homogenous

material and its mechanical properties can differ from one sample to another, two samples were used from wood formed in the years prior to the CLASS and two samples from wood formed in the years after treatment (Figure 3.1). Specimens were dried to 12% moisture content in a conditioning room. Three-point bending tests were performed with an MTS Alliance RT/100 machine (TestResources Inc., Shakopee, MN) according to the ASTM D-143 standard for small clear specimens (ASTM, 2010). The specimens were placed pith side up with a span of 110 mm (L) and speed of 1.3 mm min^{-1} . The MOE and MOR (in N mm^{-2}) were then calculated as follows:

$$\text{MOE} = \frac{P_1 L^3}{4bd^3 y_1} \quad (3.3)$$

$$\text{MOR} = \frac{3PL}{2bd^2} \quad (3.4)$$

where b and d are the width and thickness (mm) of the specimen, P_1 and y_1 represent the load (N) and the deflection (mm) at the limit of the range of elasticity and P is the maximum load (N) before rupture (Poncsák *et al.*, 2006; Shmulsky and Jones, 2011). For each specimen, cambial age, distance from pith and number of rings in the sample were also noted. An average of the MOE and MOR of the two samples tested both prior to and after treatment was used for further analyses.

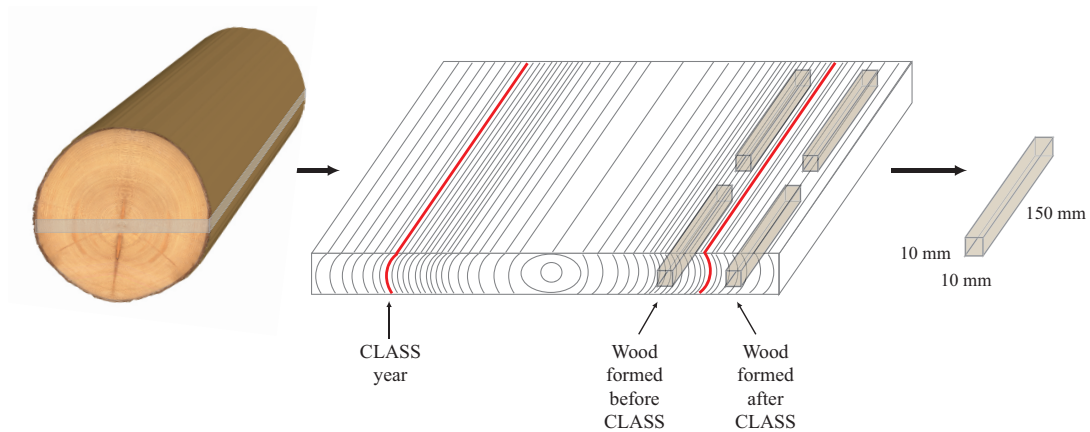


Figure 3.1 Schematic representation of sample preparation for bending strength and stiffness testing.

3.3.3 Statistical Analyses

Growth and wood quality parameters of treated and control trees were compared after treatment using a covariance analysis for repeated measurements and a nested data structure. The MIXED procedure in SAS was used, with the estimation of the restricted maximum likelihood (REML), and an autoregressive covariance structure AR(1) was applied to model the autocorrelation of individual measurements within trees (SAS Institute Inc., 2013). A covariate was used to account for differences between the selected trees. The covariate was calculated as the mean of the growth or wood quality parameter for the 20 years prior to the CLASS treatment. For tracheid length, the mean of the six years prior to treatment was used as covariate and for MOE and MOR, the covariate was the mean of the two samples containing wood

formed before treatment. The SLICE option of the LSMEANS statement was used when the interaction term Treatment×Year was found to be significant to identify which years differed between the control and treated trees (Littell *et al.*, 2006).

In the end, the study produced a multivariate dataset that was analysed with a canonical discriminant analysis using proc CANDISC in SAS. This type of analysis finds linear combinations of the quantitative variables that provide maximal separation between classes or groups (SAS Institute Inc., 2013). The pre- and post-treatment periods were used as the classification variable and the measured wood quality parameters were used to perform the canonical discriminant analysis to derive canonical variables. For this analysis, only the treated trees were used to see if we could find a distinct separation in the wood properties before and after the application of the CLASS.

Data were log-transformed when necessary to meet the normality and homoscedasticity assumptions (Quinn and Keough, 2002). Differences between mean values were considered significant when P was <0.05 . Statistical analyses were performed using SAS 9.1 software (SAS Institute Inc., 2013) and R 3.1.2 (R Development Core Team, 2014).

3.4 RESULTS

There was a clear positive growth effect on the residual trees after the CLASS. Two thirds of the treated black spruce trees showed a radial growth increase at breast height after treatment, whereas nearly 95% of balsam fir trees showed a growth increase. In the trees treated with CLASS, black spruces had a mean radial growth increment of 145% on average (maximum 290% increase) while balsam firs had an average of 360% (maximum 1120% increase). Ring width at breast height was similar between the two species before CLASS but was higher for balsam fir after treatment, the mean values for the latter species having more than tripled (Figure 3.2A). A significant difference between treated and control trees appeared in the fourth year after treatment for black spruce and the third year for balsam fir (Table 3.3A, Figure 3.2A). By the tenth year after CLASS, ring width values tended to decrease for both species, but remained higher than pre-treatment values. The standard error was higher after treatment for the two species, indicating that the CLASS induced more variability in the data.

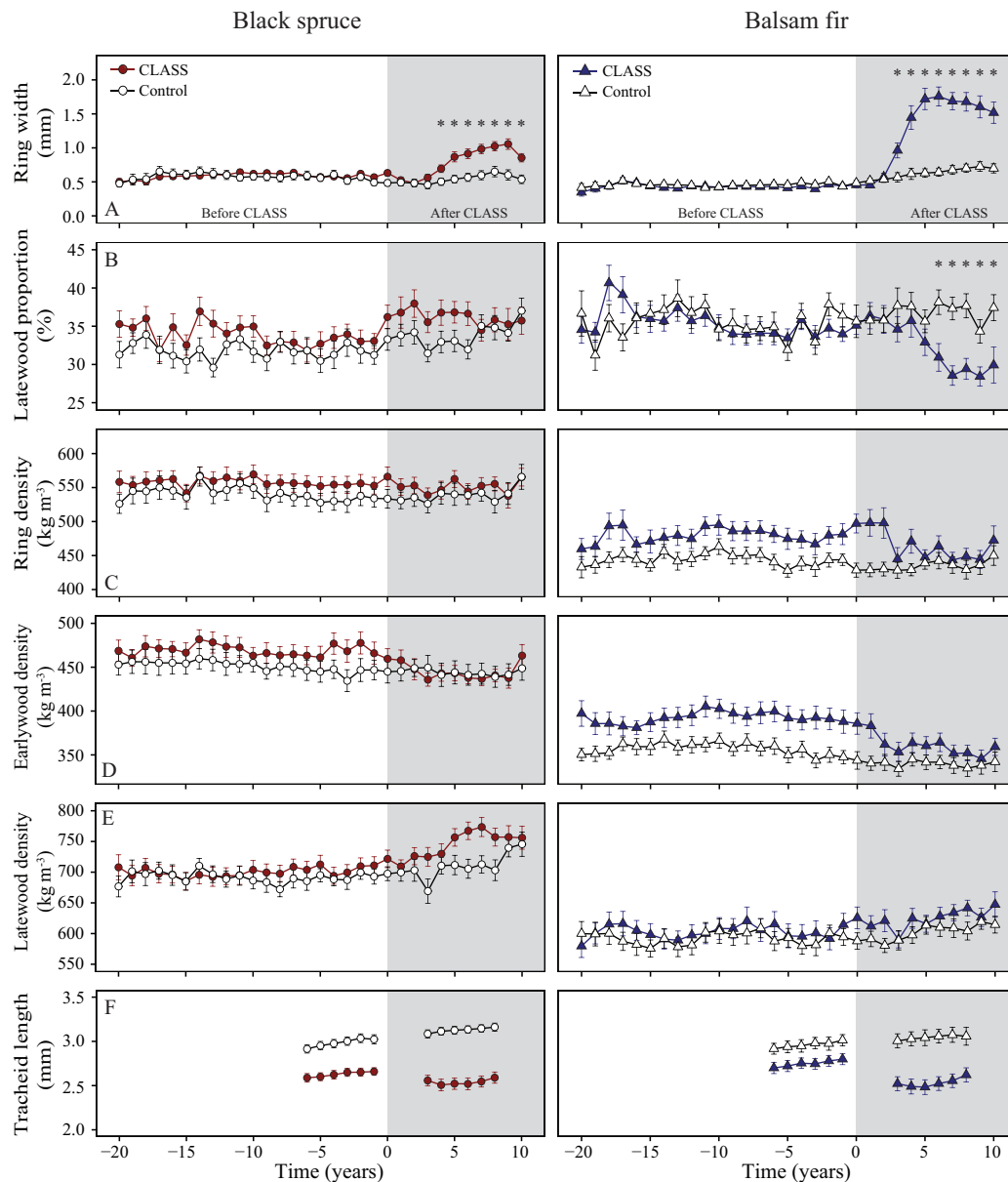


Figure 3.2 Radial growth, latewood proportion, average ring density, earlywood density, latewood density and tracheid length of residual black spruce and balsam fir stems before and after CLASS. The shaded area represents the years after treatment, with year 0 being the treatment year. Stars indicate a significant difference between treated and control trees for a given year, as determined by a slice test.

Table 3.3 Repeated measures ANOVA results of the measured growth and wood quality parameters for black spruce and balsam fir. The covariate represents the mean of the 20 years prior to CLASS for each parameter, or the mean of the preceding six years in the case of tracheid length. Significant results are presented in bold.

Parameter	Effect	Black spruce			Balsam fir		
		DF	<i>F</i>	<i>P</i>	DF	<i>F</i>	<i>P</i>
A) Ring Width	Treatment	1	15.06	0.0015	1	29.80	0.0098
	Year	9	32.12	<.0001	9	64.61	<.0001
	Treatment×Year	9	8.61	<.0001	9	29.55	<.0001
	Covariate	1	48.19	<.0001	1	35.70	<.0001
B) Latewood %	Treatment	1	0.18	0.7007	1	13.76	0.0015
	Year	9	0.84	0.5791	9	1.78	0.0693
	Treatment×Year	9	1.49	0.1498	9	3.60	0.0002
	Covariate	1	54.58	<.0001	1	25.94	<.0001
C) Ring Density	Treatment	1	0	0.9612	1	0.42	0.5307
	Year	9	1.73	0.0800	9	1.83	0.0612
	Treatment×Year	9	0.79	0.6214	9	2.30	0.0164
	Covariate	1	113.92	<.0001	1	94.59	<.0001
D) Earlywood Density	Treatment	1	6.16	0.0250	1	3.04	0.1086
	Year	9	1.22	0.2796	9	4.63	<.0001
	Treatment×Year	9	0.92	0.5040	9	1.37	0.2007
	Covariate	1	250.82	<.0001	1	164.26	<.0001
E) Latewood Density	Treatment	1	7.13	0.0487	1	1.38	0.2624
	Year	9	4.54	<.0001	9	3.73	0.0002
	Treatment×Year	9	1.30	0.2335	9	1.46	0.1622
	Covariate	1	71.80	<.0001	1	87.24	<.0001
F) Tracheid Length	Treatment	1	6.08	0.0183	1	5.74	0.0281
	Year	5	1.36	0.2418	5	0.38	0.8626
	Treatment×Year	5	0.19	0.9661	5	0.90	0.4807
	Covariate	1	78.23	<.0001	1	75.81	<.0001
G) MOE	Treatment	1	0.36	0.5706	1	0	0.9778
	Covariate	1	14.61	0.0005	1	1.46	0.2349
H) MOR	Treatment	1	0.82	0.4250	1	1.06	0.4066
	Covariate	1	4.90	0.0331	1	8.85	0.0067

There was no significant difference in latewood proportion between treated and control trees for black spruce (Table 3.3B, Figure 3.2B). The latewood percentage for balsam fir was similar before and for the first five years after treatment but then became significantly lower in the treated than in control trees in years six to ten after CLASS. Average ring density at breast height showed a similar pattern to latewood proportion, as there was no difference between treated and controls trees for black spruce (Table 3.3C, Figure 3.2C). For balsam fir, statistical analyses detected a change in the slope of the treated trees as opposed to control trees, but could not pinpoint a single year where treatments were different. For both species, earlywood density tended to decline after treatment (Figure 3.2D) and latewood density tended to increase (Figure 3.2E), but those changes were not significant (Table 3.3D-E). While the latewood proportion values were similar for both species, ring density values were on average 15% to 20% lower for balsam fir than black spruce.

Tracheid length at breast height tended to be lower after treatment (3.5% and 8% for black spruce and balsam fir respectively, compared to pre-treatment values) but the difference was not significant in either species (Table 3.3F, Figure 3.2F). Tracheid length did differ between treated and control trees but that difference was already present before CLASS.

The modulus of elasticity in bending did not differ significantly between treated and control trees (Table 3.3G, Figure 3.3). Black spruce had higher MOE values compared to balsam fir. Modulus of rupture exhibited exactly the same pattern as MOE (Table 3.3H, Figure not shown).

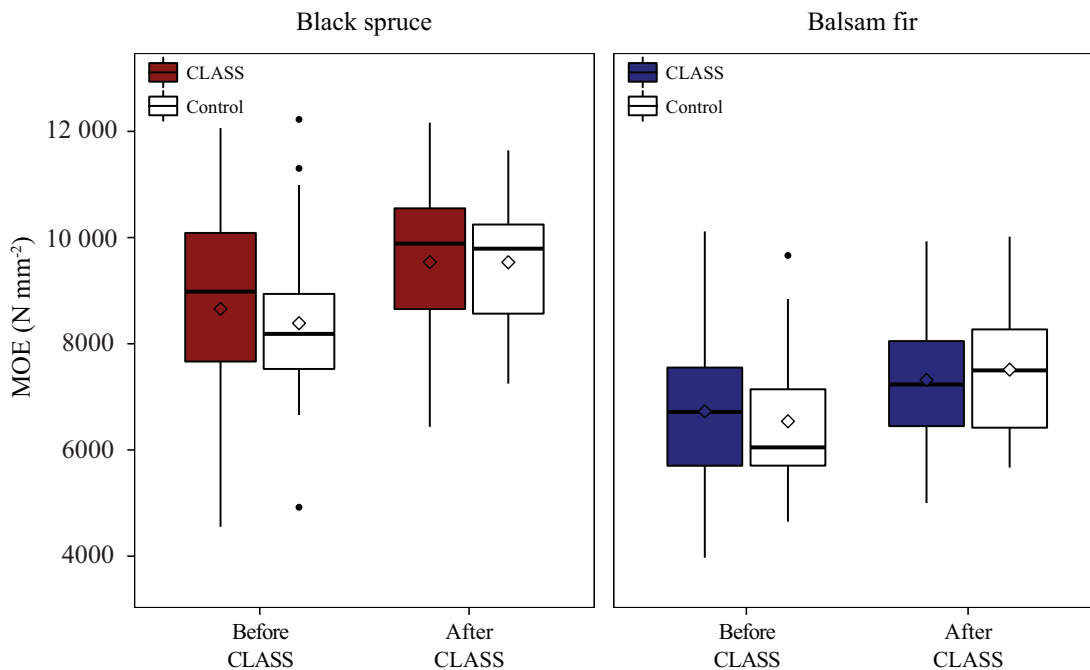


Figure 3.3 Modulus of elasticity (MOE) values before and after CLASS for black spruce and balsam fir. The black horizontal line represents the median and the diamond is the mean.

The canonical discriminant analysis showed that for both species, there was no significant difference in the wood properties of treated trees between the periods before and after treatment (Wilks' Lambda statistic: $P=0.0820$ for black spruce and $P=0.4233$ for balsam fir). We can observe that there is more variability in the canonical variables representing the wood quality parameters in the period after CLASS, but both groups are relatively close to each other (Figure 3.4) and could not be statistically separated. The same was observed for control trees (results not shown).

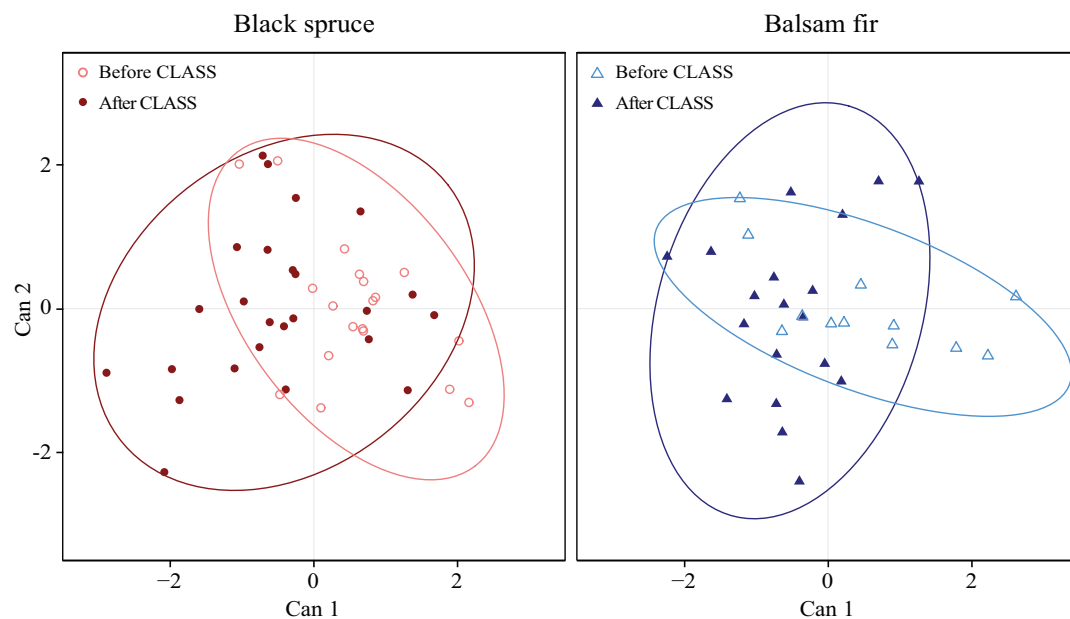


Figure 3.4 Canonical representation of the wood quality parameters in the periods before and after CLASS for black spruce and balsam fir. Ellipses represent 95% of the data.

3.5 DISCUSSION

3.5.1 Growth response

Results confirmed that careful logging around small merchantable stems (CLASS) increases the growth of residual stems in the years after harvest. A large proportion of individuals showed an increase in radial growth at breast height following the treatment, both when compared with untreated controls and pre-treatment growth. Several studies have already shown a positive radial growth response of residual stems following a release from their neighbours, either through a commercial thinning (Mäkinen and Isomäki, 2004; Vincent *et al.*, 2009; Pamerleau-Couture *et al.*, 2015) or with other types of partial cuts (Bebber *et al.*, 2004; Thorpe *et al.*, 2007; Deal *et al.*, 2010; Pamerleau-Couture *et al.*, 2015).

In black spruce, a significant radial growth increase following CLASS was only observed four years after treatment. This delay in the treatment response was also observed by Vincent *et al.* (2009) and Thorpe *et al.* (2007) for black spruce and Bebber *et al.* (2004), Latham and Tappeiner (2002) and Youngblood (1991) for other species. It is likely that in the first three years, the additional resources are allocated to root growth as a priority rather than shoot growth (Kneeshaw *et al.*, 2002; Ruel *et al.*, 2003; Vincent *et al.*, 2009), which can improve tree stability (Krause *et al.*, 2014).

In addition, such a response may increase the uptake and transport capacities for water and nutrients so that trees can cope with the greater wind penetration in the stand (Ruel, 1995) and the associated higher evapotranspiration (Kneeshaw *et al.*, 2002).

As was the case for black spruce, a radial growth increase was observed after treatment in balsam fir stems. However, at three years, the response delay was shorter, which is similar to what has been observed in other studies on the same species (Solomon and Frank, 1983; Doucet and Blais, 2000). The growth increase was also greater in balsam fir, which is also in line with previous results by Doucet and Blais (2000). True firs (*Abies* genus) usually show a faster response to release than spruce species (McCaughey and Ferguson, 1988) since they tend to show more plasticity in their shoot and crown morphology in relation to light availability (Kohyama, 1980; O'Connell and Kelty, 1994). Hence, balsam fir is better adapted to react rapidly to the environmental changes following the CLASS.

Our study addressed short-term response to CLASS treatment; however, over a longer period of time, balsam fir may eventually lose the advantage it had first acquired over black spruce. Even though the response of black spruce occurred later and its growth rate was lower than that of fir in the first few years, the species is

known to have a more “conservative” growth pattern as it can maintain its growth over a longer period of time and ultimately surpass fir (Doucet and Boily, 1995; Doucet and Blais, 2000).

3.5.2 Wood properties

For black spruce, the latewood proportion did not change after CLASS and stayed similar to controls in the years after cutting. Likewise, no significant effect of the treatment was detected on average ring density for this species. After thinning in conifer stands, it is generally considered that the growth response of the earlywood part of the ring is proportionally greater than that of the latewood, possibly as a result of the increased need to transport water in the sapwood (Barbour *et al.*, 1994; Kneeshaw *et al.*, 2002). The resulting decrease in the proportion of high-density latewood also leads to a decrease in the overall ring density (Zhang, 1995; Koga *et al.*, 2002; Jaakkola *et al.*, 2005a; Franceschini *et al.*, 2013). However, in this study, even if the CLASS had a significant positive effect on the radial growth, this growth increase comprised an increase in the width of both earlywood and latewood. Peltola *et al.* (2007) and Tasissa and Burkhart (1998) also noted that a thinning operation did not alter the proportion of the ring in earlywood or latewood and as a result had no effect on wood density. Furthermore, a high intensity thinning tends to decrease the density of earlywood and increase the density of latewood, which results in no change

in the average ring density (Moschler *et al.*, 1989; Peltola *et al.*, 2007). This is exactly what was observed here after CLASS (Figure 3D-E), which could explain the results obtained with average ring density.

Black spruce trees showed an increasing trend in tracheid length in the period preceding the treatment, and this trend was only maintained in the control trees after treatment. This might be explained by the fusiform initials of the cambium, which tend to grow in length with cambial age as a result of the declining ratio of anticlinal to periclinal divisions (Lachenbruch *et al.*, 2011). Hence, with increasing cambial age, longer tracheids tend to be formed from these initials (Dinwoodie, 1961; Shmulsky and Jones, 2011). This might also explain the difference that was present even before treatment between treated and control trees, as treated trees were generally of lower cambial age than control trees.

For many conifer species, an increase in radial increment following thinning is linked to a decrease in mechanical properties, such as the moduli of elasticity and rupture (Jozsa and Middleton, 1994; Zhang, 1995; Shmulsky and Jones, 2011). In our study, MOE and MOR values were unaffected by the CLASS treatment in both black spruce and balsam fir. Thus, the accelerated growth in the years after the CLASS had no effect on the bending strength and stiffness, as was reported in studies by Gagné *et al.*

(2012), Guller (2007) and Vincent *et al.* (2011), which examined wood properties in conifers following thinning treatments.

Aside from the results for tracheid length and mechanical properties, balsam fir showed a somewhat different trend than black spruce with regards to wood properties. Contrary to the results for black spruce, a significant decrease in the latewood proportion is noticeable in balsam fir from years six to ten after CLASS (Figure 3.2B), in years when the ring was on average more than three times wider than it was before treatment. Average ring density also decreased in the years following treatment. Jaakkola *et al.* (2005a) noted that large increases in tree growth, higher than those achieved by conventional thinning treatments, are required to create substantial reductions in wood density. This could be the case here with balsam fir, where a decrease in the average ring density is visible when the radial growth increase is at its strongest. Lindström (1997) asserted that wood density depends on latewood proportion and radial diameter of earlywood tracheids. Indeed, it appears that the latewood proportion is not the only factor determining ring density since, after the CLASS treatment, the observed ring density decrease in balsam fir occurs from the third year after treatment (Figure 3.2C) while the decrease in latewood proportion occurs only from the sixth year after the partial cutting (Figure 3.2B). The ring density reduction could be interpreted as a result of a decrease in the width of the earlywood cell walls after CLASS (Pamerleau-Couture, 2011), albeit not sufficiently

important to cause a statistically significant reduction in earlywood density, combined with the change in latewood proportion that was observed.

Balsam fir is known for the low quality of its wood (Zhang and Koubaa, 2009), especially in terms of mechanical properties (Mullins and McKnight, 1981). This was confirmed in our study, with an average ring density 17% lower and with MOE and MOR values around 23% lower than black spruce. However, latewood proportion is similar for both species. Given this result, the difference in average ring density is likely due to anatomical differences between the two species. Tracheids of both species are the same length on average, but the balsam fir tracheid diameter is slightly larger (30 to 40 μm) than black spruce (25 to 30 μm) (Zhang and Koubaa, 2009). With cell walls of similar size in earlywood and a little thinner in latewood (Krause *et al.*, 2010), balsam fir is left with a smaller cell wall-lumen ratio than black spruce, which could explain the lower density, given that the density of cell walls shows little variation across species (Butterfield, 2003). These inferior wood density values combined with a higher lignin content in balsam fir than black spruce (Zhang and Koubaa, 2009) could also induce a lower mechanical resistance since the tension strength and resistance to rupture decreases as the amount of lignin increases (Zobel and Van Buijtenen, 1989).

3.5.3 Growth vs Wood quality

The CLASS treatment led to a significant growth response of the residual stems of both species without major changes in the wood properties observed. However, pre-treatment comparisons of wood properties from treated vs. control trees contrasted with those of radial growth for both species. Whereas the mean ring width and, to a lesser extent, latewood percentage profiles over time were very similar before treatment, those of ring density and tracheid length tended to show some differences. These add complexity to the interpretation of the treatment effect. In our specific case, differences were to be expected because of the stand structure changes due to the treatment. Indeed, the CLASS harvest implies that all stems with a DBH over 14 cm are harvested in a stand with an irregular structure. Residual stems will therefore unavoidably be smaller than the pre-harvest stand average. They are also likely to have developed in the shade prior to the CLASS treatment, and in this study results showed that they tended to be younger on average than the control stems. The higher density and shorter tracheids of treated trees prior to the year of treatment are characteristics of wood found near the pith. Telewski (1989) referred to this as “flexure wood”, and explained that such wood forms under the influence of flexural stresses and has the function of resisting the complex loading patterns to which small stems are submitted. Therefore, a potential unexpected outcome of the application of the CLASS treatment is that the stems harvested at the end of the next rotation may contain more flexure wood than stems that have regenerated after a clearcut or other

major disturbance. A similar pattern could explain the observation of Torquato *et al.* (2014) that wood from irregular stands has lower stiffness than wood from even-aged stands.

Despite this, the comprehensive examination of the wood properties of the treated trees contained in the canonical discriminant analysis (Figure 3.4) did not reveal any significant differences between the periods before and after treatment for either black spruce or balsam fir. This means that overall, wood properties in treated trees were not significantly affected by the CLASS in the 10 years following treatment, although some wood quality parameters taken individually were affected, mainly in the case of balsam fir. It could be argued that in such a situation wood quality could still be adversely affected by the treatment due to a change in the uniformity of growth rings (Moschler *et al.*, 1989). However, the benefits of the gain in volume per stem are very likely to surpass the limited negative effects that could be linked to the treatment (Bendtsen, 1978).

3.6 CONCLUSIONS

In light of the results obtained, CLASS appears to be a good silvicultural option to preserve greater structural variability in uneven-aged stands while stimulating the radial growth of residual black spruce and balsam fir stems, which supports our first hypothesis regarding the effect of the treatment on stem growth. As for the quality of the wood produced in the years following CLASS, we had hypothesised that the increased radial growth would cause a decrease in latewood proportion and ring density. This was not the case for black spruce, but was confirmed for balsam fir. However, our third hypothesis regarding a decrease in mechanical properties was refuted, as we did not observe any measurable consequence of the increased growth and lower wood density on the MOE and MOR values. A canonical discriminant analysis revealed that in general, the wood properties compared before and after treatment did not differ, which leads us to believe that the changes observed on the individual wood properties would not reduce the value or change the suitability of the wood for a given end-use. A study over a longer period of time remains necessary to assess the extent of the treatment effect on ring width and wood properties. Additional studies on other parameters such as stem taper, branch diameter, proportion of compression wood, wall thickness and lumen diameter could also provide further information concerning the wood quality of the stems after CLASS.

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CHAPITRE IV

COMPARISON OF WOOD DENSITY IN ROOTS AND STEMS OF BLACK SPRUCE BEFORE AND AFTER COMMERCIAL THINNING

PUBLISHED RESEARCH PAPER

Title: Comparison of wood density in roots and stems of black spruce before and after commercial thinning

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4.1 ABSTRACT

Roots play an important physiological and mechanical role in the survival and growth of a tree, but also in the success of silvicultural treatments. Studies comparing the xylem in roots and stems have shown that conifer tracheids tend to be wider and longer in roots, which renders root wood less dense and more susceptible to cavitation and embolism. The increased radial growth often observed after thinning may induce changes in wood anatomy that could alter wood properties, such as wood density, in the stem and roots. The aim of this study was to compare growth, wood density and tracheid dimensions between the stem and roots of black spruce trees growing in the boreal forest. We also evaluated whether these wood properties were altered by the application of a commercial thinning treatment. Six black spruce trees were harvested in four commercially thinned stands. Samples were collected from the stem and two locations of each root. Radial growth, wood density and tracheid dimensions were measured on each sample. Results show that all wood density components, especially earlywood density, were higher in the roots than in the stem in black spruce. This denser wood in roots might provide increased safety against cavitation in a part of the xylem where hydraulic stresses are higher. After thinning, growth was increased in the stem and particularly in roots, resulting in slight wood density decreases, which should not influence the vulnerability of roots to cavitation or wood quality in the stem. These results lead us to suppose that the hydraulic network of the black spruce root system may not be so vulnerable to cavitation.

4.2 INTRODUCTION

The stem and roots of trees are both physiologically and mechanically important, but survival and growth are to a great extent determined by the root system. Roots provide anchorage and stability (Danjon and Reubens, 2008), as well as the water and nutrients needed for growth and development, and are important for storage of reserves and synthesis of certain growth hormones (Pallardy, 2008). Despite its importance, the root system of mature trees receives less scientific attention than the stem because of the difficulty in accessing the roots and the lack of commercial interest in this part of the tree (Fayle, 1968; Marcati *et al.*, 2014).

Most of the water taken up and transported by the root system is returned to the atmosphere via transpiration (Jackson *et al.*, 2000). This long-distance water transport in the soil-plant-atmosphere continuum requires an efficient conduit network (Holbrook and Zwieniecki, 2005) that is also resistant to cavitation and embolism. Cavitation, which refers to the formation of water vapor bubbles in columns of water subjected to tensile stresses that exceed the tensile strength of water, results in the formation of an embolism that breaks the continuity of the water column, preventing water transport in this part of the xylem (Tyree and Sperry, 1989; Hacke *et al.*, 2001; Niklas and Spatz, 2012).

Vulnerability to cavitation is known to be influenced by the structure of the xylem (Hacke *et al.*, 2001). Strong conduits with a high proportion of wall material per unit volume will be resistant to implosion and provide protection against cavitation (Sperry, 2003). The amount of cell wall material is a strong determinant of wood density because the density of the cell wall material itself is rather constant in wood (Panshin and De Zeeuw, 1970; Saranpää, 2003). Denser wood is thus considered to be more resistant to xylem cavitation and confers a greater hydraulic safety (Meinzer *et al.*, 2003; Jacobsen *et al.*, 2005). However, density is also determined by the dimensions of the cells (Butterfield, 2003), and in turn their length, diameter, and wall thickness can all influence xylem flow resistance, protection against cavitation and risk of wall collapse (Sperry *et al.*, 2006).

Studies comparing the vulnerability of root and stem xylem have shown that roots are more vulnerable to cavitation (Alder *et al.*, 1996; Hacke and Sauter, 1996), suggesting that they might be the weakest point along the hydraulic network from soil to atmosphere (Jackson *et al.*, 2000). Conduits tend to be wider and longer in roots than in stems (Bannan, 1965; Fayle, 1968; Patel, 1971), which presumably renders root wood less dense and more susceptible to cavitation and embolism. The earlywood part of the growth ring, which is where the lowest wood density values are generally found, presents the highest vulnerability to cavitation in the xylem of roots and stems (Dalla-Salda *et al.*, 2009). On the contrary, maximum wood density values

are normally obtained in the latewood, which gives the mechanical resistance (Stokes and Mattheck, 1996).

Roots also play an important role in the success of silvicultural treatments. For instance, the canopy opening following commercial thinning makes forest stands more susceptible to windthrow (Cucchi and Bert, 2003; Riopel *et al.*, 2010; Lavoie *et al.*, 2012), due to the greater wind penetration into the residual stand (Achim *et al.*, 2005). Tree stability, which depends greatly on the development of the root system, must be maintained or increased in order to withstand wind-induced loading and support the enhanced growth that is expected after thinning (Vincent *et al.*, 2009; Krause *et al.*, 2014). Thinning is also associated with higher transpiration at tree level, and thus a greater need for water uptake from the roots (Gebhardt *et al.*, 2014; Boczoń *et al.*, 2016). In parallel, the increased radial growth often observed after thinning may induce changes in the wood anatomy that could alter wood properties of the stem and roots, especially wood density and tracheid dimensions (Lemay *et al.*, 2016; Pamerleau-Couture, 2016). Such changes could have an impact on water transport and vulnerability to cavitation. Stem and root wood anatomy have been reported to vary in similar ways, but to a greater extent in the roots (Cutler, 1976). Roots could thus be more affected by thinning, which could increase their vulnerability to cavitation.

This study focuses on black spruce (*Picea mariana* (Mill.) B.S.P.), which is one of the most widely distributed conifer species in the North American boreal forest (Viereck and Johnston, 1990). It is a slow-growing species, and has a great economic importance due to its abundance and the quality of its wood (Zhang and Koubaa, 2008). The root system of black spruce consists of several coarse lateral roots extending from the stem near the soil surface, i.e. mostly concentrated in the top 20-30 cm of soil (Strong and LaRoi, 1983). Although water is generally not a primary limiting factor for tree growth in the eastern boreal forest of North America, the shallow depth of their roots makes black spruces somewhat more susceptible to dry spells. In drier periods, the first layer of soil can dry out rapidly, and with a plate root system that limits the ability to draw water from deeper soil layers, vulnerability to cavitation can increase (Cochard, 2006).

The aim of this study was to compare growth, wood density and tracheid dimensions between the stem and roots of black spruce trees growing in the boreal forest. We also evaluated whether these wood properties were altered by the application of a commercial thinning treatment. Our hypotheses were that 1) mean and earlywood density are lower and tracheid dimensions larger in the roots than in the stem, 2) thinning has a proportionally greater effect on radial growth in the roots than in the stem, and 3) all wood density components and tracheid dimensions are lower in both parts of the tree as a result of the increase in radial growth.

4.3 MATERIAL AND METHODS

4.3.1 Study sites and tree sampling

Four even-aged black spruce stands covering an east–west gradient were sampled in the Saguenay-Lac-Saint-Jean, Abitibi-Témiscamingue and Côte-Nord regions of Quebec, Canada, between $48^{\circ} 41'$ and $50^{\circ} 30'$ N and $68^{\circ} 47'$ and $70^{\circ} 22'$ W (Figure 4.1). All stands had similar characteristics in terms of species composition, density and stem diameter. A commercial thinning had been conducted in each stand about ten years prior to sampling, i.e. between 1997 and 2000.



Figure 4.1 Localisation of the study sites.

At each site, 6 black spruce trees were chosen randomly from the dominant or codominant stems in 400 m² plots. Sample trees were healthy-looking, free of visible injuries or defects and located at least 2 m away from a logging trail. For each tree, height, diameter at breast height (DBH, 1.3 m above the ground), and proportion of live crown were recorded at the time of sampling (Table 4.1).

Table 4.1 Mean tree characteristics (\pm standard deviation). AT: Abitibi-Témiscamingue, CN: Côte-Nord, LSJ: Lac-Saint-Jean.

Site	Number of roots	DBH (cm)	Height (m)	Crown ratio (%)	Age at thinning
AT	10.5 (4.2)	14.6 (2.3)	14.8 (0.7)	54.2 (16.0)	86.0 (2.5)
CN	8.7 (1.9)	17.7 (3.1)	14.1 (2.1)	47.2 (6.7)	71.2 (2.2)
LSJ1	9.2 (2.3)	17.8 (1.4)	16.8 (1.6)	49.4 (10.5)	70.2 (4.3)
LSJ2	9.8 (2.9)	15.9 (1.3)	14.3 (0.8)	68.1 (11.6)	70.8 (2.7)

Samples from the stem and roots were collected from each tree. On the stem, two adjacent discs were harvested at 1.3 m to measure radial growth and wood properties (wood density and tracheid dimensions). The root systems were excavated within a radius of 60 cm around each tree. In this way, we obtained the part of the root system responsible for tree stability and anchorage (Coutts, 1987; Danjon *et al.*, 2005; Danquechin Dorval *et al.*, 2016) since most soil movements induced by mechanical loads on the stem occur between 35 and 50 cm around the stem (Stokes, 1999).

Within the root system, all roots exhibiting a diameter >2 cm were sampled at two different locations (Figure 4.2A). A first 10-cm-thick section was taken close to the root-trunk interface (proximal part of the root) and a second one at a distance of 60 cm from the root–trunk interface (distal part). These were used to measure root radial growth and wood properties (density and tracheid dimensions). In the event that a root branched, we collected distal samples from all branches. A total of 615 root sections were sampled on 229 roots, from 24 harvested trees.

4.3.2 Radial growth

All stem and root discs were dried and sanded to increase the contrast of the tree-ring delineations. With the first disc collected at breast height, annual ring widths were measured to the nearest 0.01 mm along four radii using the WinDendro software (Regent Instruments Inc. Québec, QC, Canada). When discontinuous or very narrow growth rings were present, a LINTAB measurement table together with the TSAP-Win program (Rinntech, Heidelberg, Germany) were used instead. A similar procedure was applied to each disc from both sampling locations in the roots, but due to the eccentric growth of the roots and the sometimes large number of discontinuous rings, only one radius per root section was measured where the most growth rings were visible (Krause and Eckstein, 1993), which was generally on the upper part of the root (Figure 4.2B). As black spruce is a slow-growing species, growth rings were

generally narrow; in the stem, mean ring width was 0.96 mm, while in the proximal and distal roots, ring width was on average 1.01 and 0.53 mm, respectively.

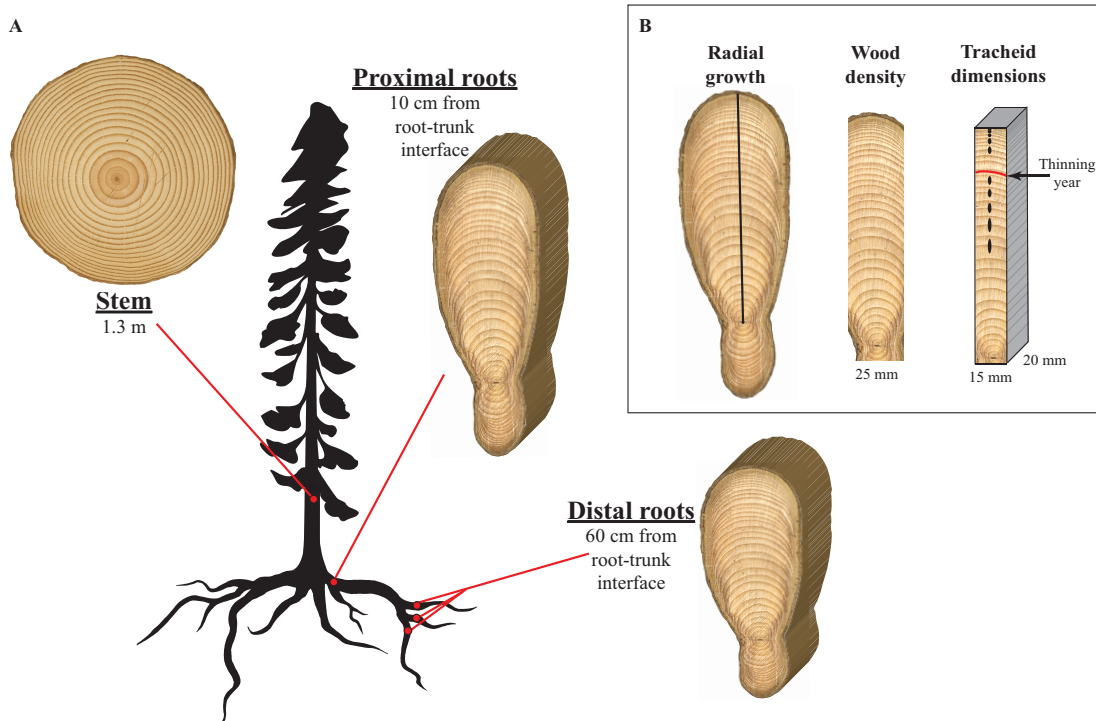


Figure 4.2 Sampling locations in the stem and roots (A). All roots in the root system were sampled in the same way. An example of sample preparation in the roots for measurements of radial growth, wood density and tracheid dimensions is shown in B.

The ring width series in the stem were corrected by visual cross-dating (Stokes and Smiley, 1968; Fritts, 1976) and statistically verified by the COFECHA program (Holmes, 1983). The cross-dated mean curve of the stem allowed a comparison of ring widths in the corresponding proximal and distal roots sections. Overall, 97% of

root sections were successfully dated. Cross-dating was not possible in 17 of the 615 root series (2.7%), due either to decay or because the series were too short. Only the 598 accurately cross-dated sections were used for successive analyses.

Data were standardized using the Arstan program by selecting a negative exponential function in the stem samples and a horizontal mean for the roots series (Cook and Holmes, 1986). Auto-correlation within the data was not removed to keep the ecological signal of the thinning event (Krause *et al.*, 2014).

4.3.3 Wood density

In the stem, wood properties measurements were taken on radial segments from the second disc collected at breast height. For the underground part, five roots per tree were selected, which had to be at least 4 cm wide to allow adequate sample preparation for wood density analyses.

Wood density profile measurements were taken on radial segments in the stem and in the proximal and distal roots (Figure 4.2B). Wood strips 1.63 mm thick (longitudinal) and 25 mm wide (tangential) were dried under restraint to 12% moisture content in a

conditioning room at 20 °C and 65% relative humidity (Alteyrac *et al.*, 2006). Measurements were taken from bark to pith, or bark to stele in the roots, on unextracted samples using a QTRS-01X Tree Ring Scanner and X-ray densitometer (Quintek Measurement System, Knoxville, TN, USA). Working from the raw data from the wood density profiles and using an algorithm developed by Genet *et al.* (2013) using the R statistical software (R Development Core Team, 2014), the boundary between consecutive growth rings was defined as the point where the maximum change in density was reached (Mothe *et al.*, 1998; Lemay *et al.*, 2016). Mean ring density and several within-ring density characteristics were obtained, including mean earlywood and latewood density, minimum earlywood density and maximum latewood density.

4.3.4 Tracheid dimensions

Because the process of sample preparation and measurement is very time consuming, tracheid dimensions were measured on a subsample of only one site (the CN site). A 20-mm-thick (longitudinal) and 15-mm-wide (tangential) piece of wood from the breast height disc in the stem and from both sampling locations in the roots was used to determine tracheid length and width (Figure 4.2B).

Five samples were analysed both before and after thinning, each comprising 2 consecutive growth rings separated manually with a razor blade. All samples were macerated in a solution of glacial acetic acid and hydrogen peroxide (1:1, v/v) at 75 °C for 15 h (Franklin, 1945). The macerated samples were carefully rinsed with distilled water and gently shaken to obtain a uniform suspension to be measured with an L&W FiberTester (Lorentzen & Wettre, Kista, Sweden). For each sample, a length-weighted mean tracheid length and width was calculated based on image analysis (Robertson *et al.*, 1999). This method allows rapid determination of tracheid length and width and is less sensitive to the presence of a large number of fines generated during preparation (Robertson *et al.*, 1999; Mäkinen *et al.*, 2015). A total of 5000 tracheids were measured per sample.

4.3.5 Statistical analyses

Growth and wood quality parameters for the periods before and after thinning were compared using an analysis of covariance (ANCOVA) for repeated measurements. As the data were hierarchical, linear mixed-effect models were used. All models were fitted using the “lme” function of the “nlme” package (Pinheiro *et al.*, 2017), with estimation of the restricted maximum likelihood (REML). An autoregressive covariance structure AR(1) was applied to model the autocorrelation of individual measurements within stem and roots. A covariate, calculated as the mean of the

growth or wood quality parameter for the 10 years prior to analysis, was used to account for differences between the selected trees. Separate models were tested for the period before and after thinning.

Factors such as the sample location (stem, proximal root, distal root), year and their interaction were entered in the models as fixed effects, as well as the 10 years-before mean as covariate. Roots were nested within their corresponding tree, and trees were nested within their corresponding site, which were considered as random factors. To analyse how growth and wood properties differed according to sample location, we used orthogonal contrasts to test whether there were differences between stem and roots, and between the two roots locations. Standard procedures for model diagnostics were conducted and verified for all analyses.

For each growth and wood property, a paired t-test was used to assess the overall difference between before and after thinning, and to determine whether this difference was statistically significant. As we disposed of a period of only 10 years after thinning, a mean of the 10 years before thinning was tested against a mean of the 10 years after thinning.

Data were log transformed (or $\log(x + 0.1)$ in the case of growth index data) when necessary to meet ANOVA assumptions. Data presented in figures are means (± 1 SE) of untransformed data. Differences at $P < 0.05$ were considered significant. All analyses were performed using R version 3.3.3 (R Development Core Team, 2017).

4.4 RESULTS

4.4.1 Radial growth

Dendrochronological analyses showed that the root samples were younger than the stem samples. Stems contained 73 ± 14 rings, while roots were 10 and 15 years younger in the proximal (63 ± 17) and distal (58 ± 17) sampling locations, respectively. Time series correlations between stem and roots were acceptable to good, ranging from 0.302 to 0.512 between stems and proximal roots, and from 0.305 to 0.429 between stems and distal roots. The two root sections had a mean correlation of 0.665, with a minimum of 0.611 and maximum of 0.725.

Growth indices of the stem and roots of black spruce varied between 0.7 and 1.2 in the years prior to commercial thinning, but varied differently in time in each part of the tree (Figure 4.3, Table 4.2). The root growth indices were slightly higher at first

and decreased slowly until the thinning year, while the stem growth index was more constant during the same period. After thinning, the growth indices increased significantly in both stem and roots, especially in the distal root sections. Growth trends in the stem and the two root locations were different over time as the interaction between sample location and year was highly significant. Contrasts showed that the growth index was significantly higher in distal than in proximal roots, but that growth in the two root locations taken together was not significantly different from that of the stem (Table 4.2).

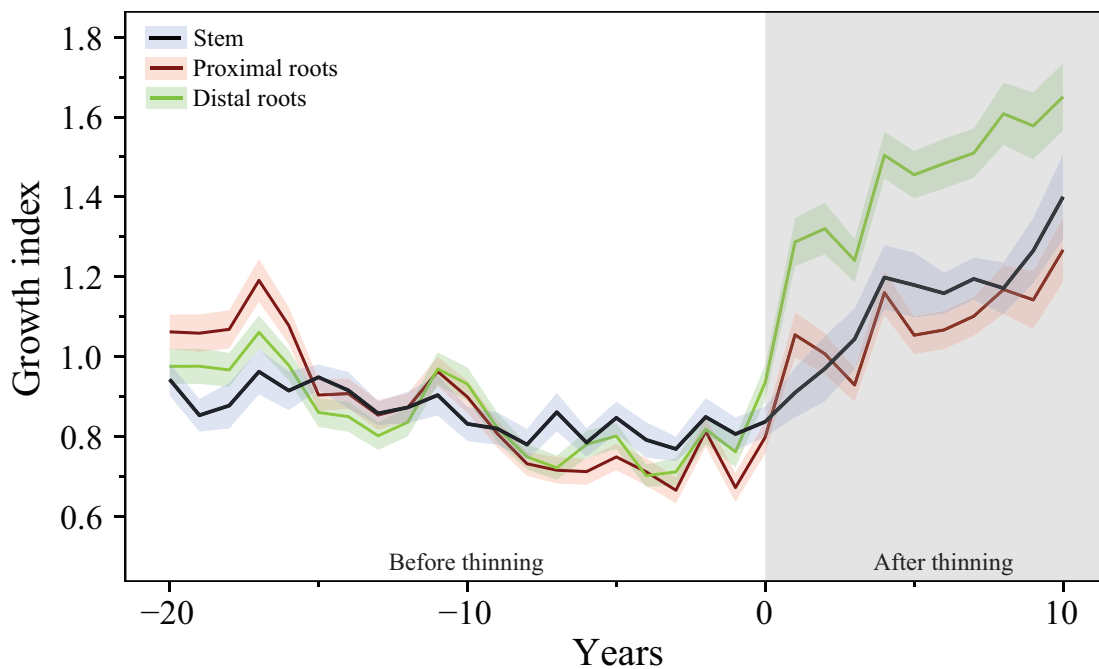


Figure 4.3 Radial growth index of stem and roots of residual black spruce trees before and after commercial thinning. The shaded area represents the period after thinning, with year 0 being treatment year.

Table 4.2 Repeated measures ANCOVA results for growth and wood quality parameters in black spruce tested in the periods before and after commercial thinning. The 20-year before mean represents the mean value of the 20 years prior to thinning for each parameter.

		Before thinning		After thinning	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Radial growth	Location	11.41	<.0001	26.95	<.0001
	– Stem vs roots		<.0001		0.9046
	– Proximal vs distal roots		0.0601		<.0001
	Year	17.53	<.0001	13.06	<.0001
	20-year before mean	143.06	<.0001	16.87	<.0001
	Location: Year	2.91	<.0001	1.68	0.0352
Mean ring density	Location	117.10	<.0001	56.03	<.0001
	– Stem vs roots		0.0133		0.0283
	– Proximal vs distal roots		0.0431		0.0954
	Year	7.90	<.0001	6.48	<.0001
	20-year before mean	507.80	<.0001	244.85	<.0001
	Location: Year	0.90	0.5704	0.71	0.7995
Earlywood density	Location	493.30	<.0001	225.40	<.0001
	– Stem vs roots		0.0004		0.0484
	– Proximal vs distal roots		0.1718		0.3192
	Year	5.70	<.0001	5.50	<.0001
	20-year before mean	1985.70	<.0001	805.80	<.0001
	Location: Year	1.10	0.4327	1.10	0.2987
Latewood density	Location	9.19	0.0001	17.88	<.0001
	– Stem vs roots		<.0001		0.0694
	– Proximal vs distal roots		0.5934		0.0748
	Year	3.47	0.0003	2.17	0.0214
	20-year before mean	1753.92	<.0001	622.93	<.0001
	Location: Year	1.59	0.0555	1.16	0.2817
Minimum density	Location	124.80	<.0001	46.78	<.0001
	– Stem vs roots		0.0310		0.0183
	– Proximal vs distal roots		0.0053		0.1174
	Year	7.01	<.0001	5.18	<.0001
	20-year before mean	321.24	<.0001	118.23	<.0001
	Location: Year	1.40	0.1117	0.99	0.4631

Maximum density	Location	4.61	0.0101	0.20	0.8002
	– Stem vs roots		<.0001		0.0055
	– Proximal vs distal roots		0.4506		0.6352
	Year	4.64	<.0001	3.60	0.0002
	20-year before mean	875.90	<.0001	266.60	<.0001
Location: Year		1.43	0.1064	0.90	0.5385
Tracheid length	Location	1294.35	<.0001	141.98	<.0001
	– Stem vs roots		0.0177		0.0402
	– Proximal vs distal roots		0.3132		0.3405
	Year	3.26	0.0127	5.73	0.0002
	10-year before mean	1169.13	<.0001	79.44	<.0001
Location: Year		1.90	0.0617	1.43	0.1826
Tracheid width	Location	70.50	<.0001	4.53	0.0117
	– Stem vs roots		0.0435		0.0075
	– Proximal vs distal roots		0.0950		0.2861
	Year	14.00	<.0001	1.32	0.2640
	10-year before mean	7734.60	<.0001	79.15	<.0001
Location:Year		2.50	0.0133	1.06	0.3900

4.4.2 Wood density

Mean ring density was significantly lower in the stem compared to both root locations (Figure 4.4, Table 4.2). In the stem, the mean ring density ranged between 500 and 550 kg m⁻³, while in the proximal and distal roots, ring density varied between 600 and 675 kg m⁻³, which is 18-22% higher than in the stem. Before thinning, the distal root sections had a higher ring density than proximal root sections, but density decreased in distal root sections after thinning to become similar to that of the proximal root sections.

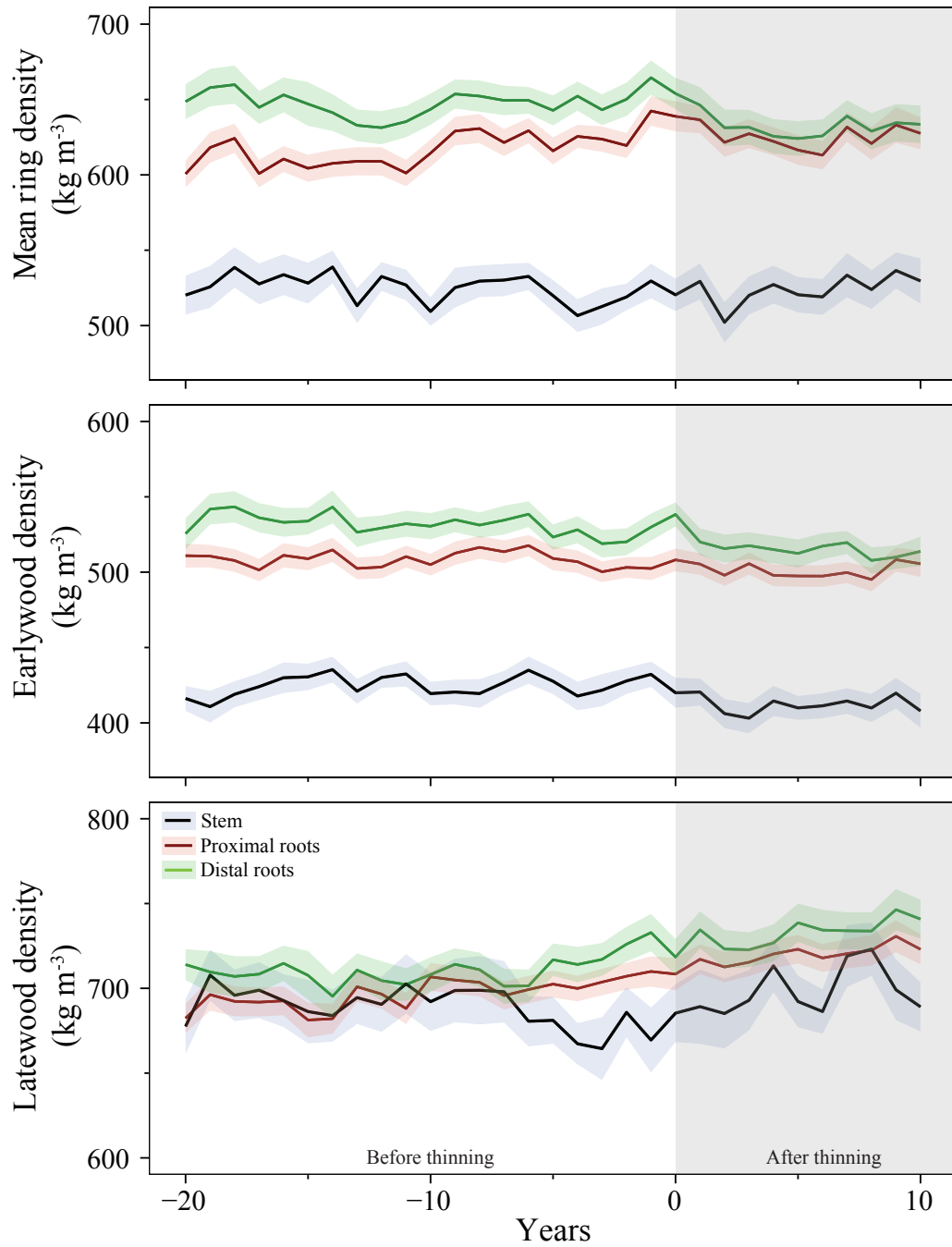


Figure 4.4 Ring density components of stem and roots of residual black spruce trees before and after commercial thinning. The shaded area represents the period after thinning, with year 0 being treatment year.

Earlywood density (EWD) showed similar patterns to those obtained for mean ring density. Stem EWD values ranged from 400 to 430 kg m⁻³, while EWD values in the roots were about 20-25% higher, varying between 490 and 550 kg m⁻³. Stem EWD was significantly lower than in the roots, both before and after thinning, whereas no difference was detected between the two root sampling locations during the whole study period.

Latewood density (LWD) values showed less overall variation than the previous two ring density components with a range of 650 to 750 kg m⁻³ (Figure 4.4). LWD values were similar between stem and roots at the beginning of the monitoring period, but became significantly lower in the stem in the years before thinning (Table 4.2). After thinning, inter-annual variations in the stem were larger but values were not different from those in the roots.

Stems had significantly lower minimum earlywood density (MinD) values (350-380 kg m⁻³) than roots, which were 35% higher and ranged between 450-550 kg m⁻³ (Figure 4.5, Table 4.2). Before thinning, MinD was 9% higher on average in distal than in proximal roots. After thinning, MinD decreased in both root locations, but the decrease was more marked in distal roots, enough to reach values similar to those in

proximal roots. Both stem and roots showed a significant decrease in MinD after thinning (Table 4.3).

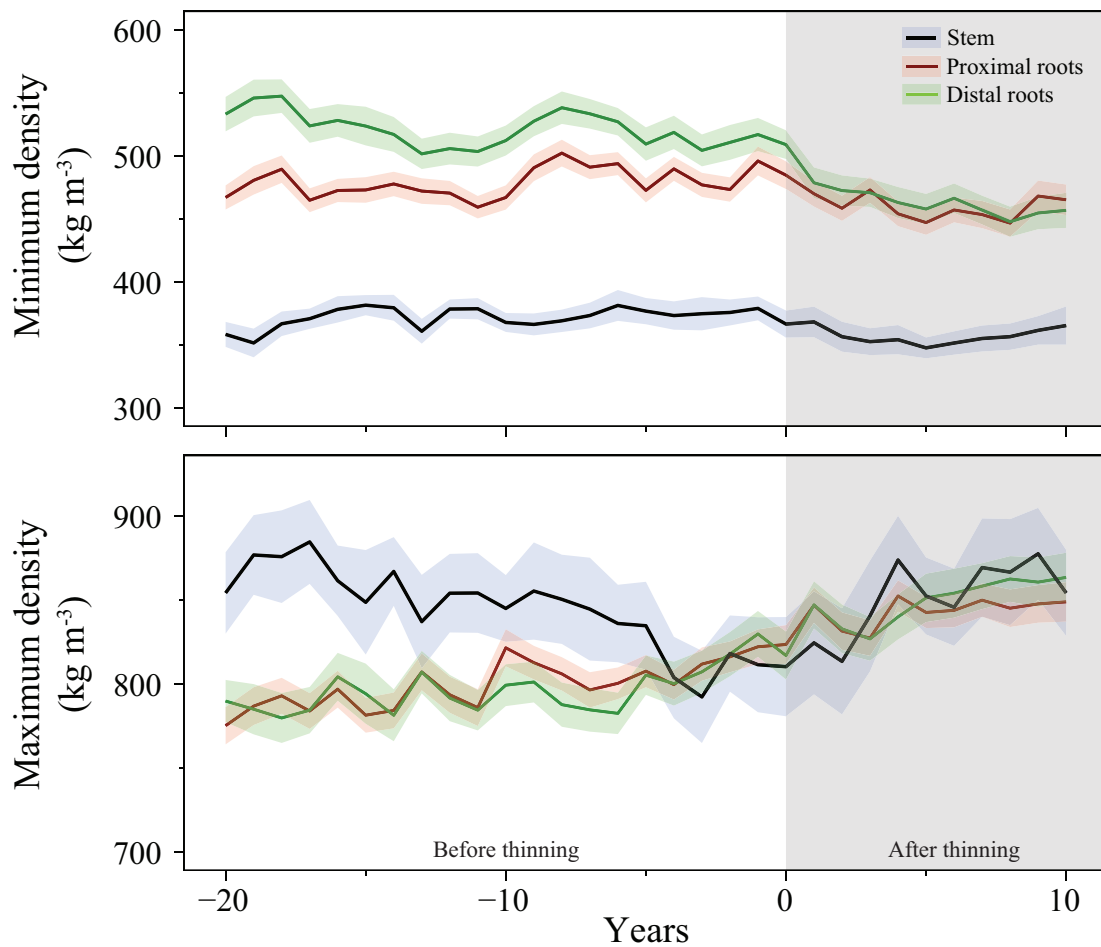


Figure 4.5 Minimum earlywood and maximum latewood density of stem and roots of residual black spruce trees before and after commercial thinning.

The shaded area represents the period after thinning, with year 0 being treatment year.

Maximum latewood density (MaxD) values varied between 775 and 900 kg m⁻³ in stem and roots (Figure 4.5). MaxD values were similar in proximal and distal roots during the whole study period and showed an upward trend that accentuated after thinning. MaxD values in the stem were decreasing before thinning but started to increase after thinning.

For all density components, trends were similar over time as the interaction between sample location (stem, proximal or distal root) and year was never statistically significant (Table 4.2).

4.4.3 Tracheid dimensions

Tracheids were significantly longer in the stem with a length varying between 3.15 and 3.30 mm, while tracheid length in the roots was 20-25% lower, reaching 2.47 mm in proximal roots and 2.65 mm in distal roots (Figure 4.6). No difference was detected between the two locations in the roots, either before or after commercial thinning (Table 4.2).

Variability in tracheid widths was greater, especially in the stem. During the entire study period, values were significantly lower in the stem, while no significant difference was detected between proximal and distal roots.

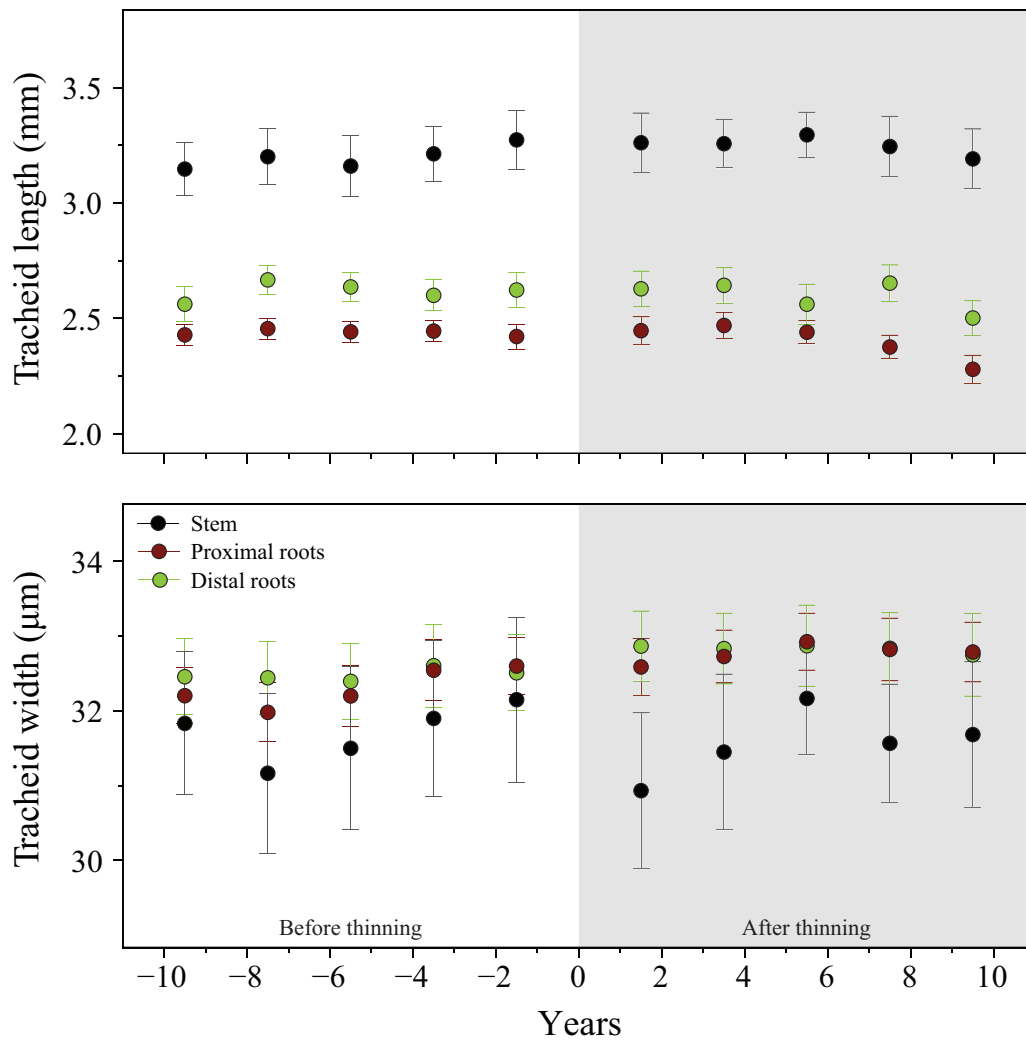


Figure 4.6 Tracheid dimensions of stem and roots of residual black spruce trees before and after commercial thinning. The shaded area represents the period after thinning, with year 0 being treatment year.

4.4.4 Summary of the thinning effect

In the 10 years after thinning, mean radial growth significantly increased in all three locations studied (Figure 4.3, Table 4.3). Wood density was also affected by thinning, especially minimum and maximum density. EWD slightly decreased in all three locations, as well as MinD, which also decreased in both stem and roots up to a mean decrease of 60 kg m^{-3} in the proximal roots. Mean LWD and MaxD significantly increased after thinning, but only in roots and not in the stem (Table 4.3). This resulted in mean ring density remaining within the natural variability in the stem and proximal roots after thinning, although it slightly decreased in the distal root samples. Thinning did not seem to have an important influence on tracheid dimensions as length and width remained within natural variability, except for the mean tracheid width in the proximal roots, which increased by an average of $0.43 \text{ }\mu\text{m}$ in the years after thinning (Table 4.3).

Table 4.3 *P*-values of paired t-test comparing the 10-year before mean to the 10-year mean after thinning for several growth and wood quality parameters.

	Stem	Proximal roots	Distal roots
Radial growth	0.0003	<0.0001	<0.0001
Ring density	0.8879	0.2194	0.0323
Earlywood density	0.0082	0.0011	<0.0001
Latewood density	0.2456	<0.0001	<0.0001
Minimum density	0.0132	0.0031	<0.0001
Maximum density	0.7450	<0.0001	<0.0001
Tracheid length	0.0826	0.3399	0.7590
Tracheid width	0.6417	0.0436	0.1785

4.5 DISCUSSION

4.5.1 Radial growth

Growth in the roots of black spruce is linked to stem growth, a fact that was already observed by (Fayle, 1968) and others more recently (Krause and Eckstein, 1993; Krause and Morin, 1998; Vincent *et al.*, 2009). Trends were similar in both parts of the trees, with a higher growth index in the stem generally corresponding to higher growth in the roots. The correlations between stems and roots, which averaged 0.393 and 0.378 for the proximal and distal roots, respectively, also confirm these trends. In addition, our observations of stem and root growth are in general agreement with

previous studies where thinning induced growth increases (Vincent *et al.*, 2009; Krause *et al.*, 2014).

The growth increases in the stem and proximal sampling location in the roots were similar after thinning, while a stronger response was observed in distal roots, a finding that is consistent with observations from Vincent *et al.* (2009) and Krause *et al.* (2014). An increased growth in roots close to the stem has the effect of increasing the stiffness and strength of the root plate, which provides a greater capacity to resist the higher wind penetration in the stand (Nicoll and Ray, 1996; Coutts *et al.*, 1999). These large roots are the most important for stability (Nicoll and Ray, 1996). Increased growth in root sections located further from the stem may in turn be driven mainly by the need to transport more water and nutrients, since the remaining black spruce trees are more exposed to sunlight and wind after thinning, which causes higher transpiration (Gebhardt *et al.*, 2014). This leads to a greater need for water uptake by fine roots and more transport that has to be assumed by the distal roots. However, these roots also have a mechanical function and even though the increase in proximal root diameter may have a negligible effect on the rigidity of the root plate, it still increases the tensile strength of the roots and therefore tree stability. Thus, the water transport and mechanical functions of the proximal roots cannot be completely dissociated.

4.5.2 Wood density

Greater cavitation resistance requires stronger implosion-resistant conduits with more wall material per unit volume and, hence, denser wood (Sperry, 2003). The roots in our study had higher wood density than stems, except for maximum latewood density. This denser wood in roots might provide increased safety in a part of the xylem where hydraulic stresses are higher. Small roots are especially vulnerable to cavitation (Hacke and Sauter, 1996), which might explain why wood density was higher in distal than in proximal sampling locations.

The higher earlywood density observed in roots could also be interpreted as the result of a cavitation protection mechanism. The earlywood part of the growth ring, comprised of large diameter tracheids, is more efficient in transporting water (Domec and Gartner, 2002) and is responsible for most of the water movement, while the small latewood tracheids often conduct little to no water (Pallardy, 2008). Since most water transport occurs in the earlywood part of the annual ring, it is mainly this part that requires cavitation resistance in the roots. A higher mean and minimum ring density has been linked to higher cavitation resistance by Dalla-Salda *et al.* (2009), and higher wood density to a higher resistance to drought-induced embolism (Hacke *et al.*, 2001).

Our results showed that tracheid width in black spruce was slightly but significantly higher in roots than in the stem. Because density of the cell wall is relatively constant (Panshin and De Zeeuw, 1970), this implies that earlywood tracheid cell walls has to be much thicker in roots for the earlywood density to be higher despite the increased cell width. This is consistent with the observation made by Krause *et al.* (2010) that cell radial diameter and cell wall thickness in earlywood are higher in the roots than in the stem of black spruce, and that lumen area is smaller in roots. Accordingly, the cell wall/lumen ratio in the earlywood is higher in roots, which results in a higher earlywood density that could help roots to preserve their hydraulic system and prevent wall collapse (Hacke *et al.*, 2001; Pittermann *et al.*, 2006b; Sperry *et al.*, 2006).

Based on data from several studies, Sperry *et al.* (2006) suggested that roots are generally less mechanically challenged by bending than the stem. However, Sperry *et al.* (2006) did not distinguish between the type of root (horizontal roots, taproots) or the location in the root system (close to or further away from the stem). Roots are still subjected to important mechanical stresses when the tree is exposed to wind, and the external forces on the stem have to be transferred to the root system. It has been shown that species with plate root systems, such as black spruce, have relatively

stronger wood further along the lateral root (at a distance of 50-100 cm along the root) compared to roots from heart or tap systems, and that the root-wood strength decreased further away from the tree after a strength maximum had been reached (Stokes and Mattheck, 1996). This could explain why proximal roots have a high latewood density because denser wood results in higher compression strength (Stokes and Mattheck, 1996). Another possible benefit of the higher latewood density in roots could be that it provides a better defence against decay, as it has been shown that species with low wood density decayed faster than high-density species (Mackensen *et al.*, 2003).

4.5.3 Tracheid dimensions

Studies on tracheid dimensions in roots are scarce and generally include very few samples per tree and a low number of trees due to the time-consuming analysing process and the difficulty in accessing the samples. The rare findings comparing xylem anatomy in roots and shoots have shown that roots typically have longer and wider conduits (Bannan, 1965; Fayle, 1968; Patel, 1971). Contrary to what is reported in these studies, we observed that tracheids were significantly shorter in roots compared to the stem of black spruce. Fayle (1968) also observed shorter tracheids in the roots of *Picea* species. Pittermann *et al.* (2006b) showed that stronger tracheids, characterised with a higher cell wall/lumen ratio tended to be shorter. We can

suppose that the high wood density values that we obtained in the roots reflect thicker cell walls, which would imply shorter tracheids.

However, our observation that root tracheids were shorter differs from the results Pittermann *et al.* (2006a) and Pittermann *et al.* (2006b), who observed longer and wider tracheids, as well as a lower cell wall/lumen ratio, in the roots of several conifer species. This difference might be explained by the fact that only small roots and stems were sampled in those studies, typically 8-10 mm in diameter in the stem and 6 mm or less in the roots, which thus comprised only juvenile wood. The primary function of such small roots is to transport water and their biomechanical function is mainly associated with the resistance to tensile stress, unlike larger roots that also have to resist bending stresses. Sample roots in our study were much larger, often reaching a diameter of 10 cm even at a distance of 60 cm from the stem, and the period we studied comprised mainly mature wood. Although roots in the distal sampling location are not the most important in the mechanical support of the tree, they are still subjected to bending forces that they must be able to withstand. Patel (1971) showed that tracheid size was greater near the stele in roots and decreased towards the outer rings, which could explain the discrepancy between our results and those of Pittermann *et al.* (2006a) and Pittermann *et al.* (2006b).

The younger cambial age of the roots compared to the stem sampled in our study

might also explain the difference in tracheid length between stem and roots because tracheid length is known to increase from pith to bark, at least in the stem of mature trees (Sanio, 1872; Bannan, 1965; Mvolo *et al.*, 2015). Conversely, it has been reported that tracheids in the inner roots, near the stele, are longer than in the outer rings (Sanio, 1872; Bannan, 1965). Yet, (Patel, 1971) observed much longer and wider tracheids even though the roots were younger than the stems in 37 years old *Pinus radiata*. The authors explained their finding by simply stating that it was generally well accepted that tracheids were longer and wider in the conifer roots than in the stem. Only Fegel (1941) seems to have observed longer tracheids in the stems of many conifer species other than pines. Since we sampled both the stem and roots in the outer rings, near the bark, we obtained wood samples in which the tracheids were the longest in the stem but not in the roots. The fact that we had a small sample number, coming from only one site for the tracheid measurements, might also have had an influence on the results. However, our results show that tracheids cannot be assumed to be systematically longer in the roots than in the stem of conifer trees.

4.5.4 Thinning effect

Although not to the same extent as radial growth, thinning had an effect on wood density. While growth was significantly increased in the stem and both root locations in the years after thinning, some components of wood density tended on the contrary

to decrease following thinning. Mean ring density, earlywood density and minimum density decreased in the years after thinning, especially in the roots. Lemay *et al.* (2016) showed that in black spruce, wood density in the stem was not significantly reduced after a high intensity partial cut, which is in line with our observations. However, no comparable result could be found for roots, in any species. We observed that wood density in the roots was reduced on average by 2-4% compared to before thinning, which is similar to previously observed effects of thinning on wood density in the stem (Jaakkola *et al.*, 2005; Mäkinen and Hynynen, 2014). This lower ring density in the roots might be explained by the increase in ring width after thinning, which is often associated with a higher proportion of earlywood in the ring (Mäkinen *et al.*, 2002b; Todaro and Macchioni, 2011). As earlywood is characterised by cells with large lumens and thin walls, and thus has a low density, a more important proportion of earlywood after thinning results in a lower mean ring density. Furthermore, a faster growth rate reduces cell wall thickness and increases lumen diameter (Mäkinen *et al.*, 2002a; Pamerleau-Couture, 2011). A larger lumen can transport more water, which is necessary to support the higher demand due to the increased tree transpiration after thinning (Gebhardt *et al.*, 2014; Boczoń *et al.*, 2016). Latewood and maximum density seemed to increase after thinning, but the increasing trend was already present in the years before thinning. It was not possible to verify that the increase was really attributable to thinning because control (unthinned) trees were not included in the analysis. Nevertheless, the increasing latewood density in the years after thinning in both the stem and roots suggests that the wood was more

mechanically resistant, which could help trees resist the increased biomechanical stimuli (Ruel, 1995; Achim *et al.*, 2005).

4.6 CONCLUSIONS

Our study of growth, wood density and tracheid dimensions in the stem and roots of black spruce adds some valuable new information about the variation of wood properties in trees, particularly in the roots, which are often overlooked. We observed that wood density was higher in the roots than in the stem in black spruce, and that tracheids were shorter, which refutes our first hypothesis. Black spruce being a slow-growing species suggests that it does not have very high water requirements and instead benefits from a resistant and safe hydraulic network. These results lead us to formulate a subsequent hypothesis that the hydraulic network of the black spruce root system is less vulnerable to cavitation than usually portrayed, and may not be the weakest link in the system. Further studies on cavitation are necessary to verify this.

Commercial thinning resulted in increased growth in both the stem and roots, but the increase was greater in the distal roots. This faster growth had a slight effect on wood density, especially in the earlywood part of the growth ring, which should not influence the vulnerability of roots to cavitation or wood quality in the stem. Overall,

the higher wood density values in roots also make the tree more resistant, which could limit the risk of windthrow after thinning.

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CHAPITRE V

CONCLUSIONS GÉNÉRALES

CONCLUSIONS GÉNÉRALES

5.1 CONTRIBUTIONS DE LA THÈSE

Cette thèse de doctorat avait comme objectif d'évaluer l'effet d'une coupe partielle sur la croissance et les propriétés du bois de l'épinette noire et du sapin baumier en forêt boréale. En s'intéressant à deux espèces, à trois différentes coupes partielles, à différentes échelles temporelles (intra et interannuelle) et à plusieurs propriétés du bois dans deux parties de l'arbre, la thèse a fait ressortir plusieurs résultats inédits et a permis de faire avancer les connaissances sur la réaction des arbres résiduels à la suite d'une coupe partielle, ce qui est essentiel à l'amélioration des méthodes actuelles en sylviculture. De plus, avec les trois chapitres publiés, la thèse s'intéresse à des enjeux pratiques, reliés à la production de bois et la qualité de ce bois à la suite d'une coupe partielle, de même qu'à des éléments de recherche plus fondamentale, comme par exemple l'étude des processus qui expliquent la réaction de croissance des arbres à une coupe partielle. La thèse fait ainsi le lien entre des disciplines telles que la sylviculture, la science du bois, la dendrochronologie et la formation du bois.

L'étude de la xylogénèse et du développement intra-annuel du cerne de croissance en lien avec la pratique d'une coupe partielle apporte de nouvelles informations qui permettent de mieux comprendre comment la xylogénèse est modifiée après une ouverture du couvert forestier. En effet, puisqu'aucun changement n'a été observé dans le *timing* ou la durée des phases de la xylogénèse, c'est plutôt une augmentation du taux de trachéides produites après la coupe partielle qui est responsable de l'augmentation de croissance observée dans les années après la coupe. Ces résultats,

qui s'appliquent autant pour l'épinette noire que le sapin baumier, apportent une meilleure compréhension de la dynamique de la formation du bois, qui est étroitement liée aux propriétés du bois qui est produit par l'arbre.

La thèse apporte également de nouvelles informations sur les effets des coupes partielles sur les propriétés du bois de l'épinette noire et du sapin baumier, des connaissances qui sont essentielles pour l'utilisation du bois transformé. Dans le contexte actuel et futur de convergence vers les produits du bois à haute valeur ajoutée, les propriétés du bois doivent d'être à la hauteur des normes de l'industrie de la transformation. Cette étude permet de s'assurer que les coupes partielles maintiennent un produit final de qualité. Contrairement à plusieurs études qui font état d'une diminution des propriétés du bois chez plusieurs espèces lorsque la croissance est augmentée (Barbour *et al.*, 1994; Koga *et al.*, 2002; Mäkinen *et al.*, 2002b, a; Saranpää, 2003; Jyske *et al.*, 2010), les résultats obtenus dans la thèse démontrent bien que ce n'est pas le cas chez l'épinette noire et que le sapin baumier reste également peu affecté. L'épinette noire est très résiliente à toute modification de son environnement et même de sévères stress l'affectent peu (Balducci *et al.*, 2013; Beliën, 2015). C'est une espèce bien adaptée à différentes conditions et qui réagit peu au changement en raison de sa croissance lente (Viereck et Johnston, 1990). Une coupe partielle, même de forte intensité comme dans le cas de la CPPTM, ne devrait donc pas réduire l'aptitude du bois provenant d'une tige résiduelle d'épinette noire à être utilisé pour un usage précis. Quant au sapin baumier, ce dernier est une espèce qui réagit plus fortement à une ouverture du milieu (McCaughey et Ferguson, 1988; Sullivan et Peterson, 1994; Ministère des ressources naturelles, 2013). Après la coupe partielle, le sapin a effectivement montré une réaction de croissance plus rapide et surtout plus forte que l'épinette noire, qui a entraîné une diminution de certains des paramètres de qualité du bois étudiés dans les années après coupe. Toutefois, en

considérant globalement les propriétés du bois mesurées, il en est ressorti que les propriétés du bois avant et après traitement n'étaient pas significativement différentes chez le sapin, malgré le fait que certains paramètres de qualité du bois pris individuellement montraient une diminution significative. Les usages que l'on pourra faire du bois provenant d'une tige résiduelle de sapin baumier ne devraient donc pas être modifiés. Les résultats obtenus démontrent bien qu'une coupe partielle peut augmenter la production de bois de l'épinette et du sapin, sans toutefois modifier significativement les propriétés du bois à court terme.

Jusqu'à maintenant, le système racinaire avait été encore très peu étudié en raison du manque d'intérêt commercial pour cette partie de l'arbre et de l'accès plus difficile aux racines en comparaison avec la tige. Les résultats obtenus dans la thèse apportent une importante contribution aux connaissances sur la structure du xylème des racines et offrent ainsi une meilleure compréhension de la fonction des racines chez l'épinette noire. L'augmentation de croissance observée dans les racines confirme ce qui avait été mentionné dans de précédentes études sur l'épinette noire à la suite d'une éclaircie (Vincent *et al.*, 2009; Krause *et al.*, 2014). La comparaison des propriétés du bois entre les racines et la tige a fait ressortir un résultat très intéressant, soit l'importante différence de masse volumique entre les racines et la tige. En effet, la masse volumique moyenne du cerne de croissance est environ 20% plus élevée dans les racines que dans la tige. En séparant les composantes de la masse volumique, les résultats ont montré que la différence est encore plus grande pour la masse volumique du bois initial et la masse volumique minimale. La majorité du transport d'eau ayant lieu dans le bois initial (Domec et Gartner, 2002; Pallardy, 2008), la masse volumique plus élevée dans cette partie du cerne de croissance confère possiblement aux racines une protection accrue contre les embolies dues à la cavitation (Hacke *et al.*, 2001; Dalla-Salda *et al.*, 2009). Cette protection supérieure dans les racines par rapport à la

tige est nécessaire puisque les racines, particulièrement les racines fines, sont plus vulnérables à la cavitation, (Alder *et al.*, 1996; Hacke et Sauter, 1996), étant généralement considérées comme le maillon faible de la chaîne de transport de l'eau allant du sol jusqu'aux feuilles (Jackson *et al.*, 2000). Après la coupe partielle, la masse volumique moyenne et les masses volumiques du bois initial et minimale ont légèrement diminué dans les racines lignifiées. Toutefois, ces diminutions étaient associées à une augmentation de la masse volumique du bois final et de la masse volumique maximale, ce qui a limité l'effet sur la masse volumique moyenne des cernes. Le système racinaire de l'épinette noire semble ainsi bien protégé contre la cavitation et une coupe partielle ne devrait pas augmenter les risques de cavitation dans les racines ou la tige. De plus, l'augmentation de la densité du bois final des racines et de la tige après l'éclaircie suggère également que le bois est plus résistant mécaniquement, ce qui pourrait aider les arbres à mieux résister aux stimuli biomécaniques accrus et éviter d'augmenter la susceptibilité aux chablis (Achim *et al.*, 2005).

La thèse a permis d'en apprendre plus sur les deux espèces étudiées, particulièrement concernant les propriétés du bois. Les résultats viennent confirmer une fois de plus que l'épinette noire est une espèce très résiliente, qui réagit peu face aux différents stress qui peuvent l'affecter par rapport à d'autres espèces. En effet, que ce soit un important stress hydrique (Belien *et al.*, 2012; Balducci, 2015) ou une coupe partielle de forte intensité comme dans le cas du troisième chapitre de cette thèse, l'épinette noire change peu sa croissance et les propriétés de son bois, possiblement en raison de sa croissance lente résultant de réactions physiologiques et morphologiques plus lentes. La réaction de croissance est tout autre dans le cas du sapin baumier. Ce dernier réagit fortement dans le cas d'une ouverture de la canopée (chapitres II et III de la thèse; McCaughey et Ferguson, 1988; Doucet et Blais, 2000) et est souvent

fortement affecté à la suite d'une défoliation (Krause et Morin, 1995). Pourtant, il semble que le sapin soit malgré tout assez résilient face aux perturbations. En effet, les propriétés du bois ont été peu affectées après une coupe partielle de forte intensité (chapite III) et l'anatomie du xylème du sapin n'a pas été significativement modifiée après une importante défoliation (Rossi *et al.*, 2009). Les deux espèces paraissent donc bien adaptées pour faire face aux réalités de l'aménagement forestier; elles devraient pouvoir continuer à produire un bois de qualité en plus grande quantité après différents types de coupes partielles.

5.2 IMPLICATIONS DES RÉSULTATS, LIMITES ET PERSPECTIVES

Les résultats du deuxième chapitre montrent qu'une ouverture du couvert forestier a augmenté la production cellulaire dans les tiges et les racines de l'épinette noire et du sapin baumier sans pour autant changer le début et la fin de la xylogénèse. Puisque la saison de croissance n'est pas décalée dans le temps ou étendue sur une plus longue période, cela laisse supposer qu'une coupe partielle ne place pas les arbres dans une situation de risques accrus de dommages dus aux gels au moment de l'initiation de la croissance ou plus tard en fin saison. Ce résultat devrait être rassurant pour les gestionnaires de la forêt, particulièrement dans le contexte actuel de changements climatiques, où de plus en plus de conditions extrêmes sont à prévoir. Par contre, comme l'expérience a uniquement été appliquée à un faible nombre d'individus, dans une seule localisation et avec une coupe partielle expérimentale appliquée localement, il serait précipité de généraliser à plus grande échelle. Il serait judicieux de répéter l'expérience sur plusieurs sites, avec un gradient de différentes intensités de coupes partielles, avec un nombre plus important d'individus et sur une plus longue période de temps pour consolider les résultats obtenus. Il serait également très intéressant d'effectuer ce suivi sur différentes espèces de la forêt boréale. Dans un contexte où

l'on cherche à augmenter la productivité des forêts, il serait ainsi pertinent de s'intéresser à plusieurs espèces pour déterminer lesquelles sont les plus aptes à augmenter leur croissance suite à une coupe partielle.

Le troisième chapitre est particulièrement intéressant pour les gestionnaires de la forêt et les industriels, car l'étude sur la CPPTM confirme bien l'augmentation de la croissance radiale des tiges résiduelles d'épinette noire et de sapin baumier en forêt boréale. Ces dernières années, des questions ont été soulevées quant à l'impact d'une telle augmentation de croissance sur la qualité du bois. Les résultats démontrent clairement que les paramètres de qualité du bois mesurés n'ont pas été significativement affectés chez l'épinette noire et très peu dans le cas du sapin baumier. Cette étude sur la qualité du bois est l'une des premières portant sur le sapin baumier et l'intégration des résultats obtenus aux modèles prédisant le rendement et le panier de produits est maintenant possible. Les résultats supportent également l'application à plus grande échelle de coupes partielles telles que la CPPTM. Il semble en effet que la CPPTM puisse apporter un juste équilibre entre production de bois et qualité. On obtient ainsi une amélioration de la productivité des forêts aménagées et le maintien de la qualité des arbres récoltés, ce qui aura un effet direct sur la diversité et la valeur des produits tirés de la récolte.

Il aurait néanmoins été intéressant d'étendre l'étude du troisième chapitre à un plus grand nombre de peuplements, couvrant un plus grand territoire de la forêt boréale. De plus, malgré que l'étude analyse déjà une période de 10 ans après l'intervention, il aurait été pertinent de pouvoir analyser une période de temps plus longue. Cela aurait permis de voir la durée réelle de l'effet de l'ouverture de la canopée sur la croissance, qui est toujours plus élevée après 10 ans, et de vérifier que les propriétés du bois du

sapin reviennent véritablement vers les niveaux qui prévalaient avant la coupe. Toutefois, les premiers dispositifs sur la coupe avec protection des petites tiges marchandes ne sont implantés que depuis 1997 (Ministère des Ressources Naturelles, 2002). Il serait également approprié de s'intéresser à d'autres paramètres de qualité du bois qui peuvent également avoir une influence sur les usages que l'on peut faire du bois, comme par exemple le diamètre des branches, la proportion de bois juvénile, la présence de bois de compression, etc. La taille des branches peut influencer les propriétés mécaniques du bois d'œuvre car elles créent une zone de faiblesse dans le bois qui pourrait diminuer la qualité des bois de sciage (MacDonald et Hubert, 2002; Shmulsky et Jones, 2011). La présence d'une plus grande proportion de bois juvénile et de bois de compression dans la tige pourrait avoir le même résultat. En effet, le bois juvénile présente des propriétés inférieures au bois mature, notamment en ce qui concerne la masse volumique et les propriétés mécaniques (MacDonald et Hubert, 2002; Shmulsky et Jones, 2011). Quant au bois de compression, celui-ci est plus dense, mais moins résistant en flexion et en tension (Shmulsky et Jones, 2011) et il contient plus de lignine (MacDonald et Hubert, 2002). Ces caractéristiques pourraient donc rendre les tiges moins intéressantes pour le bois de sciage et la pâte à papier. L'étude des paramètres cellulaires (aire du lumen, épaisseur des parois cellulaires, ratio paroi/lumen), qui sont fortement liés au rôle mécanique et physiologique de l'arbre, pourrait également bonifier la compréhension des propriétés du xylème.

Les résultats tirés du chapitre IV, qui montrent que la masse volumique est plus élevée dans les racines que dans la tige, ce qui rend le réseau hydraulique des racines sécuritaire et résistant. Cette information est importante pour la compréhension de la physiologie de l'épinette noire. Le système racinaire de surface de l'épinette noire subit également des forces mécaniques plus importantes en raison de la pénétration du vent plus importante dans le peuplement après l'éclaircie commerciale (Achim *et*

al., 2005). Une masse volumique plus élevée permet donc à l'arbre d'être davantage résistant, ce qui peut limiter les risques de chablis quand l'intensité des coupes partielles est faible ou modérée. Le résultat pourra donc être inclus dans les modèles qui analysent la stabilité de l'espèce. Le territoire couvert par l'étude permet d'appliquer les résultats à une grande partie de la forêt boréale du Québec, mais il serait tout de même pertinent d'augmenter le nombre d'arbres analysés par site et le nombre de peuplements échantillonnés. Les résultats obtenus portent à croire que le système racinaire de l'épinette noire est peut-être moins vulnérable à la cavitation que l'on suppose. Des études supplémentaires sur la cavitation, incluant des analyses anatomiques, sont toutefois nécessaires pour vérifier cette hypothèse. Comme les informations sur les propriétés du bois des racines sont rares, il serait aussi intéressant d'effectuer des études sur différentes espèces et d'étendre les analyses à d'autres propriétés du bois, comme par exemple la résistance mécanique. Il serait alors possible de relier les résultats de masse volumique et de résistance mécanique des racines avec la charge mécanique exercée dans cette partie de l'arbre, pour mieux évaluer l'adaptation du système racinaire aux coupes partielles.

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