UNIVERSITÉ DU QUÉBEC

IMPACT DE TROIS INTERVENTIONS SYLVICOLES SUR LA STRUCTURE DES PEUPLEMENTS, LA CROISSANCE ET LA QUALITÉ DU BOIS DE L'ÉPINETTE NOIRE (*PICEA MARIANA* (MILL.) B.S.P.) EN FORÊT BORÉALE

PAR

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RÉSUMÉ

Traditionnellement, les forêts d'épinette noire de l'Est du Canada sont exploitées par la coupe totale. Ce type de coupe est, toutefois, associé à la simplification de la structure et de la composition des forêts. De ce fait, différents types de coupe partielle ont récemment été mis au point afin de réduire les écarts entre les forêts aménagées et celles naturelles, selon le principe de l'aménagement écosystémique. De plus, les coupes partielles visent à augmenter la croissance des arbres résiduels grâce à la diminution de la compétition, et par le fait même à augmenter la rentabilité des futures interventions. Par contre, l'augmentation de la largeur des cernes de croissance, à la suite de coupes partielles, peut nuire à la qualité du bois.

L'objectif de cette étude était d'évaluer l'effet de trois types de coupe partielle appliqués à des peuplements d'épinette noire, équiens et inéquiens, sur la structure des peuplements (la répartition spatiale, la distribution diamétrale et la structure d'âge des arbres résiduels, ainsi que la quantité et la distribution diamétrale des arbres morts) et la croissance radiale des arbres résiduels. L'effet d'une augmentation de la croissance radiale sur les propriétés du bois (masse volumique, caractéristiques des trachéides, propriétés mécaniques) et sur le diamètre des branches a aussi été évalué.

Les coupes partielles étudiées sont la coupe avec protection des tiges à diamètre variable (CPTDV), la coupe avec protection des petites tiges marchandes (CPPTM) et l'éclaircie commerciale (EC). Cinq blocs, correspondant à une station traitée jumelée à une station témoin (120 à 400 m^2), ont été échantillonnés pour chaque type de coupe partielle. La structure des peuplements ainsi que la croissance radiale des arbres résiduels ont été évaluées avec l'ensemble des épinettes noires présentes dans chaque station. Afin d'analyser les propriétés du bois et le diamètre des branches, cinq épinettes noires par station ont été récoltées aléatoirement parmi celles ayant une augmentation de croissance d'au moins 20 % comparativement aux 10 années précédant la coupe dans les stations traitées et parmi l'ensemble des arbres dans les stations témoins.

Après l'application des trois types de coupe partielle, la structure d'âge ainsi que la distribution du diamètre des arbres résiduels étaient semblables à celles des stations témoins. Ces résultats démontrent que les coupes partielles peuvent maintenir la structure initiale des peuplements et convenir à un aménagement écosystémique des forêts. Toutefois, une quantité de bois mort inférieure a été observée à la suite des coupes partielles, ce qui peut nuire à la biodiversité associée à ces legs biologiques.

La croissance radiale des épinettes noires résiduelles a été augmentée à la suite de la CPPTM et de l'EC grâce à la diminution de la compétition. Toutefois, la croissance radiale moyenne était limitée à la suite de la CPTDV, en raison de la présence de grappes d'arbres résiduels. La croissance radiale était positivement influencée par le temps depuis le traitement et la longueur du houppier, tandis qu'elle était diminuée par le degré de compétition et l'âge des arbres.

L'augmentation de la largeur des cernes de croissance, à la suite des coupes partielles, ne cause pas d'effet néfaste sur la qualité du bois de l'épinette noire. En effet, seuls de faibles changements de propriétés du bois ont été observés. À 1,3 m de hauteur, bien que la masse volumique moyenne des cernes de croissance n'ait pas changé à la suite des coupes partielles, celle du bois initial a diminué à la suite de la CPPTM et de l'EC. Toutefois, cette diminution n'a pas nui aux propriétés mécaniques du bois; aucune corrélation n'a été observée entre ces deux attributs. De plus, seules de faibles corrélations ont été détectées entre certaines caractéristiques cellulaires et la masse volumique du bois, et aucune corrélation avec les propriétés mécaniques n'a été observée.

La masse volumique a également été évaluée à différentes hauteurs le long de la tige. Les propriétés mécaniques de l'ensemble de la tige n'ont pas semblé affectées par les coupes partielles, car aucune diminution de la masse volumique n'a été observée le long de la tige. Toutefois, des branches de plus fort diamètre, principalement dans la première moitié du houppier, ont été observées à la suite des coupes partielles. Cette différence a été davantage observée après la CPPTM et l'EC, ce qui pourrait nuire à la classification du bois provenant de ces deux types de coupe.

Bien qu'elles nécessitent quelques ajustements (p. ex. plus de bois mort de fortes dimensions, moins de grappes d'arbres résiduels), ce projet démontre que les coupes partielles étudiées pourraient être adéquates, en peuplement d'épinette noire, afin de maintenir les bénéfices écologiques et économiques. L'ensemble des résultats de cette thèse contribue aux connaissances générales sur les coupes partielles, tout en contribuant au développement durable des peuplements forestiers.

ABSTRACT

Traditionally, black spruce stands in eastern Canada were harvested through clear-cutting. This method of cutting simplified the structure and composition of forests. Therefore, using an ecosystem-based management approach, different types of partial cutting treatments have recently been developed to reduce differences between managed and natural forests. In addition, partial cutting treatments are designed to increase the radial growth of residual trees by decreasing inter-tree competition and thus enhance the economic benefits of the treatments. However, an increase of ring width after partial cutting treatments could lead to a decrease in wood quality.

The aim of this study was to evaluate the effect of three types of partial cutting treatments within even- and uneven-aged black spruce stands, on stand structure (spatial repartition, diameter distribution and age structure of residual trees, and on the quantity and diameter distribution of dead trees) and on the radial growth of residual trees. The effect of increased radial growth on wood properties (wood density, cell characteristics, mechanical properties) and branch diameter, was also evaluated.

The three studied partial cutting treatments were: 1) careful logging around stems with variable diameter (CLVD), 2) careful logging around small merchantable stems (CPPTM), and 3) commercial thinning (CT). Five blocks, each comprised of one treated plot combined with one control plot (120 to 400 m^2), were sampled for each type of partial cutting treatment. Stand structure and the radial growth of residual trees were evaluated using all black spruce present in each plot. To analyze wood properties and branch diameter, five black spruce per plot were then randomly sampled among those trees presenting a post-treatment radial growth at least 20% larger than that of the 10 years pre-treatment period, as well as among all trees in control plots.

After the three partial cutting treatments, the age structure and diameter distribution of residual trees were similar to that found in control plots. These results demonstrated that partial cutting treatments could maintain the initial stand structure and be suitable for ecosystem-based management. However, a lower quantity of deadwood was also observed after partial cutting, potentially affecting the biodiversity associated with these biological legacies.

The radial growth of residual black spruce trees increased after CPPTM and CT due to a decrease of inter-tree competition. However, mean radial growth was limited after CLVD because of a higher presence of tree clusters. Radial growth was positively influenced by the time since treatment and crown length, while it decreased with inter-tree competition and tree age.

The increased ring width observed after partial cutting treatments did not lead to a detrimental effect on the wood quality of black spruce trees. In fact, only small changes were observed for wood properties. At a height of 1.3 m, while ring wood density was not altered by partial cutting, earlywood density decreased after CPPTM and CT. However, this decrease did not negatively affect the mechanical properties of the wood; no correlation was observed between mechanical properties and earlywood density. Also, only weak correlations were detected between some cellular characteristics and wood density, and no correlation with mechanical properties was observed.

Wood density was also evaluated at different sampling heights along the stem. The mechanical properties of the entire bole should not be affected by partial cutting treatments as no decrease in wood density was observed along the tree. However, larger diameter branches, especially in the lower half of the crown, were observed after partial cutting treatments. This difference was observed in particular after CPPTM and CT, which could negatively affect wood classification after use of these type of partial cutting.

Although some adjustments are required (e.g. a greater amount of large-sized deadwood, fewer residual tree clusters), this project demonstrated that the studied partial cutting treatments could be suitable, in black spruce stands, for maintaining ecological and economic benefits within harvested stands. The overall results of this thesis contribute to our general knowledge of partial cutting treatments and improve our understanding of the sustainable development of boreal forest stands.

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INTRODUCTION

L'épinette noire (*Picea mariana* (Mill.) B.S.P.) est une espèce dominante de la forêt boréale de l'est du continent nord-américain (Gagnon, 1995; Bergeron, 1996; Saucier *et al.*, 1998). La superficie de la pessière noire à mousses représente 28 % du territoire québécois et est le plus vaste domaine forestier de la province (Gagnon et Morin, 2001). De ce fait, l'épinette noire a une grande importance écologique, en plus de représenter une grande valeur pour l'industrie forestière du Nord-Est canadien en raison de son abondance et de la qualité de sa fibre (e.g. Gagnon et Morin, 2001; Zhang et Koubaa, 2009).

Structure des peuplements

Grâce à ses cônes semi-sérotineux, l'épinette noire se régénère efficacement à la suite de feux de forêts (Gagnon et Morin, 2001). Toutefois, en l'absence de cette perturbation, les peuplements développent graduellement une structure d'âge inéquienne où la presque totalité de la régénération de cette espèce se fait par marcottage (enracinement des branches basses) (Doucet, 1988; Groot et Horton, 1994; Gagnon et Morin, 2001). Ces structures inéquiennes sont façonnées par la dynamique des trouées, lesquelles sont formées par la mort d'arbres individuels ou de petits groupes d'arbres causée par des perturbations mineures (McCarthy, 2001). À l'est du Québec, près de 70 % des forêts naturelles dominées par l'épinette noire ont une structure irrégulière (Boucher *et al.*, 2003), modulée par un long intervalle de feux, qui peut atteindre jusqu'à 500 ans (Bouchard *et al.*, 2008). Comparativement aux forêts équiennes, leur structure irrégulière ainsi que leur grande quantité de bois mort créent une hétérogénéité d'habitats permettant à une grande variété d'espèces d'y habiter (e.g. Lowe *et al.*, 2011). Toutefois, la proportion de ces types de peuplements (mûrs et surannés), comparativement aux peuplements en régénération, est en diminution sur le territoire québécois (MRNF, 2009). Les méthodes de récolte uniforme, particulièrement la coupe totale et la coupe avec protection de la régénération et des sols (CPRS) utilisées depuis des décennies en forêt boréale, sont responsables de cette diminution. En effet, la coupe totale simplifie la structure et la composition des écosystèmes, entraînant des inquiétudes sur la préservation de la biodiversité et des processus écologiques ainsi que sur la résilience des écosystèmes (Gauthier *et al.*, 2008; Jetté *et al.*, 2008; Kuuluvainen, 2009) .

Le concept d'aménagement écosystémique a émergé au Québec dans les années 1990 (Bergeron et Harvey, 1997) et cette approche fut introduite dans la législation en 2005. La base de ce concept soutient qu’une bonne façon de maintenir la diversité biologique et les fonctions écologiques des écosystèmes serait de faire des interventions qui favoriseraient le développement de peuplements ayant des structures et compositions similaires à celles qui sont présentes naturellement dans l’écosystème (Franklin, 1993; Gauthier *et al.*, 1996; Bergeron *et al.*, 2002). À long terme, cette façon de faire devrait contribuer à maintenir les différentes fonctions écologiques de l’écosystème, et par le fait même nous permettre de continuer à tirer profit de ses bénéfices sociaux et économiques (Gauthier *et al.*, 2008). Ainsi, différents types de coupe partielle ont émergé afin de réduire les écarts entre les forêts aménagées et naturelles. Comme elles ne récoltent qu'une partie des arbres d'un peuplement, les coupes partielles tentent d'émuler les perturbations secondaires naturelles, comme les épidémies d'insectes, ce qui devrait accélérer le retour des peuplements à leur structure initiale.

En effet, les coupes partielles ont démontré leur capacité à accélérer le développement (p. ex. la succession forestière) des peuplements en forêt boréale mixte, en plus d'augmenter leur complexité structurale (Prevost et Pothier, 2003; Witte *et al.*, 2013). Toutefois, certains types de coupe partielle, comme les coupes à diamètre limite, peuvent simplifier la structure des peuplements à court terme, en favorisant une structure équienne plutôt qu'inéquienne (Cimon-Morin *et al.*, 2010). De plus, les coupes forestières conservent très peu de legs biologiques (arbres morts ou affaiblis) comparativement aux perturbations naturelles qui en laissent un bon nombre (Gauthier *et al.*, 2008). Ces derniers sont particulièrement importants pour maintenir certains processus écologiques (p. ex. le drainage, le cycle nutritif), en plus de participer à la régénération d'espèces végétales et de servir d'habitats à plusieurs espèces animales (Gauthier *et al.*, 2008). En contrepartie, l'ouverture des peuplements, à la suite de coupes partielles, peut augmenter les risques de mortalité par chablis, ce qui peut entraîner des pertes économiques importantes (Riopel *et al.*, 2010). Toutefois, la mortalité est dépendante du type et de l'intensité de la coupe partielle appliqué, les arbres plus petits avec une faible vigueur étant associés, pour différentes espèces nord-américaines, à un plus grand risque de mortalité (Caspersen, 2006; Powers *et al.*, 2010). Très peu d'études se sont intéressées, pour le moment, à la structure des peuplements, ainsi qu'à la quantité de bois mort retrouvée à la suite de différents types de coupe partielle en peuplement d'épinette noire (e.g. Cimon-Morin *et al.*, 2010). Cette information pourrait mener à une meilleure gestion de la principale ressource forestière québécoise et favoriserait l'application adéquate du principe d'aménagement écosystémique.

Croissance radiale

Afin d'être utilisées à grande échelle, les coupes partielles doivent avoir un attrait économique pour l'industrie. La valeur des conifères boréaux étant directement liée à leur diamètre, l'augmentation de croissance à la suite d'une coupe partielle peut générer des gains financiers (Liu *et al.*, 2007). Ainsi, le diamètre des tiges est l'un des critères économiques les plus importants, surtout pour les résineux, car il a un impact direct sur le rendement au sciage (Doucet *et al.*, 2009). En raison de son importance économique, la croissance des arbres après une coupe partielle a fait l'objet de plusieurs études ces dernières années, autant en forêt tempérée (e.g. Jones et Thomas, 2004; Bevilacqua *et al.*, 2005) qu'en forêt boréale canadienne (e.g. Thorpe *et al.*, 2007; Vincent *et al.*, 2009). De manière générale, la diminution de la densité des peuplements, à la suite d'une coupe partielle, favorise l'accroissement radial des arbres résiduels grâce à l'augmentation du rayonnement solaire, de la température du sol et de la disponibilité de l'eau (Thibodeau *et al.*, 2000). Bien que la réaction de l'épinette noire à la suite d'une éclaircie commerciale en forêt régulière ait été quantifiée (Weetman, 1975; Vincent *et al.*, 2009), très peu d'information est disponible sur l'effet de différents types de coupe partielle, spécialement dans les peuplements d'épinette noire inéquiens. De plus, plusieurs études ont observé que la réaction des arbres résiduels était très variable. Les arbres de petite taille, avec un faible taux de croissance avant la coupe, ainsi qu'un faible niveau de compétition à la suite de celle-ci, seront ceux ayant la plus forte augmentation de croissance radiale relative (Vincent *et al.*, 2009; Krause *et al.*, 2011). Ainsi, la réaction des arbres à une coupe partielle peut varier en fonction de l'espèce, du type de peuplement dans lequel elle est effectuée (équien ou inéquien) et du statut social des arbres préservés. Par exemple, en récoltant majoritairement les arbres dominants, les coupes partielles en peuplement inéquien conservent les arbres petits et opprimés dans le peuplement. Conséquemment, les coupes partielles devraient avoir un effet plus prononcé sur la croissance de ces arbres résiduels comparativement à l'éclaircie commerciale par le bas en peuplement régulier qui conserve les arbres dominants et codominants.

Qualité du bois

La productivité des peuplements est une priorité pour l'industrie forestière, mais une augmentation de la croissance radiale pourrait être liée à une diminution de la qualité du bois due à des changements dans ses caractéristiques intrinsèques (e.g. Dutilleul *et al.*, 1998; Makinen *et al.*, 2002a). La qualité du bois peut être définie comme une mesure des caractéristiques influençant les propriétés des matériaux produits à partir de celui-ci (Shmulsky et Jones, 2011). Ainsi, considérant les multiples utilisations du bois, l'ensemble des caractéristiques de celui-ci peut être considéré comme un facteur de qualité (Alteyrac, 2005). Au Québec, l'épinette noire est principalement utilisée pour le bois d'œuvre, mais peut également être utilisée dans la fabrication de pâtes et papiers, comme combustible, et dans plusieurs produits secondaires à valeur ajoutée (p. ex. le bois MSR) (Zhang et Koubaa, 2008).

La masse volumique du bois est considérée comme étant l'un de ses principaux critères de qualité, car elle est directement reliée aux propriétés mécaniques de la tige, en plus d'être un bon indicateur du rendement et de la qualité de la pâte, et de la transmission de la chaleur lors de la combustion (Saranpää, 2003; Shmulsky et Jones, 2011). La masse volumique est principalement déterminée par les structures cellulaires du bois (Saranpää, 2003; Shmulsky et Jones, 2011). Ayant des parois cellulaires plus épaisses que celles du bois initial, le bois final a une masse volumique supérieure (Raven *et al.*, 2000). Chez les conifères, la largeur du bois final demeure relativement constante malgré une largeur de cernes variable (Shmulsky et Jones, 2011). Or, à la suite d'une coupe partielle, l'augmentation de la croissance radiale pourrait diminuer la proportion de bois final et conséquemment, la masse volumique du bois (Makinen *et al.*, 2002a). De plus, des cernes de croissance plus larges ont déjà été associés à une augmentation de la taille des cellules et à une diminution de l'épaisseur des parois cellulaires (Makinen *et al.*, 2002b), contribuant également à la baisse générale de la masse volumique. Le lien existant entre la largeur des cernes de croissance et la masse volumique du bois a fait l'objet de nombreuses études sur différentes espèces de la forêt boréale (e.g. Corriveau *et al.*, 1987; Koubaa *et al.*, 2000). Toutefois, aucun consensus n'existe. Spécifiquement pour l'épinette noire, Xiang *et al.* (2014) ont observé une corrélation négative entre la masse volumique et la largeur des cernes de croissance dans le bois mature, tandis que Vincent *et al.* (2011) n'ont pas observé ce lien à la suite d'une éclaircie commerciale.

La masse volumique varie naturellement en fonction de l'âge cambial. Chez l'épinette noire, elle est faible dans le bois des premières années cambiales, ce qui correspond à la période de bois juvénile, pour ensuite augmenter jusqu'à la formation du bois mature. L'âge de transition entre les bois juvénile et mature se situe entre le 11^{e} et le 21^{e} cerne de croissance pour cette espèce (Yang et Hazenberg, 1993; Alteyrac *et al.*, 2006). La masse volumique varie également en fonction de la hauteur dans l'arbre. Celle-ci diminue avec la hauteur en raison d'une plus grande proportion de bois juvénile au sommet de l'arbre qu'à sa base (Singh, 1986; Zobel and Sprague, 1998). Selon Koubaa *et al.* (2000), la corrélation négative observée entre la masse volumique et la largeur des cernes de l'épinette noire est plus importante dans le bois juvénile et diminue dans le bois mature. De ce fait, l'effet des coupes partielles pourrait se faire ressentir davantage dans le haut de la tige, endroit où une forte proportion de bois juvénile est retrouvée. Toutefois, l'augmentation de croissance pourrait être plus faible dans cette section, limitant ainsi l'effet négatif des coupes partielles sur la masse volumique du bois. En effet, l'augmentation de la croissance est généralement supérieure dans le bas de la tige à la suite d'une coupe partielle (e.g. Sharma and Zhang, 2004). Ce changement de forme de la tige permettrait aux arbres résiduels d'augmenter leur stabilité, afin de résister à une plus grande exposition au vent (Dean and Long, 1986). En revanche, ce changement de défilement de la tige, bien que positif en termes de masse volumique, pourrait causer des problèmes sur le volume et les dimensions des planches pouvant être produites.

Bien que souvent absente des études sur la qualité du bois à la suite de coupes partielles, la longueur des trachéides est une caractéristique importante à considérer. De longues trachéides sont souhaitables, car elles ont un impact considérable sur la qualité du papier, notamment par leur influence sur sa résistance aux déchirures (Shmulsky and Jones, 2011). De manière générale, une augmentation de la largeur des cernes a été associée à une diminution de la longueur des fibres pour plusieurs espèces de la forêt boréale (Dutilleul *et al.*, 1998; Makinen *et al.*, 2002b). Les coupes partielles pourraient ainsi avoir un effet négatif sur une des principales utilisations de l'épinette noire, soit celle de la fabrication du papier.

Utilisant un système de classification visuelle (NLGA, 2008), le bois d'œuvre en Amérique du Nord est classifié selon divers défauts mécaniques et biologiques, dont la largeur des nœuds. En effet, les nœuds représentent un défi pour l'industrie, car ils créent une zone de faiblesse dans le bois causée par la discontinuité et la déviation des fibres (Jozsa and Middleton, 1997), en plus de nuire à l'apparence des produits (Shmulsky and Jones, 2011). Les nœuds sont également indésirables dans les procédés papetiers, en raison des caractéristiques du bois qui sont différentes de celles de la tige (Macdonald and Hubert, 2002; Walker, 2006). Parce qu'elles sont influencées par les mêmes facteurs environnementaux que la tige, les branches peuvent augmenter leur diamètre à la suite d'une coupe partielle. En effet, l'augmentation de la lumière et de l'espace disponible permet une plus longue rétention des branches, favorisant ainsi un diamètre plus important (Makinen and Hein, 2006; Weiskittel *et al.*, 2007b). Les branches à la base du houppier semblent plus bénéficier de l'ouverture du peuplement que celles au sommet. Ces dernières recevant déjà beaucoup de lumière, certaines études ont constaté qu'elles ne sont pas affectées par l'ouverture du peuplement à la suite d'une coupe partielle (Makinen and Hein, 2006; Weiskittel *et al.*, 2007a).

La qualité du bois des arbres résiduels, à la suite d'une coupe partielle, peut différer selon la structure du peuplement initial (équien ou inéquien). En effet, les coupes à diamètre limite, appliquées en peuplement inéquien, récoltent les arbres dominants tout en conservant les petits arbres opprimés. Ces arbres ont des profils radiaux de croissance et de masse volumique différents des arbres dominants, qui varient en fonction de la durée et de l'intensité de leur oppression. L'ouverture du peuplement, à la suite d'une coupe partielle en peuplement inéquien, peut créer de plus grandes variations des caractéristiques intrinsèques du bois, comparativement aux arbres dominants conservés en peuplement équien. De plus, Garber and Maguire (2005) ont observé que les arbres provenant de différentes classes sociales ont des distributions foliaires différentes, la densité maximale de feuillage des arbres opprimés étant située plus haut que dans le cas des arbres dominants (Makela and Vanninen, 2001). Ainsi, différents types de coupe partielle appliqués à différentes structures pourraient entraîner des réactions différentes. Pour l'instant, très peu d'information est disponible sur l'effet d'une augmentation de la croissance à la suite d'une variété de coupes partielles en forêt boréale canadienne (Bose *et al.*, 2014). Il existe donc très peu de connaissances sur les propriétés du bois de l'épinette noire à la suite de ce type de traitement, malgré son omniprésence au Canada.

Objectifs et hypothèses

L'objectif de cette étude est d'évaluer l'effet de trois types de coupe partielle appliqués à des peuplements d'épinette noire, équiens et inéquiens sur (i) la structure des peuplements, (ii) la croissance radiale et (iii) la qualité du bois des arbres résiduels.

Spécifiquement, l'étude s'intéresse à

(i) l'effet des coupes partielles sur la répartition spatiale, la distribution diamétrale et la structure d'âge des arbres résiduels. La quantité et la distribution diamétrale du bois mort seront également évaluées. L'hypothèse est que les coupes partielles simplifieront la structure d'âge et la distribution diamétrale des arbres résiduels, en plus d’uniformiser leur répartition spatiale. Elles réduiront la quantité de bois mort présent dans les peuplements traités, en plus d'éliminer le bois mort de fortes dimensions. En effet, les coupes partielles entraînent généralement une diminution du bois mort de grandes dimensions (e.g. Fraver *et al.*, 2002), nuisant ainsi aux espèces qui en sont dépendantes.

(ii) l'effet des coupes partielles sur la croissance radiale des arbres résiduels le long de leur tige. L'hypothèse testée est que les arbres résiduels augmenteront leur croissance radiale de façon plus importante dans le bas de la tige. Toutefois, une importante variabilité devrait être observée entre les arbres résiduels.

(iii) l'effet d'une augmentation de la croissance, après les coupes partielles, sur la qualité du bois, qui est évaluée par la masse volumique du bois (moyenne, bois initial et bois final), la proportion de bois final, les propriétés des trachéides (longueur des trachéides, l'épaisseur des parois et l'aire du lumen du bois initial et final), les propriétés mécaniques (module d'élasticité et de rupture) ainsi que le diamètre des branches. Le profil de ces caractéristiques le long de la tige sera également évalué. L'augmentation de la croissance devrait affecter négativement tous les facteurs de qualité du bois avec un effet plus prononcé à la base des arbres, particulièrement dans les peuplements inéquiens.

Territoire étudié et approche méthodologique

Trois types de coupe partielle ont été étudiés, soit l'éclaircie commerciale (EC), la coupe avec protection des petites tiges marchandes (CPPTM) et la coupe avec protection des tiges à diamètre variable (CPTDV). L'éclaircie commerciale est appliquée dans des forêts équiennes, contrairement à la CPPTM et la CPTDV qui sont appliquées dans des forêts inéquiennes.

L'EC par le bas récolte généralement entre 30 et 35 % de la surface terrière du peuplement, constituée principalement des petits arbres, opprimés et de moins bonne qualité, laissant sur pied les arbres dominants et codominants (Doucet *et al.*, 2009). L'EC consiste à régulariser la qualité de la production ligneuse dans le temps et peut, de surcroît, augmenter la valeur du peuplement (Doucet *et al.*, 2009). Elle est que récemment appliquée aux peuplements naturels d'épinette noire (Vincent *et al.*, 2009).

De leur côté, la CPPTM et la CPTDV récoltent l'ensemble des tiges de plus de 14 cm de diamètre, tout en protégeant les petites tiges marchandes (9-14 cm). La CPPTM récolte généralement entre 70 et 90 % du volume marchand du peuplement, tout en retenant environ 900 tiges par ha de 2 à 14 cm dont près de 125 d'entre elles entre 10 et 14 cm (Doucet *et al.*, 2009; Pouliot *et al.*, 2011). La CPTDV est appliquée dans des peuplements comprenant moins de petites tiges marchandes que ceux convenables pour la CPPTM ou lorsque la distribution des arbres est discontinue (Pouliot *et al.*, 2011). Elle récolte jusqu'à 95 % de la surface terrière du peuplement, tout en retenant environ 375 tiges par ha de 4 à 14 cm dont 75 d'entre elles entre 10 et 14 cm (Pouliot *et al.*, 2011). Ces coupes ont été initialement appliquées afin de réduire les longues rotations associées à la coupe totale, et non afin d'émuler les perturbations naturelles. Toutefois, il s'agit d'exemples de grande valeur afin d'évaluer l'effet des coupes partielles (Thorpe et Thomas, 2007), car elles sont présentes, spécialement la CPPTM, à une échelle opérationnelle en forêt boréale du Québec. En forêt boréale, l'implantation des premiers dispositifs d'études sur la CPPTM a débuté vers la fin des années 1990 (e.g. Riopel *et al.*, 2010).

Cinq blocs ont été échantillonnés par type de coupe partielle, un bloc correspondant à un peuplement traité jumelé à un peuplement témoin. Pour la CPPTM, trois peuplements traités faisaient partie d'une étude expérimentale dans laquelle cette intervention était évaluée à travers le Québec (Riopel *et al.*, 2010). La sélection des stations est décrite en détail dans le chapitre 1. Une attention particulière a été portée à la sélection des peuplements témoins, afin qu'ils aient une structure semblable à celle retrouvée initialement dans les peuplements traités. Tous les peuplements ont été échantillonnés dans la forêt aménagée du Saguenay Lac-Saint-Jean entre le 47°51´ et 50°35´N et le 70°11´ et 72°11´O, dans le domaine bioclimatique du sapin baumier (*Abies balsamea* (L.) Mill.) - bouleau jaune (*Betula alleghaniensis* Britt.) et sapin baumier - bouleau blanc (*Betula papyfera* March.) (MRNF, 2003-2016). Une carte présentant l'emplacement de chacun des blocs ainsi qu'un tableau regroupant des informations supplémentaires sur ceux-ci sont présentés au chapitre 1 (Fig. 1.1; Supplementary data Table S1.1).

Chaque chapitre contient le détail de l'échantillonnage et des méthodes utilisées spécifiquement à chacun. En résumé, chaque peuplement a été échantillonné à deux reprises. Lors du premier échantillonnage, la hauteur totale ainsi que la longueur du houppier, le diamètre à 0,2 m et 1,3 m (DHP) et la position cartésienne de l'ensemble des épinettes noires résiduelles ont été mesurés (DHP ≥ 4 cm). De plus, le diamètre des arbres des autres espèces présentes a été mesuré afin de calculer la densité des peuplements ainsi que la surface terrière. Le bois mort a été mesuré à hauteur de poitrine et caractérisé.

Un échantillon de bois a été prélevé à 0,2 m sur toutes les épinettes noires, afin de déterminer l'âge des arbres et d'évaluer l'accroissement radial. Grâce à cette dernière mesure, cinq arbres par station ont été sélectionnés, de façon aléatoire, parmi ceux ayant une augmentation de croissance de plus de 20 % comparativement aux 10 années précédant la coupe dans les peuplements traités et parmi l'ensemble des arbres dans les peuplements témoins. Lors du deuxième échantillonnage des stations, les arbres ainsi sélectionnés ont été abattus et des rondelles ont été prélevées à 0 m, 0,5 m, 1,3 m, 2 m et tous les 2 mètres jusqu'au sommet. L’ensemble des rondelles a servi aux analyses densitométriques, tandis que celle à 1,3 m a également servi aux analyses cellulaires. Une section entre 0,5 m et 1 m a été prélevée afin de réaliser les tests mécaniques. Lors de cet échantillonnage destructif, la longueur du houppier a été divisée en cinq sections et le diamètre des cinq plus grosses branches, par section, a été mesuré.

Structure de la thèse

Cette thèse est présentée sous forme de recueil d'articles scientifiques rédigés en anglais, comprenant trois chapitres principaux dont le premier a été publié et les deux autres sont en voie de soumission. La thèse se termine par une conclusion générale.

Le premier chapitre présente l'effet des coupes partielles sur la structure des stations, ainsi que sur la croissance des arbres résiduels. Spécifiquement, la croissance radiale, la structure d'âge, la distribution des diamètres et la distribution spatiale des arbres résiduels, ainsi que la quantité et la distribution des diamètres du bois mort ont été évaluées et comparées avec des stations témoins.

L'effet d'une augmentation de la croissance à la suite des coupes partielles sur la qualité du bois de l'épinette noire est traité dans les chapitres 2 et 3. Dans le chapitre 2, les effets étudiés à 1,3 m sont la masse volumique du bois (bois initial et final), la proportion de bois final, les caractéristiques anatomiques (longueur des trachéides, épaisseur des parois cellulaires et l'aire du lumen du bois initial et final) ainsi que les propriétés mécaniques (module d'élasticité et de rupture; évaluées entre 0,5 et 1,0 m). En plus de comparer les propriétés du bois entre les peuplements traités et témoins, la corrélation entre les diverses propriétés a été déterminée.

Quant au chapitre 3, l'effet des coupes partielles sur les propriétés du bois à différentes hauteurs dans la tige a été étudié. La masse volumique moyenne, ainsi que celle du bois initial et final, la proportion du bois final et la largeur des cernes de croissance ont été évaluées. De plus, le diamètre des branches après les traitements a été comparé avec les stations témoins.

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CHAPITRE 1

EFFECT OF THREE PARTIAL CUTTING PRACTICES ON STAND STRUCTURE AND GROWTH OF RESIDUAL BLACK SPRUCE TREES IN NORTH-EASTERN QUEBEC

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Effect of three partial cutting practices on stand structure and growth of residual black spruce trees in north-eastern Quebec

Abstract

Partial cutting practices are increasingly used in boreal forests for two major reasons: (1) maintaining age structure and tree diameter distribution according to the principles of ecosystem-based management and (2) increasing tree growth by decreasing competition. This study evaluated the effects of three different partial cutting treatments applied to even- and uneven-aged black spruce (*Picea mariana* (Mill.) B.S.P.) stands in north-eastern Quebec, Canada. The effect of partial cutting was assessed by comparing treated and control plots in terms of age structure, diameter and spatial distribution, amount of deadwood and tree radial growth. Age structure and diameter distribution were not different from control plots after partial cuttings applied in both uneven-aged and even-aged stands, but lower deadwood basal area was observed. Tree radial growth generally increased following treatments in uneven-aged stands but can be limited by tree age and inter-tree competition. In even-aged stands, tree removal was more uniformly distributed and the overall reduction in inter-tree competition resulted in an increased tree radial growth. Overall, these results suggest that the studied partial cuttings were adequate for maintaining structural attributes and increasing tree growth, but adjustments should be made to treatments to increase the amount of deadwood to a level observed in natural forests and to lower inter-tree competition.

Keywords: Partial cuttings, structural attributes, spatial distribution, black spruce, mortality, tree radial growth.

Introduction

Black spruce (*Picea mariana* (Mill.) B.S.P.) is a widespread species across North America, and its abundance and wood properties make it highly valued by the forest industry in north-eastern Canada (Viereck and Johnston, 1990; Saucier, 1998; Zhang and Koubaa, 2008). Natural structures of black spruce forest in eastern Quebec are heavily influenced by long fire return intervals that can reach over 500 hundred years because of high precipitation and cold temperatures (Foster, 1983; Bouchard *et al.*, 2008). This long fire cycle is also associated with secondary disturbances, such as spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks, which create uneven-aged forest. Consequently, 60 - 70 per cent of black spruce-dominated stands are uneven-aged (Boucher *et al.*, 2003; Côté *et al.*, 2010). Compared with even-aged stands, uneven-aged stands have a wider range of age distribution (Rossi *et al.*, 2009), which is generally associated with a higher proportion of small-diameter trees (10-14 cm; inverse J-shaped diameter distribution) or an irregular diameter distribution (Boucher *et al.*, 2003) and a large amount of deadwood (McGee *et al.*, 1999). The complexity of uneven-aged structures is generally accompanied by a distinct biodiversity as high heterogeneity offers habitats for a wide variety of birds, insects and plants (Bergeron and Noël, 2008; Lowe *et al.*, 2011).

However, black spruce stands are traditionally harvested through clear-cutting (Youngblood and Titus, 1996), which promotes a regular, even-aged stand structure. In addition, clear-cutting can also decrease the long-term abundance and recruitment of deadwood (Bergeron *et al.*, 1999) and thus alter the biodiversity compared with irregular, uneven-aged forests (Hansen *et al.*, 1991; McComb *et al.*, 1993). In recent years, partial cuttings have increasingly been used in black spruce stands of eastern Canada. The objective is to hasten the return to their initial structural attributes (age and diameter distributions). According to the principle of ecosystem-based management, they aim at harvest forests within the observed limits of occurrence of natural disturbances (Hunter, 1990; Bergeron *et al.*, 1999). As they remove a portion of the stems, partial cuttings applied in uneven-aged stands emulate secondary disturbances which might accelerate the return to their initial structure. Nevertheless, in the short term (3 years or less), some partial harvesting treatments could simplify the stand structure (i.e. transform uneven-aged structure into even-aged) if the removal intensity is too high (Cimon-Morin *et al.*, 2010; Ruel *et al.*, 2013). Given that stand structure changes over time due to tree growth and recruitment, the negative effect of high intensity partial cutting may decrease with time.

Tree mortality after silvicultural treatments is increasingly evaluated due to its importance on both biodiversity and productivity. By decreasing stand density, partial cutting can reduce the density-dependent mortality (self-thinning) by decreasing the relative density, which is the ratio between the observed stand density and the maximum density attainable in a stand with the same mean volume (Drew and Flewelling, 1979), which is beneficial from a productivity point of view. However, deadwood is important in the ecosystem as it creates habitats for a wide variety of species (Bergeron and Noël, 2008; Jetté *et al.*, 2008). For example, cavity- and snag-dependent species could be reduced (e.g. Vanderwel *et al.*, 2009) with decreasing mortality of large-diameter trees after partial harvesting (Fridman and Walheim, 2000; Fraver *et al.*, 2002). Dead large-diameter trees provide more advantages for biodiversity since they persist for a longer period of time and a wider range of vertebrates can use them when compared with smaller trees (Conner *et al.*, 1975; Cline *et al.*, 1980; DeGraaf and Shigo, 1985). In contrast, increased wind penetration in the stand following a partial cutting can increase the risk of windthrow. After intense tree removal in an irregular stand, 11 per cent (Groot, 2002) to 32 per cent (Riopel *et al.*, 2010) of residual trees can be lost due to windthrow during the first 5 years. In natural forests, the risk of mortality generally increases with increasing tree size (Canham *et al.*, 2001; Rich *et al.*, 2007) although partial cuttings removing a large number of codominant and dominant trees, and thus leaving smaller trees with low vigour, could be associated with a greater risk of mortality (Caspersen, 2006; Powers *et al.*, 2010). Mortality is therefore highly dependent upon the type of partial cutting method used (Powers *et al.*, 2010). However, to our knowledge, only a few studies have compared the amount of deadwood in post-harvested black spruce stands with unmanaged stands as well as compared different partial cutting methods (e.g. Cimon-Morin *et al.*, 2010).

Tree spatial distribution, or horizontal structure, is another key characteristic of forest stands because it can affect productivity, stand dynamics, and structural diversity (Homyack *et al.*, 2004). The horizontal structure is closely related to stand dynamics through processes such as competition, growth, mortality and tree recruitment (Cale *et al.*, 1989; Nathan and Muller-Landau, 2000). Parameters such as soil, climate, topography and disturbance regimes can also influence the horizontal structure of a stand (Bonan, 1989). However, very little information is available on stand spatial structure following intermediate silvicultural treatments as most emphasis has been placed on stand composition and vertical structure (Gauthier *et al.*, 2008).

After partial cutting, residual tree growth is generally stimulated through increases in soil temperature, nutrient cycling (Thibodeau *et al.*, 2000), moisture availability (Fayle, 1983) and solar radiation. Because stem value is largely dependent on its diameter, improved radial growth of residual trees may thus lead to higher financial returns at the stand level despite the reduced tree density (Liu *et al.*, 2007). While tree growth responses to partial cutting of different intensities have been studied across the Canadian boreal forest *(e.g. Abies balsamea (L.) Mill:* Raulier *et al., 2003;* Bourgeois *et al.*, 2004), little has been done on black spruce stands, except after commercial thinning (Vincent *et al.*, 2009; Krause *et al.*, 2011). While single-tree growth response was highly variable within a stand, a better growth response was observed on trees with the lower growth before thinning (Krause *et al.*, 2011) and with less individual tree competition afterwards (Vincent *et al*., 2009). Therefore, tree growth response is expected to vary depending on the partial cutting method and the residual stand structural attributes (e.g. stand diameter distribution and spatial distribution). Although black spruce response to commercial thinning and fertilization has been quantified (e.g. Weetman 1975), knowledge on its growth response after partial cutting treatments, particularly in uneven-aged stands, is limited.

This study evaluated the effects of three different partial cutting treatments applied to even-aged and uneven-aged black spruce stands in the boreal forest of eastern Canada. The three main objectives of the study were to examine the effect of partial cuttings on: (i) tree age, diameter and spatial distributions, (ii) amount of deadwood and (iii) radial growth of residual trees. We expected that compared with untreated controls, partial cuttings would simplify stand age structure and tree diameter distribution, increase spatial uniformity, reduce the amount of deadwood and increase the radial growth of residual trees.

Understanding the effect of partial cuttings on different stand types will help improve practices within a perspective of sustainable forest management.

Methods

Study site

The study was conducted in managed boreal stands of Quebec, Canada, between 47°51' and 50°35' N and 70°11' and 72°11' W, in the bioclimatic zones of balsam fir (*Abies balsamea* (L.) Mill.) - yellow birch (*Betula alleghaniensis* Britt.) (mixed forest) and balsam fir-white birch (*Betula papyrifera* Marsh.) (boreal forest) (MRNF, 2003-2011) (Fig. 1.1, Supplementary data Table S1.1). The mean temperature in the coldest month is -14.3°C (January) and in the warmest month 17.5°C (July); average annual precipitation is 980 mm (average from 1981 to 2010- Environment Canada (2015)).

Three silvicultural treatments were studied: careful logging around small merchantable stems (CPPTM in Québec, a variant of HARP in Ontario), Careful Logging around stems with Variable Diameter (CLVD, Coupe avec Protection de Tiges à Diamètre Variable in Québec) and Commercial Thinning from below (CT). CPPTM and CLVD are generally applied in uneven-aged stands and consist of removing all trees with a diameter at breast height (DBH) of >14 cm (diameter limit cutting). CLVD is applied in stands with fewer saplings and smaller merchantable stems than stands suitable for CPPTM or where the stem distribution is discontinuous (Pouliot *et al.*, 2011). CT is applied in even-aged stands and generally removes 30-35 per cent of the initial stand basal area, mostly in smaller-diameter trees. A description of each partial cutting treatment is given in Table 1.1.

Five blocks were selected for each partial cutting treatment. A block corresponds to one treated plot (partially cut by the industry) combined with one control plot (i.e. five treated plots + five control plots per partial cutting treatment) (Fig. 1.2). For the CPPTM treatment, three treated plots were part of an experimental study where CPPTM was evaluated in softwood stands across Quebec (Riopel *et al.,* 2010). The other treated and control plots were selected using the forest maps from the *Ministère des Forêts, de la Faunes et des Parcs du Québec* (GIS, third inventory). They were selected based on the time elapsed since treatment application (at least 4 years after to observe the effect of time) and their post-harvest tree species composition (at least 50 per cent of black spruce basal area). The other tree species were mostly balsam fir with minor presence of yellow birch, white birch and jack pine (*Pinus banksiana* Lamb.). The plots were all on sites with a gentle slope and good drainage to limit environmental variations and were established systematically between skidding trails. The control plots were selected within a radius of 1 km from the treated plots to minimize any effect of climate or soil. To be selected, the control plots had to have the same site conditions (e.g. tree composition, soil and slope) and the same initial structure as the treated plots, i.e. even-aged for CT, and uneven-aged for CPPTM and CLVD. The stand age had to be similar to that of the corresponding treated plots, and they had to be exempt from any anthropogenic disturbance. According to an *a priori* power analysis conducted by Vincent *et al*. (2009) on black spruce stands, at least 35 trees per stand were required to cover stand variation and ensure the statistical power of the analysis. The size of the plots therefore ranged from 120 to 400 m^2 to include a sufficient number of trees.

Plot measurements and compilation

In each treated and control plot, the diameter at stump height (DSH; 0.2 m) and at 1.3 m (DBH), total tree height (TH), crown length (CL) and Cartesian coordinates of every black spruce tree (DBH ≥ 4 cm) were noted for a total of 1098 trees (Tables 1.2 & 1.3; Fig. 1.2 & 1.3). For further analyses, the crown ratio (CR = CL/TH) was used instead of CL. In the treated plots, the stump diameter of harvested trees and their position were also noted. Plot mortality was evaluated by measuring the DBH and noting the type of mortality (lying or standing snags) of each dead tree. However, even if their DBH was measured, no type of mortality was recorded for some dead trees, which prevented conducting a statistical analysis on mortality type. For the coarse woody debris (lying snags), only those with a visible stump were measured to ensure that they originated from the plot and to have an exact DBH measurement. The year of mortality was not identifiable due to decomposition. Therefore, this study evaluated the amount and diameter of deadwood found in plots after harvest and not the cause of mortality. Finally, the DBH and position of all other tree species in each plot were noted. All of these data were used to calculate stem density and basal area per hectare (Table 1.3). A schematic representation of the experimental design and plot measurements is shown in Fig. 1.2.

Relative densities were calculated according to an equation parameterized by Newton and Weetman (1993) for black spruce:

$$Rd = \frac{N_o}{(v/10^{7.691})^{-0.618}} \tag{1}$$

where Rd is the relative density, N_o is the observed density (stem ha^{-1}) and v is the mean tree volume (dm^3) calculated as follows:

$\log_{10}(v) = b_1 + b_2 \times \log_{10}(H_d) + b_3 \times \log_{10}(DBH)$ (2)

where $b_1 = -1.5154$, $b_2 = 0.7429$, $b_3 = 2.2832$, H_d is the dominant height and DBH is the mean tree diameter (Newton and Weetman, 1994). The zone of imminent competition mortality is bounded by a minimum relative density (0.50 for black spruce) and the maximum size-density boundary (Newton and Weetman, 1993).

Site quality was evaluated through calculation of the site index (SI), defined as TH at a reference age of 50 years. The SI was calculated according to an equation parameterized by Pothier and Savard (1998) for black spruce:

$$SI_1 = 0.9604 \times H_d^{0.9412}(1 - e^{-0.03379 \times A})^{-0.697 \times H_d^{0.1046}} \quad (3)$$

where H_d is the dominant height, which corresponds to the mean height of the largest 100 trees per ha and A is the mean stand age. The number of years required to reach 1 m was calculated and corrected for the fact that age was measured at 0.2 m instead of 1 m (Pothier and Savard, 1998):

$$SI = SI_1 - 0.8\,(310 \times SI_1^{-1.751}) \quad (4)$$

To improve SI estimations of uneven-aged stands (CPPTM and CLVD), whose age-height trajectory deviates from that of even-aged stands, we used the age-height relationship developed by Ouzennou *et al*. (2008) for black spruce stands. This method consists in introducing the Shannon evenness index based on tree diameters into a Chapman-Richards age-height equation.

Radial growth and competition index

In each stand, a wood core was sampled at 0.2 m above the root collar (to determine tree age without influence of roots) on every black spruce. The cores were air-dried and sanded before measuring tree ring width using either WinDENDRO^{TM} system (Guay *et al.*, 1992) or a manual Henson micrometer (precision of 0.01 mm). The measurements made on each wood core were cross-dated using the COFECHA program (Holmes, 1983). We established a minimum tree age (not every core had the pith) and determined the ring width of each year. To assess the diameter growth variability among treated trees, a diameter increment ($\Delta DSH = DSH_j$ - DSH_i) since the year of cutting was computed, where DSH_j is the tree diameter at the sample year and DSH_i is the diameter the year prior to the cutting. The DSH_i was obtained by subtracting, from the DSH_j, the ring width values measured each year.

To evaluate the effect of competition on radial growth at tree level, Heygi's competition index (CI_i) was calculated for all black spruce trees (equation 5) as proposed by Mailly *et al.* (2003). Using living tree coordinates at the sampled year and ArcGIS, we determined the distance between the subject tree and each neighbour within a 4 m radius ($Dist_{ij}$):

$$CI_i = cf \times \sum_{j=1}^{n} \left(\frac{DBH_i}{DBH_j} \times \frac{1}{Dist_{ij}} \right) \quad (5)$$

Since no trees were sampled outside the plots, a correction factor (*cf*), which was the inverse of the proportion of the circle centred on i (mirror effect), was added to the CI_i equation. To minimize the error introduced by this *cf*, only trees at 2 m from the plot edge were considered.

Data analysis

Stand structural attributes

A linear mixed-model analysis of variance (ANOVA) was used to detect significant differences in dead tree basal area and density between each partially cut plot and its respective control, as well as between the three partial cutting treatments. The "lme" function in the "nlme" package (Pinheiro and Bates, 2007) in R (R Core Team, 2014) was used to fit the linear mixed-model by maximizing the restricted log-likelihood (REML). The model took into account both SI and time since treatment (TST). The same TST of treated plots was attributed to control plots to compare the same calendar year, which limited the effect of climate. A random effect was estimated for each block. Square-root transformations were applied when necessary to satisfy the assumptions of normality and homogeneity of variance. When the ANOVA detected a significant difference between treatment means, a Tukey pairwise multiple comparisons test, using "lsmeans" package and function (Lenth and Hervé, 2015) in R, was conducted to distinguish the effect of the treatment.

To compare age, residual tree and dead tree DBH frequency distribution among plots, non-parametric multivariate analysis of variance (PERMANOVA) was conducted using the Bray-Curtis dissimilarity method in the software package Primer 6 (Clarke and Gorley, 2006). This method compared the differences between treatments by incorporating block as a random factor. When the PERMANOVA detected a significant difference between treatment distributions, a pairwise test was conducted to examine the difference between each partial cutting and its respective control.

Spatial Analysis

Ripley's K function (Ripley, 1977) is one of the most commonly used methods to analyse tree spatial distribution (Fortin and Dale, 2005). Using the living tree coordinates of all species, we were able to determine the tree spatial distribution in treated and control plots (Fig. 1.3). Tree spatial distribution in the treated plots before the partial cutting was determined by including stump coordinates. A univariate function was used to compute the K-function based on all pairs of points (neighbour trees) separated by a distance less than a given radius r (Fortin and Dale, 2005).

$$K(r) = \frac{A}{n_k^2} \sum_{i=1}^{n_k} \sum_{j=1}^{n_k} w_{ij} I_t(i,j) \, for \, i \neq j \qquad (6)$$

with

$$I_t(i,j) = \begin{cases} 0, if d_{ij} > r \\ 1, if d_{ij} \leq r \end{cases} \qquad (7)$$

where n is the number of trees in plot k, A is the plot area and d_{ij} is the distance between trees i and j (Fortin and Dale, 2005), and w_{ij} is a weight necessary to correct the edge effect, which corresponds to the inverse of the proportion of the circle centred on i and passing through j (Goreaud and Pelissier, 1999). The K-function was estimated at distances of 0.5 m (r) from 0 to 5 m from each tree (i). It was then transformed into the L-function (equation 8) to stabilize its variance and to equal zero under complete spatial randomness (Goreaud and Pelissier, 2003). Values of L(r) < 0 and L(r) > 0 indicate segregated and aggregated spatial patterns, respectively.

$$L(r) = \sqrt{\frac{K(r)}{\pi}} - r \qquad (8)$$

Monte Carlo simulations were used to detect significant deviations from complete randomness. A thousand simulations were used to create a 95 per cent confidence envelope of L(r), using random coordinates as numerous as the number of trees per plot. If the value of L(r) departed from this envelope, it was considered to be significantly different from randomness. All spatial analyses were done in SAS 9.2 (SAS Institute Inc., Cary, NC, USA), using a routine created by Rossi *et al.* (2013).

Growth and variability

To evaluate the growth after the three partial cuttings, a ratio between ring width 5 years post- to 5 years pre-treatment was used. To compare growth ratio between treated and control plots, a linear mixed-model ANOVA was conducted in R (R Core Team, 2014) using the "lme" function in the "nlme" package (Pinheiro and Bates, 2007). SI and tree characteristics (crown ratio, age and DSH_i) were used to account for differences between individual trees, plots and treatments, whereas trees within blocks were considered as a random effect. Tukey multiple comparisons tests were conducted, using the "lsmeans" method (Lenth and Hervé, 2015), to distinguish the effect of the treatment.

A second analysis was performed to identify years during which ring widths were different than those of control plots. A linear mixed-model ANOVA with repeated measurements (years) was used on each partial cutting separately with the REML method, using the "lme" function in the "nlme" package in R (Pinheiro and Bates, 2007). Only the ring widths produced after the treatments were analysed. SI, TST and tree characteristics (crown ratio, age, DSH_i and pre-harvest growth (average of 5 years pre-treatment)) were used to account for the differences between individual trees, plots and treatments, whereas trees within blocks were considered as a random effect. Square-root transformation was applied when necessary to satisfy the assumptions of normality and homogeneity of variance.

Multiple linear regression was conducted to evaluate the relationship between ΔDSH and predictor variables (SI, TST, crown ratio, age, DSH_i and CI_i). Only data from partially cut plots were used. This allowed us to determine which factor influenced tree growth increment after partial cuttings. Multi-collinearity was assessed on predictor variables and square-root transformation on ΔDSH was used to satisfy the assumptions of normality and homogeneity of variance.

Results

Stand structure

Structural attributes

At the sample year (9, 5 and 10 years after CPPTM, CLVD and CT respectively), mean total basal areas were 56 ± 15, 49 ± 22 and 39 ± 13 per cent less for CPPTM, CLVD and CT, respectively, compared with their respective control plots (Table 1.3). Mean stand densities measured in CPPTM, CLVD and CT were 35 ± 25, 42 ± 18 and 37 ± 27 per cent lower than their respective controls (Table 1.3). Higher SI was found in CT plots than that in CLVD and CPPTM. However, partially cut plots had a lower SI when compared with their respective control plots (Table 1.2).

Mean basal area of deadwood after CPPTM and CT was 2.3 and 0.3 m^2 ha^{-1}, respectively, which correspond to 58 ± 16 and 96 ± 6 per cent less compared with their controls (Table 1.3). In contrast, CLVD plots had higher deadwood basal area (2.4 ± 1.6 m^2 ha^{-1}) than their controls (1.7 ± 1.1 m^2 ha^{-1}). The treatments had a significant effect on deadwood basal area (p=0.0008) with some block variability. Multiple comparisons indicated a significant difference for CPPTM (p=0.0077) and CT (p≤0.0001), but not for CLVD (p=0.9999) when compared with their specific controls (Fig. 1.4). Less basal area of deadwood was found after CT than all other treatments (Fig. 1.4). The dead tree density was statistically lower in CT plots than the controls (CT: p≤0.0001) with only 35 dead trees per ha compared with 729 (Fig. 1.4). Mean relative densities were below the lower limit of the zone of imminent competition-induced mortality (ZICM; 0.5) for CPPTM and CLVD, and slightly above for CT (Table 1.3). Relative densities of control plots were higher than those of treated plots and were above the lower limit of ZICM in the case of control plots associated with CPPTM and CT (Table 1.3). Dead trees found after CPPTM had a DBH distribution significantly different (p=0.029) than that of control plots according to the PERMANOVA, whereas there was no difference for CLVD and CT (Fig. 1.4).

The age structure indicated that CT plots had an even-aged structure, the majority of trees being within the 60-80 year class, while the wider age distribution associated with CPPTM and CLVD corresponded to an uneven-aged structure (Fig. 1.5). Between the three partial cuttings, CLVD had the smallest trees with the highest tree frequency in the 6-9 cm class, which was similar to its control (Fig. 1.5). Ten years after CPPTM, there was a higher tree frequency in the 9-12 cm class with a mean DBH of 10.1 ± 3.1 cm, which was 2 cm less than control plots (Table 1.2; Fig. 1.5). CT plots had the larger trees with a mean

DBH of 16.8 ± 3.4 cm with the majority of trees within the 15-18 cm class. Interestingly, the age ($p=0.229$) and diameter ($p=0.279$) distributions of the partially cut plots were not statistically different from their control plots (pairwise test shown in Fig. 1.5) according to the PERMANOVA, with some block variability for the DBH distribution ($p=0.049$).

Spatial structure

Tree spatial distribution within each plot was evaluated using the univariate Ripley's L (r) function (Supplementary data, Fig. S1.1). A summary of the frequency of plots with aggregation or segregation for each partial cutting is presented in Fig. 1.6. Few plots showed clustering before and after CPPTM, whereas the control plots were mostly randomly distributed. A higher frequency of plots showing tree aggregation can be observed after CLVD (Fig. 1.6). The spatial distribution of treated plots before the CLVD was not different from that of control plots, whereas after CLVD, more plots were observed with clusters between 2.5 and 4 m (Fig. 1.6). After CT, trees were segregated at short distance (Fig. 1.6), meaning that close competition was reduced. At longer distances, there was some clustering although there were fewer clusters after the commercial thinning than before.

Radial growth

Mean tree ring widths, 9 and 8 years after CPPTM and CT, were 0.14 and 0.13 cm $year^{-1}$ compared with 0.05 and 0.07 cm $year^{-1}$ for their respective controls. The growth ratio indicated that ring width nearly doubled after CPPTM ($p\leq0.0001$) and was 1.50 times greater after CT ($p=0.0072$; Table 1.4). The difference between tree ring width from partially cut plots and their controls increased with time as the interaction between treatment and year was significant for each partial cutting method ($p<0.0001$; Fig. 1.7). The growth increase began the first year after CPPTM and the third after CT and continued for 9 and 8 years after each partial cutting, respectively (Fig. 1.7). On the other hand, ring widths after CLVD were greater than those in the control plots starting at year 2 (Fig. 1.7). However, ring width did not increase 5 years after CLVD as the growth ratio was the same as that in the control plots ($p=0.4490$; Table 1.4).

The growth variability between trees was high after each partial cutting (Supplementary data, Fig. S1.2). Compared with their controls, there was a greater frequency of trees with a diameter increment (ΔDSH) of >2 cm after CPPTM and CT (Supplementary data, Fig. S1.2). Multiple regression analysis was used to determine what was associated with this variability in ΔDSH between trees after a partial cutting treatment ($r^2=0.4952$). Tree ΔDSH increased with greater TST ($t=9.372$, $p\leq0.0001$) and crown ratio ($t=1.984$, $p=0.0485$), but decreased with increasing age ($t=-3.890$, $p=0.0001$) and competition index (CI_i, $t=-3.300$, $p\leq0.0011$). However, DSH_i ($t=-1.198$, $p=0.2324$) and SI ($t=1.832$, $p=0.0684$) were not significantly associated with ΔDSH.

Discussion

Understanding the spatial distribution of trees after a partial cutting is important to better forecast the future stand growth and long-term stand dynamics. Trees within control plots were mostly dispersed randomly with some aggregation, as was observed in other natural mature black spruce stands (St-Pierre *et al.*, 1991; Rossi *et al.*, 2013). In natural stands originated from fire, black spruce seedlings are often observed in clusters near the burned boles of the former trees (St-Pierre *et al.*, 1991; Filion and Morin, 1996).

Afterwards, a random spatial distribution is gradually established as a result of early mortality at the juvenile stage (Kenkel, 1988) and self-thinning during later developmental stages (Carleton and MacLellan, 1994; Harper *et al.*, 2005). Nevertheless, at the mature stage, aggregation can be observed in high-density stands because of a localized incomplete self-thinning process due to a heterogeneous environment, where favourable conditions could alter the interaction among trees and thereby reduce mortality (Barot *et al.*, 1999). Commercial thinning (CT) is often applied in even-aged, high-density stands to rectify the clustered patterns apparent in pre-thinning plots (Fig. 1.6). After CT, clustering frequency and close competition are reduced by lower stand density and trees tend to be uniformly distributed at short distances (Fig. 1.6). By reducing competition, growth resources were more available and better distributed among trees so that their radial growth increased after CT compared with controls (Fig. 1.7), as already observed in other black spruce stands (Vincent *et al.*, 2009). Stem radial growth began to increase from the third year after treatment because over the short term, resources were allocated to the root system to improve both tree water supply and anchorage (Urban *et al.*, 1994; Kneeshaw *et al.*, 2002; Vincent *et al.*, 2009).

The main purpose of CT is to increase stand vigour to promote stem growth, which was observed in this study (Fig. 1.7). However, there are some structural changes in plots after CT as they had less deadwood than control plots (Fig. 1.4) as already observed by Powers *et al.* (2010) in red pine (*Pinus resinosa* Ait.) stands. Tree mortality in even-aged stands is often related to the self-thinning rule (Drew and Flewelling, 1977, 1979; Bravo-Oviedo *et al.*, 2006), which describes the relationship between mean tree size and the maximum stand density regulated by competition-induced mortality (Powers *et al.*, 2010).

Maximum size-density relationships likely explain the high mortality observed in the control plots (Powers *et al.*, 2010), as suggested by their relative density values within the zone of imminent mortality induced by tree competition (Table 1.3). The decreased stand density after CT allowed tree size to increase without increasing mortality, as the relative density was lower than that of control plots (Table 1.3). Also, compared with the other partial cuttings, CT has the lowest harvest intensity, which may limit post-harvest mortality by windthrow (e.g. Thorpe and Thomas, 2007). In addition, the improved tree vigour decreased stand vulnerability to spruce budworm outbreaks and thus contributed to reduce the long-term deadwood recruitment after partial cutting (Pothier *et al.*, 2012; Soucy *et al.*, 2012). The increased single-tree radial growth and decreased stand mortality are beneficial for overall productivity, but could be detrimental to animal and plant species associated with deadwood (Vanderwel *et al.*, 2009). However, given the aim and cost of CT, a low amount of deadwood is desired.

After CLVD and, to a lesser extent, after CPPTM, more small clusters of trees were observed compared with controls and pre-treatment observations (Fig. 1.6). In natural uneven-aged forests, gap dynamics is the principal mechanism driving tree spatial distribution, creating stand spatial heterogeneity and tree aggregation (Franklin *et al.*, 2002). According to our results, diameter limit cuttings increased the patchiness of the stand as previously observed by Meador and Moore (2011) in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests in northern Arizona. This is particularly noticeable for CLVD, which is generally applied in stands with discontinuous and clustered distribution of small trees (Pouliot *et al.*, 2011). Trees within a cluster are submitted to a high level of competition, which appears to limit their growth (Fraver *et al.*, 2014), as competition is inversely related to ΔDSH. As a consequence, CLVD did not improve tree radial growth rate due to the high frequency of clusters (Figs. 1.6 & 1.7). In contrast, there were fewer clusters after CPPTM and the majority of residual trees benefited from the decreased stand basal area from the first year following the treatment application (Figs. 1.6 & 1.7). After CPPTM, average tree ring width was twice that of the pre-harvest rate, as already observed by Thorpe *et al.* (2007). However, a high variability in growth was observed between partially cut plots (Fig. 1.7), which was likely due to heterogeneity in the application of the treatment and/or in initial stand characteristics (Table 1.3).

Since relatively few studies have examined the effect of partial cutting on tree spatial distribution, we believe that our results offer an important contribution to the understanding of black spruce stand dynamics after partial cutting in boreal forests, despite some limitations. For example, horizontal stand structure is better described in larger plots (0.1 ha), as Ripley's functions are sensitive to plot size (Larson and Churchill, 2012). Also, no skidding trails were included in our plots although they can affect both local tree density and diameter growth after partial cutting treatments (Genet and Pothier, 2013). Nonetheless, we believe that clusters of small trees after partial cutting in uneven-aged stands could alter tree radial growth. It is therefore important to avoid leaving small tree clusters in residual stands, especially with CLVD, even if tree clusters could have environmental advantages (e.g. preferred habitat for some species, reduce windthrow risk), which could make them interesting attributes in treated stands. However, considering the application cost of partial cuttings and the fact that stem value is largely dependent on its diameter, treatments without potentials for interesting financial returns might not be viable options for forest industries.

The multiple regression analysis indicated that ΔDSH of residual trees was related to TST, tree age, crown ratio and the competition index. A relationship between tree growth and age was also observed by Thorpe *et al.* (2007), who speculated that the age-dependent increase in pathogenic fungi (e.g. root-rot fungi such as *Armillaria* spp. and *Inonotus tomentosus* (Fr.) Teng. for black spruce (Whitney, 1995)) could be an important factor explaining the declining growth with age. Since the majority of saplings within clusters in uneven-aged forest are old (± 80 years) (St-Denis *et al.*, 2010), they likely have lower potential to respond positively to tree removal. However, ~ 50 per cent of tree growth variability was unexplained, indicating that other factors have influenced growth (e.g. soil conditions, root formation, root grafting, harvest injuries, etc.). This high unexplained variability could also be related to the fact that growth measurements were made at stump rather than at breast height, which can induce higher variability (Fraver *et al.*, 2011).

The treatments applied in the studied uneven-aged stands tended to maintain an age structure and diameter distribution comparable with those of control plots (Fig. 1.5) even though stand basal area and tree density were lower (Table 1.3). This resulting stand density is likely inadequate to preserve the wildlife diversity typical of old-growth forest (e.g. Fortin *et al.*, 2011) since lateral obstruction cover is important to decrease predation risks for many species (Ferron *et al.*, 1998; Turcotte *et al.*, 2000). Furthermore, lower deadwood basal area was observed after CPPTM (65 per cent less), as well as higher smaller-diameter tree mortality (Fig. 1.4), as already observed after other partial harvestings (Fridman and Walheim, 2000; Fraver *et al.*, 2002). The amount and diameter of deadwood could be insufficient to maintain some of the associated animal species (e.g.

DeGraaf and Shigo, 1985; Vanderwel *et al.*, 2009; Ruel *et al.*, 2013). The relative densities of treated plots were lower than that of control plots and were below the zone of imminent competition-induced mortality, which explain the low amount of deadwood (Table 1.3). On the other hand, dead trees were mainly found on the ground after CPPTM (Fig. 1.4), which could be related to the high mortality rate by windthrow observed soon after high intensity partial cutting (Gardiner *et al.*, 1997; Riopel *et al.*, 2010). However, the amount of deadwood found after CPPTM is still less than that in natural forests, suggesting that alternative methods should be implemented to increase deadwood volume. First, by leaving the pre-existing snags in cut stands and some reserve large-diameter trees that will eventually die and provide benefits for biodiversity. Second, by promoting deadwood recruitment through active management (e.g. removing live crowns) during the first few years after a partial cutting (e.g. Huff and Bailey, 2009) in some critical stands where few microhabitat-bearing trees are available and strong conservation issues have been identified (e.g. presence of endangered species) (Bütler *et al.,* 2013).

Over the short term, Cimon-Morin *et al.*, (2010) found that selection cutting methods were more suitable than CPPTM to maintain a higher canopy density, mean tree size and abundance of deadwood in black spruce stands. However, these approaches were also associated with higher logging costs (Moore *et al*., 2012), which could make them less appealing for the forest industry. Therefore, CPPTM and CLVD are good alternatives as they should, nevertheless, promote an irregular stand structure. The number of years elapsed since the treatment application is important to promote diameter distribution of old-growth stands given that ΔDSH is positively related to the TST. Thus, the temporal increase in basal area within most diameter classes indicates that partial cutting can maintain stand structure (Groot, 2014). The growth variability among trees will ensure, in the long term, the implementation of complex diameter distribution. Groot (2014) indicated that heavy partial cutting in uneven-aged black spruce forest can reach the pre-harvest basal area of ~45 years after harvest, but it could take between 65 and 105 years in poorer quality sites with a low level of post-harvest growing stock (Thorpe *et al.*, 2010).

Overall, these results suggest that the studied partial cuttings were adequate for maintaining structural attributes and increasing tree growth, but adjustments should be made to treatments to increase the amount of deadwood to a level observed in control plots and to lower the frequency of tree clusters. It is important to note that these results only apply to a subset of black spruce stands (black spruce composition >50 per cent after harvesting). Also, since no data on initial stand characteristics were available, some of the differences between treated and control plots could have been present prior to the treatment. However, only a few studies have evaluated the effects of partial cuttings in uneven-aged boreal forests on tree spatial distribution, age and diameter distribution and on the amount of deadwood. Our results therefore provide a good overview of the effects of partial harvesting treatments and their ability to achieve their goals.

Conclusion

Partial cuttings are increasingly used in the boreal forest to maintain natural structure (age and diameter distribution), especially in uneven-aged stands, and to increase residual tree growth. In uneven-aged forests, CPPTM and CLVD decreased tree density and stand basal area. Also, CPPTM is associated with a reduction in the abundance of deadwood, especially of larger diameter, but this may be corrected by appropriate measures. Nevertheless, the age structure and diameter distribution after partial cuttings in uneven-aged stands did not differ from those of control plots. Moreover, single-tree radial growth after CPPTM was twice the pre-harvest rate, which could be economically attractive. However, inter-tree competition and tree age could limit the growth increase, as was observed after CLVD. On the other hand, commercial thinning has long been used to promote stand vigour and growth, and our results support that this treatment is adequate for this objective in black spruce stands. Finally, partial cuttings in both even- and uneven-aged black spruce stands, with appropriate measures, can be efficiently integrated in sustainable forest management.

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Conflict of interest statement

None declared.

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Table 1.1. Characteristics of partial cutting treatments.

Partial cuttings	**Initial structure**	**Basal area harvested**	**Particularities**	
CPPTM	Uneven-aged (Irregular)	70 to 90%	Protection of small merchantable stems (9 to 14 cm)	- Leaving 900 stems/ha of 2 to 14 cm with 125 of them between 10 to 14 cm
CLVD	Uneven-aged (Irregular)	Variable (up to 95%)		- Leaving 375 stems/ha of 4 to 14 cm with 75 of them between 10 and 14 cm
CT	Even-aged (Regular)	30 to 35%		- Harvesting stems with lower quality (smaller, not straight, etc.)

Table 1.2. Mean ± standard error, minimum and maximum diameter at 1.3 m (DBH), age and height, with the time since treatment (TST) and site index (SI), for n trees in each of the p treated and control plots within the three partial cuttings.

			DBH			Age			Heigth			TST			SI		
Treatment		n	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
CPPTM	Treated	134	10.1 ± 0.3	5.0	19.1	79 ± 2.0	22	124	7.7 ± 0.2	2.8	12.3	9.0 ± 0.9	6	12	4.7 ± 0.7	2.7	6.9
	Control	176	12.2 ± 0.3	5.6	24.6	93 ± 2.0	36	175	10.2 ± 0.2	4.5	19.0	10.0 ± 1.3	6	14	7.8 ± 0.7	6.4	9.7
CLVD	Treated	172	10.0 ± 0.3	4.0	26.0	78 ± 1.7	21	144	7.6 ± 0.2	2.6	17.7	4.8 ± 0.5	4	6	5.2 ± 2.5	0.7	12.3
	Control	190	10.7 ± 0.4	4.0	28.0	74 ± 1.9	32	199	8.5 ± 0.3	3.5	21.0	6.0 ± 0.0	6	6	6.9 ± 1.9	1.9	13.1
CT	Treated	202	16.8 ± 0.2	9.2	26.1	68 ± 0.8	40	94	14.0 ± 0.2	7.0	26.0	10.2 ± 0.2	10	11	11.7 ± 1.6	7.7	16.7
	Control	252	15.5 ± 0.3	6.0	28.5	80 ± 1.6	22	182	14.9 ± 0.2	7.7	26.1	11.4 ± 0.7	10	13	13.3 ± 2.0	8.9	19.2

Table 1.3. Basal area (m^2 ha^{-1}) and density (# ha^{-1}) (mean ± standard error) for each plot within the three partial cuttings, divided by type (stump, dead, black spruce (BS) and other tree species (Other)).

		Basal Area (m^2 ha^{-1})					Density (Tree ha^{-1})					
Treatment		**Stump**	**Dead**	**BS**	**Other**	Total	**Stump**	**Dead**	**BS**	**Other**	Total	Relative density
CPPTM	Treated	24.0 ± 6.6	2.3 ± 0.1	8.8 ± 1.2	4.6 ± 2.5	13.4 ± 2.8	748 ± 283	321 ± 65	1044 ± 183	416 ± 224	1460 ± 198	0.24 ± 0.04
	Control	0.0 ± 0.0	6.8 ± 1.9	28.7 ± 4.9	1.4 ± 0.3	30.6 ± 4.8	0 ± 0	447 ± 123	2227 ± 269	127 ± 37	2373 ± 275	0.56 ± 0.09
CPTDV	Treated	25.2 ± 4.7	2.4 ± 0.7	8.9 ± 2.3	2.2 ± 1.0	11.1 ± 3.1	603 ± 60	260 ± 56	1105 ± 215	335 ± 138	1440 ± 148	0.24 ± 0.09
	Control	0.0 ± 0.0	1.7 ± 0.5	19.1 ± 1.5	2.3 ± 1.2	21.4 ± 2.4	0 ± 0	218 ± 54	2167 ± 334	372 ± 202	2538 ± 180	0.45 ± 0.07
EC	Treated	22.2 ± 4.2	0.3 ± 0.2	24.1 ± 3.9	4.9 ± 3.2	29.0 ± 3.5	1256 ± 272	35 ± 24	1064 ± 113	209 ± 115	1273 ± 79	0.51 ± 0.08
	Control	0.0 ± 0.0	6.7 ± 1.0	39.2 ± 6.4	9.1 ± 2.9	48.4 ± 5.4	0 ± 0	729 ± 336	2247 ± 899	365 ± 118	2612 ± 830	0.87 ± 0.11

Total represents the value at the sample years (Total = BS+Other)

Table 1.4. Growth ratio from 5 years post- to 5 years pre-treatment (mean ± standard error) for each treated and control plots within the three partial cuttings.

Treatment		**Growth ratio**	
CPPTM	Treated	1.90 ± 0.21	BC
	Control	1.04 ± 0.05	A
CLVD	Treated	1.14 ± 0.05	AD
	Control	0.97 ± 0.03	A
CT	Treated	1.51 ± 0.07	BD
	Control	1.13 ± 0.05	AC

Same letters are not significantly different ($p>0.05$)

Supplementary Table S1.1. Additional information for each treated and control plots within each partial cutting.

Partial cuttings	Block	Plot	Latitude (N)	Longitude (W)	Year of cutting	Size (ha)
CPPTM	B3	Treated	48° 41' 10.2''	70° 21' 51,1''	1997	23.1
		Control	48° 41' 54.4''	70° 20' 54.5''	-	11.3
	B10	Treated	48° 41' 34.4''	70° 21' 33,4''	1999	7.9
		Control	48° 41' 36.3''	70° 22' 07,6''	-	2.3
	B20	Treated	48° 42' 58,6''	70° 13' 13,7''	2000	8.7
		Control	48° 43' 02,3''	70° 13' 27,4''	-	4.2
	B21	Treated	50° 15' 53,5''	72° 11' 14,7''	2000	15.3
		Control	50° 16' 03,4''	72° 11' 29,6''	-	4.1
	B5	Treated	50° 25' 26,5''	72° 00' 49,7''	2003	3.2
		Control	50° 25' 28,5''	72° 00' 51,4''	-	5.1
CLVD	CLVD1	Treated	48° 43' 52.3''	70° 11' 21,5''	2006	7
		Control	48° 43' 14.9''	70° 11' 11.9''	-	6.8
	CLVD2	Treated	48° 42' 28.9''	70° 13' 50,8''	2006	22.4
		Control	48° 43' 18.0''	70° 12' 22.4''	-	10.7
	CLVD4	Treated	50° 35' 54.0''	70° 35' 40.0''	2006	26.4
		Control	50° 34' 12.3''	70° 36' 13.6''	-	17.6
	CLVD5	Treated	50° 25' 22.9''	71° 26' 38.6''	2006	11.4
		Control	50° 22' 42.0''	71° 27' 11.3''	-	20.6
	CLVD9	Treated	50° 23' 43.0''	71° 42' 42.0''	2006	8.7
		Control	50° 21' 48.8''	71° 42' 14.0''	-	12.4
CT	LA1	Treated	47° 51' 19.5''	71° 18' 09.9''	1998	8.3
		Control	47° 51' 49.7''	71° 19' 08.6''	-	13.4
	LC1	Treated	48° 08' 58.9''	71° 52' 00.1''	1998	6.1
		Control	48° 08' 41.4''	71° 52' 51.5''	-	5.3
	LC2	Treated	48° 08' 17.2''	71° 52' 46.5''	1998	3.9
		Control	48° 08' 22.0''	70° 21' 33.0''	-	43.3
	MV3	Treated	48° 47' 38.0''	70° 21' 33.0''	1997	4.4
		Control	48° 47' 31.7''	70° 21' 29.3''	-	13.4
	MV4	Treated	48° 46' 51.7''	70° 33' 05.8''	1998	3.8
		Control	48° 46' 45.4''	70° 32' 53.0''	-	1.9

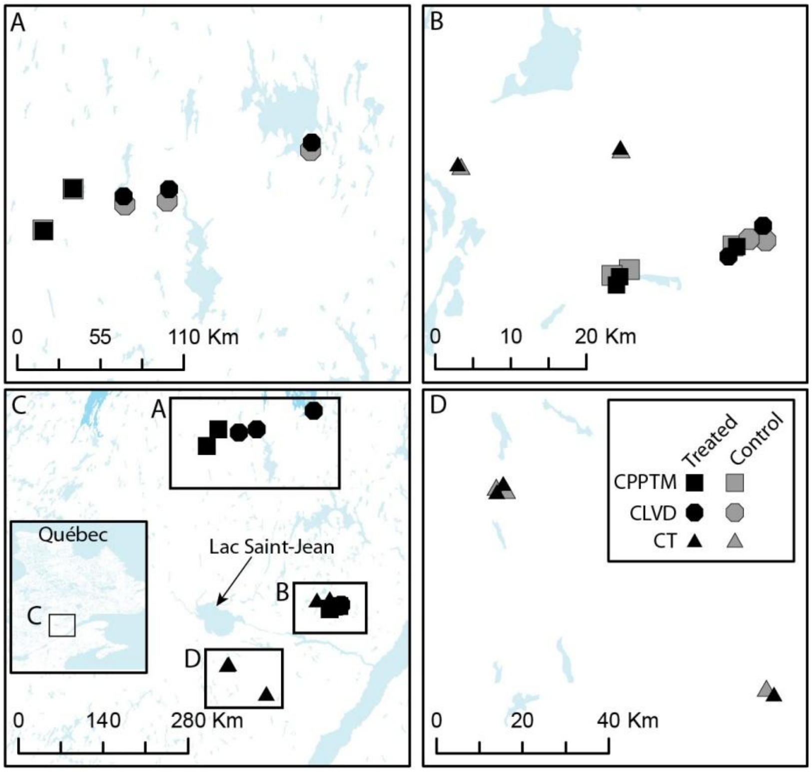


Figure 1.1. Study region (C) and location of treated and control plots for each partial cutting. A, B and D are close-ups of the three sectors shown in C.

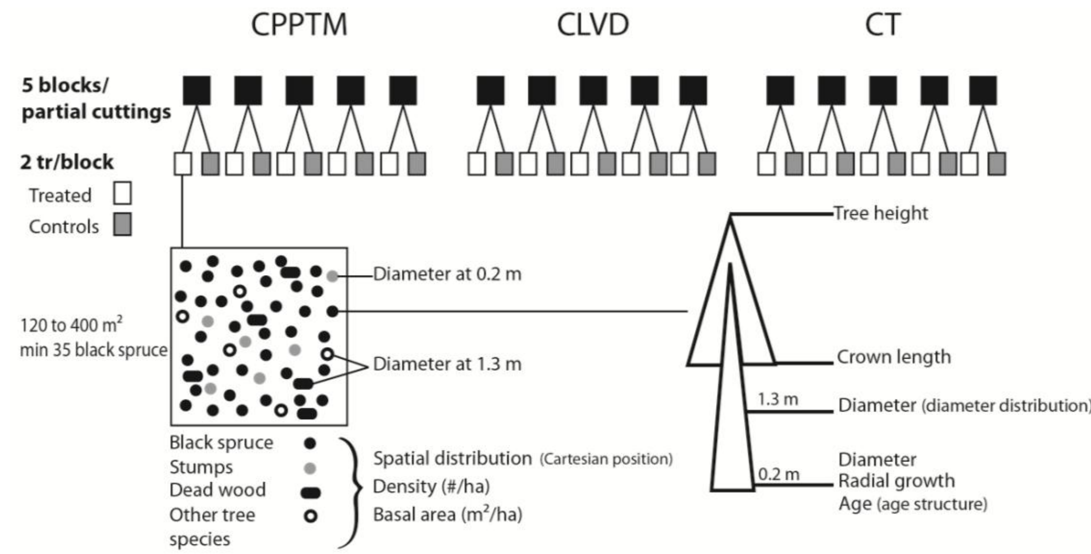


Figure 1.2. Schematic representation of experimental design and plot measurements.

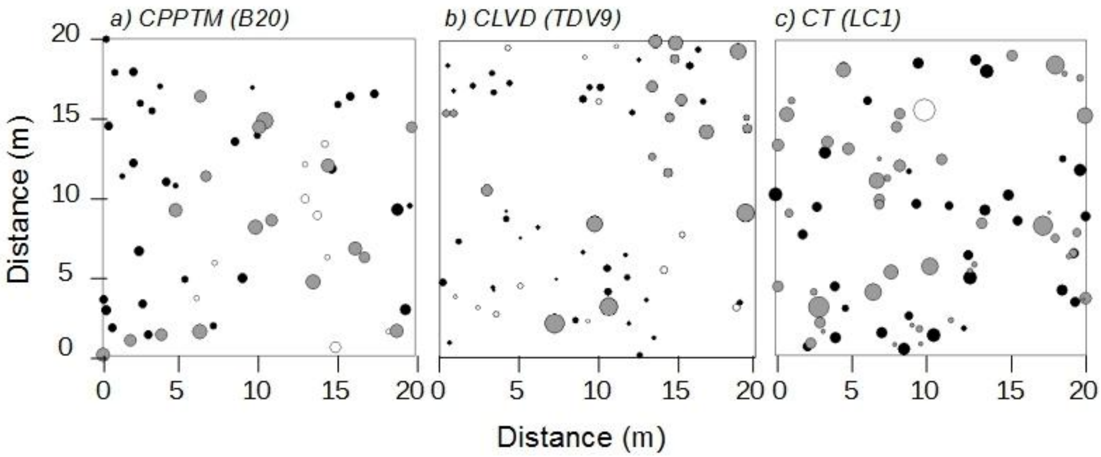


Figure 1.3. Example of the spatial distribution for each treatment. Black, white and grey dots represent black spruce, other tree species and stumps, respectively. Symbol size represents the DBH of each tree multiplied by four to facilitate the observation.

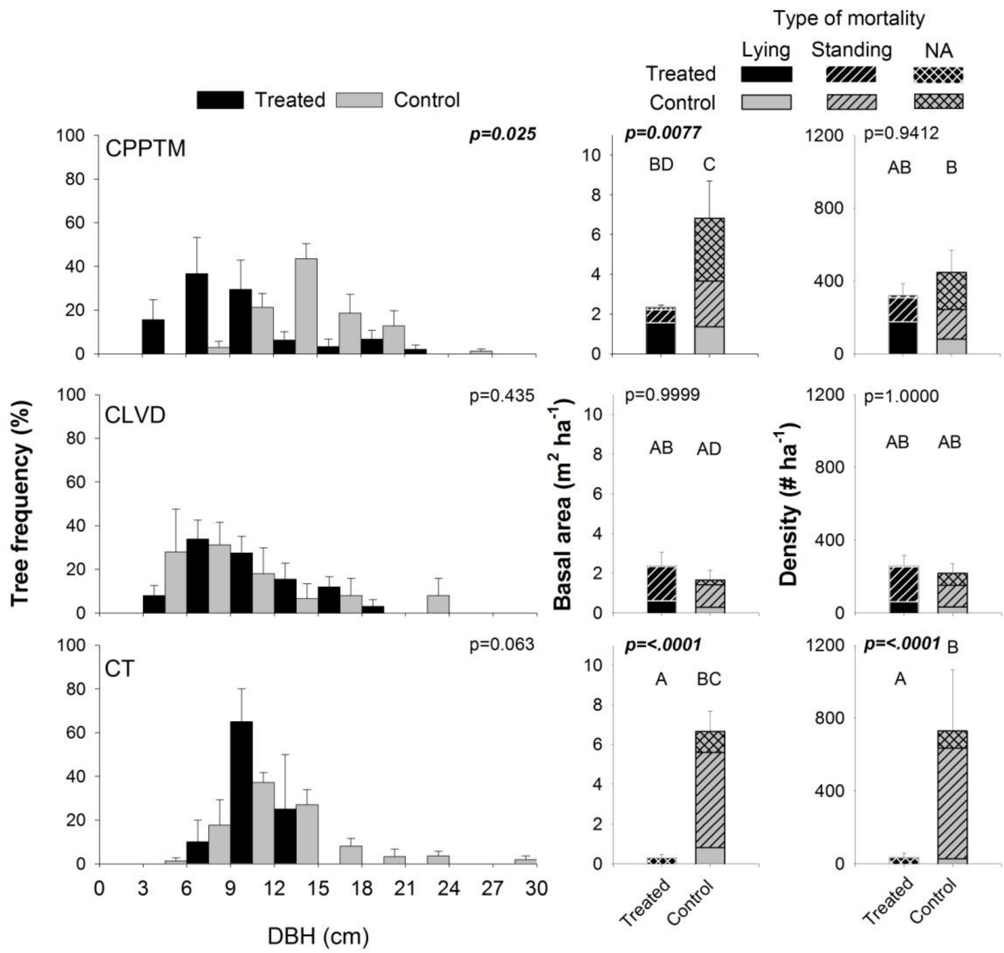


Figure 1.4. DBH distribution, mean basal area and plot density of dead trees by treatment at sample year, divided by type of mortality (lying or standing- only for basal area and density). NA represents trees with no type recorded. Vertical lines refer to the standard error. Same letters are not significantly different (p>0.05).

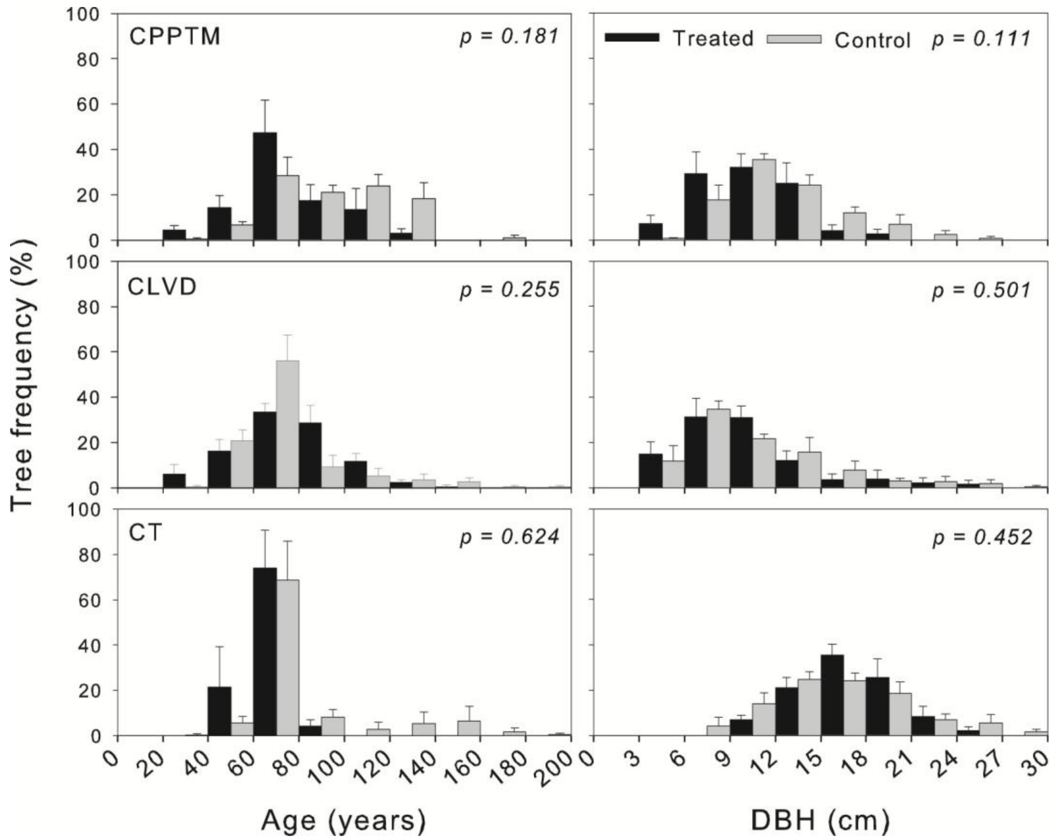


Figure 1.5. Mean frequency distribution of age and diameter at 1.3 m (DBH) of live black spruce trees measured at the sample year for the three partial cuttings and their controls, with standard error. P-values are the results of the PERMANOVA pairwise test.

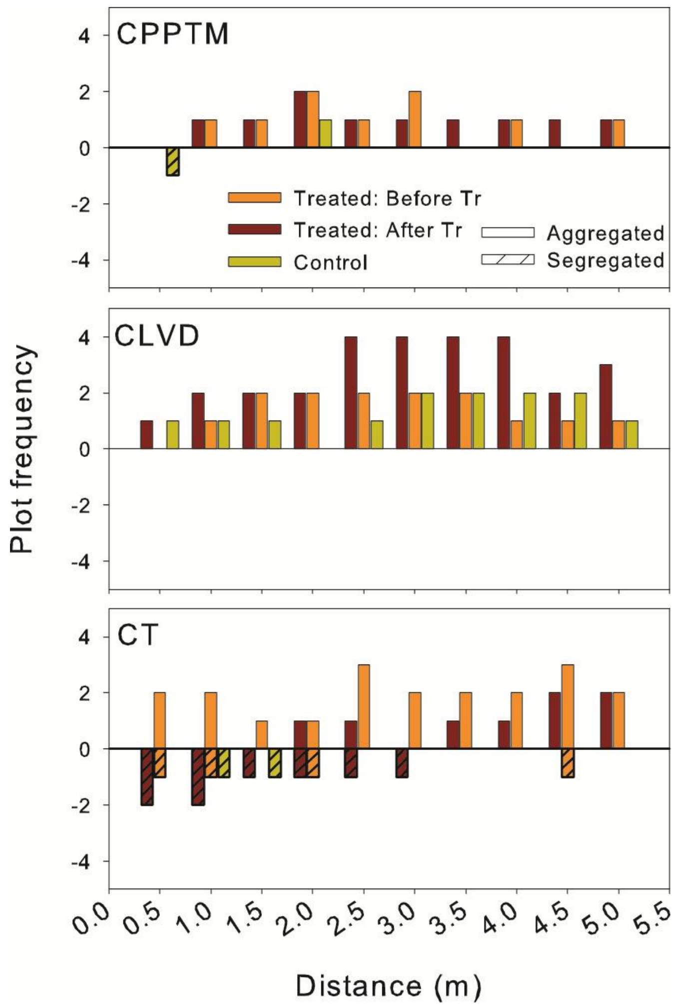


Figure 1.6. Summary for each treatment (Tr) of the univariate Ripley's L (r) function calculated on each treated and control plot (Supplementary data, Fig. S1.1). The vertical bars represent the frequency of plots that have a value of the function that is lower (negative) or higher (positive) than the envelope indicated by the Monte Carlo simulation, which means that the distribution is significantly overdispersed (segregation) or aggregated (clustering), respectively, at a distance (m) from each tree.

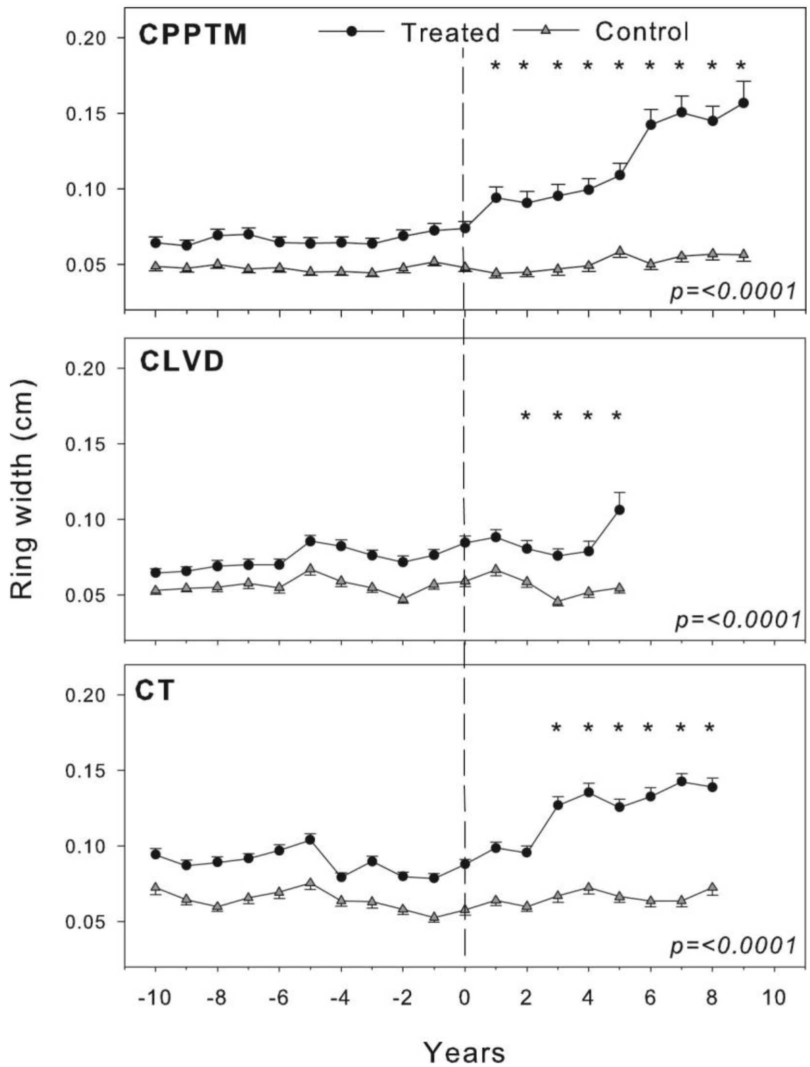
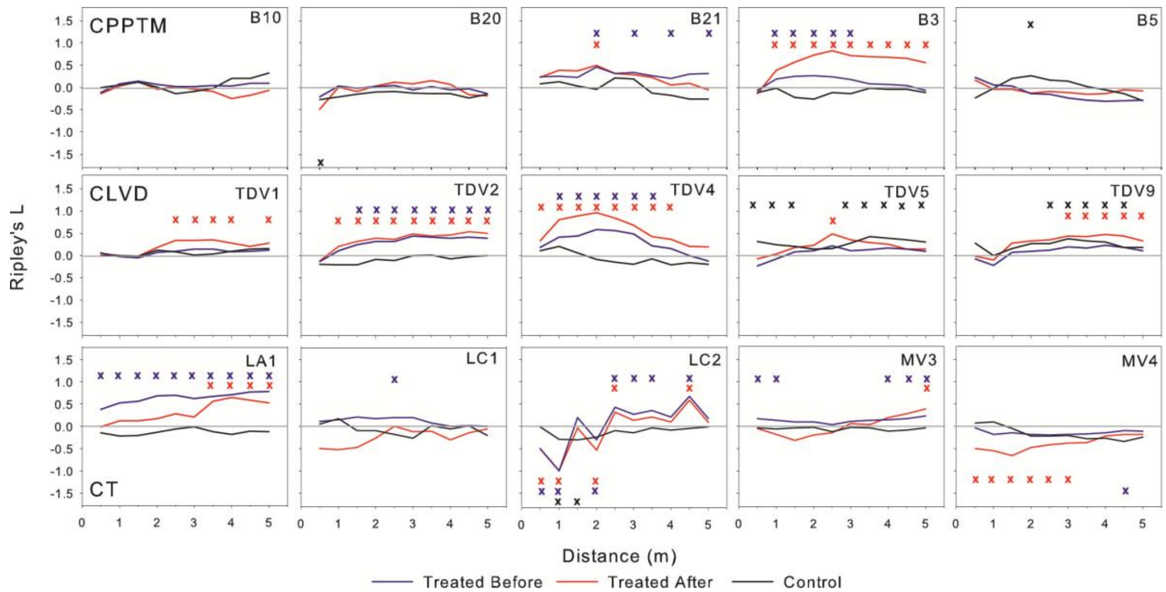
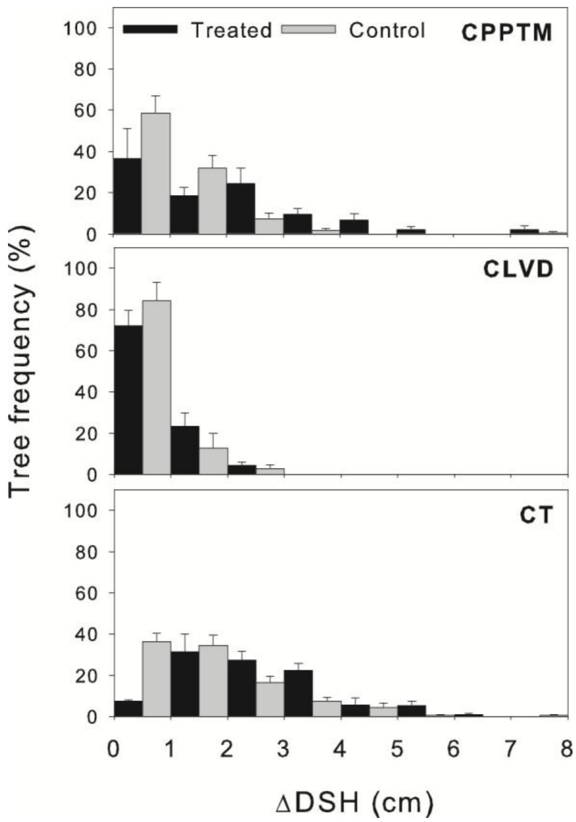


Figure 1.7. (A) Average ring width (cm) per year measured at 0.2 m for each treatment (black circles) with their controls (grey triangles). The vertical lines, at year 0, indicate year of partial cutting. Vertical bars represent the standard error. P-values are the results from the treatment and year interaction. * shows years where treated plots are different than control plots.



Supplementary Figure S1.1. Univariate Ripley's L(r) function calculated on each treated and control plot. The spatial distributions of the treated and control plots are based on all living trees within the plots at the sample year. The treated plots before the partial cuttings include the coordinates of each stump within the plots. x represents the value of the function that is lower or higher than the envelope indicated by the Monte Carlo simulation, which means that the distribution is significantly overdispersed (segregation) or aggregated (clustering), respectively.



Supplementary Figure S1.2. Frequency distribution of trees according to their increase in diameter at 0.2 m (ΔDSH) for the three partial cuttings (black) and their controls (grey). Vertical lines represent standard deviation.

CHAPITRE 2

EFFECTS OF THREE PARTIAL CUTTING TREATMENTS ON SELECTED WOOD QUALITY ATTRIBUTES OF RESIDUAL BLACK SPRUCE TREES IN NORTH-EASTERN QUEBEC

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Effects of three partial cutting treatments on selected wood quality attributes of residual black spruce trees in north-eastern Quebec

Abstract

We investigated the effect of wider growth rings following three partial cutting treatments, applied 4 to 10 years earlier, on wood and tracheid properties of black spruce (*Picea mariana* (Mill.) B.S.P.) trees in northeastern Quebec. The partial cutting treatments were commercial thinning (CT), careful logging around small merchantable stems (CPPTM) and careful logging around stems with variable diameter (CLVD). We sampled four, three and four blocks composed of a partially cut plot and an unharvested control plot for CLVD, CPPTM and CT, respectively. Five black spruce trees were randomly selected among those presenting wider growth rings in each treated plot, and among all trees in each control plot. Compared with pre-treatment values, growth rings were significantly wider by 40, 47 and 35% after CLVD, CPPTM and CT, respectively. However, only small differences compared with pre-treatment values were found in latewood proportion (3-7%), ring density (3-8%), early and latewood lumen areas (0-13%), cell wall thickness (1-6%), and tracheid length (0-4%). Compared with control trees, the modulus of elasticity (MOE; 24%) and modulus of rupture (MOR; 17%) was significantly lower after CPPTM. However, MOE was not correlated with either ring width or density, while MOR had a weak negative correlation with ring width. These results indicate that partial cutting treatments can significantly increase tree radial growth without detrimental effects on wood properties, which remain within the natural variations generally observed for black spruce trees.

Keywords: Partial cuttings, wood density, tracheid length, lumen area, cell wall thickness, mechanical properties, black spruce.

Introduction

Black spruce (*Picea mariana* (Mill.) B.S.P.) is a widespread tree species (Saucier, 1998) known to have good fiber quality and high wood stiffness and strength (Zhang *et al.*, 2002; Lei *et al.*, 2005; Liu *et al.*, 2007b). This tree species is therefore highly valued for pulpwood and lumber production (Zhang and Koubaa, 2009). Black spruce stands in eastern Canada are traditionally harvested through clear-cutting (Youngblood and Titus, 1996). However, in recent years, partial cuttings have increasingly been used in even-aged and uneven-aged black spruce stands with two main objectives (i) maintaining the initial stand structural attributes (age and diameter distributions) according to the principle of ecosystem-based management (Hunter, 1990; Bergeron *et al.*, 1999) and (ii) promoting tree growth by decreasing inter-tree competition.

By increasing soil temperature, nutrient cycling (Thibodeau *et al.*, 2000), moisture availability (Fayle, 1983) and solar radiation, partial cuttings generally stimulate radial growth of residual trees (Vincent *et al.*, 2009; Krause *et al.*, 2011). Because stem value is largely dependent on its diameter, improved radial growth of residual trees may lead to higher financial returns (Liu *et al.*, 2007a). However, even though tree growth responses to partial cutting have already been studied in black spruce stands (e.g. Vincent *et al.*, 2009; Krause *et al.*, 2011), little is known about the effect of large ring width induced by a broad range of partial cutting intensities on wood quality (Bose *et al.*, 2014). Understanding the effects of partial cuttings on wood properties variations can help improve silvicultural practices and ensure an efficient use of wood as a raw material (Jyske *et al.*, 2010).

Mechanical properties, such as strength and elasticity, are greatly influenced by wood density (Saranpää, 2003), which is considered to be one of the most important wood quality characteristics (Panshin and Zeeuw, 1980; Koubaa *et al.*, 2002). Increased growth is usually associated with a decrease in average ring density (Makinen *et al.*, 2002a; Xiang *et al.*, 2014) caused by an increasing number of earlywood cells without significant changes in the number of latewood cells (Zhang, 1998; Wang *et al.*, 2002). A decrease in earlywood and latewood density can also be expected (Makinen *et al.*, 2002a) due to changes in tracheid dimensions. In fact, larger rings widths are often characterized by wider cells with thinner cell walls (Makinen *et al.*, 2002b) and shorter tracheids (Dutilleul *et al.*, 1998; Kang *et al.*, 2004). However, contradictory results have also been reported. For example, Koubaa *et al.* (2000) found a negative correlation between ring width and ring density in black spruce trees but the correlation decreased with cambial age and was no longer significant after 25 years of age. Also, Alteyrac *et al.* (2006) stated that in natural black spruce stands, wood mechanical properties were not influenced by ring width, although this result could be explained by the limited ring width variation in natural even-aged mature stands (Torquato *et al.*, 2014). Therefore, compared with natural plots, the wider rings induced by partial cuttings might lead to detrimental changes in wood and tracheid properties of black spruce.

Differences in wood property patterns can also be expected between trees from even- and uneven-aged stands. The long fire return intervals in eastern Canada combined with spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks result in numerous uneven-aged stands dominated by black spruce (Boucher *et al.*, 2003; Cote *et al.*, 2010). Unlike in even-aged stands, gap dynamics resulting from small-scale disturbances is the principal factor affecting stand structure and tree growth in natural uneven-aged forests (Franklin *et al.*, 2002). Therefore, trees within uneven-aged stands have a more varied ring width profile, depending on the length and severity of tree suppression (Piispanen *et al.*, 2014). This usually leads to differences in wood characteristics, such as higher wood density close to the pith (suppressed stage) and lower in the outer rings (dominant phase) compared with even-aged trees whose wood density continuously increases from pith to bark (Piispanen *et al.*, 2014). Partial cuttings in uneven-aged stands generally remove most of the dominant trees, while smaller, suppressed trees are left in the stand. The release of suppressed trees after partial cuttings in uneven-aged stands might therefore create larger variations in wood properties, especially in wood density, compared with trees from even-aged stands.

This study evaluated the effects of an increased tree growth occurring after three partial cutting treatments applied in even- and uneven-aged black spruce stands in the boreal forest of eastern Canada. The studied effects were 1) wood density (earlywood and latewood density) and latewood proportion, 2) tracheid properties (tracheid length, earlywood and latewood cell wall thickness and lumen area) and 3) mechanical properties (modulus of elasticity (MOE) and modulus of rupture (MOR)). The working hypothesis is that an increased growth after partial cuttings will negatively affect all wood properties with a more pronounced effect in uneven-aged stands.

Methods

Study sites

Three partial cutting practices were studied in the managed boreal stands of the Saguenay Lac-Saint-Jean region (Quebec, Canada) between 47°51' and 50°25' North and 70°13' and 72°11' West: Careful logging around small merchantable stems (CPPTM in Québec, a variant of HARP in Ontario), Careful Logging around stems with Variable Diameters (CLVD, coupe avec protection des tiges à diamètre variables in Québec) and Commercial Thinning from below (CT). CPPTM and CLVD are diameter limit cutting (diameter >14 cm) applied in uneven-aged stand while CT is applied in even-aged stand. CPPTM, CLVD and CT removed 70, up to 95 and 35 % of stand basal area, respectively. Further information is available in Pamerleau-Couture *et al.* (2015). In this region, the mean temperature of the coldest month is -14.3 °C (January) and the warmest month is 17.5 °C (July); average annual precipitation during the 1981-2010 period was 980 mm (Environment Canada, 2015).

Five blocks were selected for each cutting treatment. A block corresponds to one treated plot combined with one control plot (i.e. 5 treated plots + 5 control plots per partial cutting treatment). The treated plots were selected based on the time elapsed since treatment application (at least 4 years) and their tree species composition (at least 50% of black spruce basal area). The plots were all established on sites with a gentle slope and good drainage to limit environmental variations. The control plots were selected within a radius of 1 km from the treated plots to minimize the effect of climate and soil conditions. Diameter distribution and age of control plots had to be similar to the initial conditions of the corresponding treated plots and they had to be without any anthropogenic disturbance. At least 35 trees per stand were required to cover stand variation, resulting in plot sizes ranging from 120 to 400 m^2 (Pamerleau-Couture *et al.*, 2015).

Tree selection and plots measurements

In each treated and control plot, a wood core at 0.2 m above the root collar was sampled from every black spruce tree (Pamerleau-Couture *et al.*, 2015). In each treated plot, five black spruce trees were randomly selected among those presenting a post-treatment radial growth at least 20% larger than that of the 10-year pre-treatment period (Vincent *et al.*, 2009), whereas this selection was made among all trees in control plots. Two CPPTM plots, one CLVD and one CT were eliminated because trees reaction were not in accordance with our selection (a decrease was observed in the average growth of selected trees in the treated plots) or missing samples. In the remaining treated plots (4 for CLVD, 3 for CPPTM and 4 for CT), 30, 67 and 64% of residual trees actually increased their radial growth after CLVD, CPPTM and CT, respectively (Table 2.1). The selected trees were used to evaluate the effect of an increased growth on wood density, as well as tracheid and mechanical properties.

We then returned in each plot to fell selected trees from which wood disks were sampled at 0 m to assess tree age, and at 1.3 m to assess wood density, latewood proportion and cell properties. A wood section sampled between 0.5 and 1 m was used to measure wood mechanical properties. Diameter at breast height (1.3 m, DBH), tree height (TH) and crown length (CL) were measured in the field (Table 2.2). For further analyses, the crown ratio (CR = CL/TH) was used instead of CL. Site index was measured according to an equation developed by Pothier and Savard (1998) for black spruce even-aged stands (CT) and from Ouzennou *et al.* (2008) for uneven-aged stands (CPPTM and CLVD) (Table 2.2).

Wood quality measurements

Ring width, latewood proportion and ring density

X-ray densitometry measurements were taken from 2 mm thick sections starting 10 years pre-treatment (QTRS-01X Tree Ring Analyser; QMS Inc., Knoxville, TN). Sample preparation included the removal of extraneous compounds by extracting with cyclohexane/ethanol (2:1) solution for 24 hours and then with hot water for a further 24 hours. Ring density (RD) was then measured by the change in X-ray intensity going through the wood according to Eq. (**1**)

$$\mathbf{RD} = (1/\mu_m t)\ln(I_0/I) \qquad (1)$$

where **RD** is the ring density, $\boldsymbol{\mu_m}$ is the mass absorption coefficient [constant], **t** is the sample thickness [constant], $\mathbf{I_0}$ is the incident intensity [measured] and **I** is the transmitted intensity [measured]. The transition between early and latewood was determined according to the maximum derivative method using a six-degree polynomial with Matlab® software (Koubaa *et al.*, 2002). Five resulting datasets were analyzed in this study: ring width (RW), latewood proportion (LWP), average ring density (RD), earlywood density (EWD) and latewood density (LWD).

Tracheid properties

Thin transversal sections were first embedded in paraffin and then cut with a rotary microtome in sections 8-10 μm thick. They were then fixed with albumin and colored with safranin (Deslauriers, 1999). We measured the four annual rings immediately preceding the partial cuttings and all the annual rings after the treatment starting at year three (a positive response of black spruce trees generally starts at year three according to Vincent *et al.* (2009)). Cell wall thickness (WT) and lumen area (LA) were measured with an image analysis system (WinCELL^{tm}) along three radial paths of each tree ring, then standardized and averaged for each tree (Vaganov, 1990; Deslauriers *et al.*, 2003; Krause *et al.*, 2010). The distinction between early and latewood was made according to Mork's procedure, which consists of defining a cell as latewood when the lumen area is less than twice the thickness of a double cell wall (Denne, 1988).

Using the same wood section, another sample (1.5 cm thick) was prepared to include 4 years prior to the treatment and 4 years after (starting at year 3). For three CLVD plots, the time since treatment was 4 years, resulting in only one year post-treatment included in this analysis. Each ring was manually separated and macerated in a solution of equal volume of glacial acetic acid and hydrogen peroxide and heated at 60 °C for 24 h (Franklin, 1945). The resulting suspension was rinsed with distilled water and then shaken for 30-45 sec for a homogenous separation of the fibers. In each sample (each year), the length of 5000 tracheids was measured using a fiber tester (Lorentsen & Wettre, Kiste, Sweden). The weight-weighted mean fiber length was used as it reduced the potential impact of fines and gives more weight to the fibers in the length determination (Bouslimi *et al.*, 2014).

Mechanical properties

To evaluate the mechanical properties of the sampled trees, small defect-free 10 mm X 10 mm X 150 mm specimens were cut in the wood formed both before and after treatment application. Due to a short post-treatment period, sample dimensions were smaller than those recommended by the American Society for Testing and Materials (ASTM, 2007), but were sufficient to characterize the changes in mechanical properties after a partial cutting treatment (e.g. Alteyrac *et al.*, 2006; Vincent *et al.*, 2011; Kuprevicius *et al.*, 2013) since they included the majority of post-treatment years. For the three treatments, especially after CLVD, some pre-treatment rings could have been included in the post-treatment samples since the TST was short. All specimens were dried under restraint, from green to 12% moisture content in a conditioning room (20 °C, 65% humidity rate) (Alteyrac *et al.*, 2006). Bending tests were conducted according to the ASTM D-143 standard test methods for small clear specimens (ASTM, 2007). Modulus of elasticity (MOE) and rupture (MOR) were evaluated on samples using the MTS-Alliance RT/100 material testing system (TestResources Inc., Shakopee, MN) according to

$$MOE = P_1L^3/4bd^3y \quad (2)$$

$$MOR = 3P_2L/2bd^2 \quad (3)$$

where *b* and *d* are the sample width and thickness, respectively, *y* represents the deflection, L is the span length (110mm), and P_1 and P_2 the maximum loads of elastic domain and rupture, respectively. Samples with visible defects (knot, compression wood) were automatically excluded from the analysis.

Statistical analysis

Using the “nlme” package and "lme" function (Pinheiro and Bates, 2007) in R (R Core Team, 2014), a linear mixed-model analysis of variance (ANOVA) with repeated measurement (year) was performed to detect significant differences in wood properties between each partially cut plot and its respective control plot after the treatment (each silvicultural treatment was analyzed separately). The restricted maximum likelihood (REML) method was used to estimate the parameters. The model took into account the site index (SI), time since treatment (TST), tree characteristics (age, DBH and crown ratio) and pre-harvest measurement (average of 4 years pre-treatment was used for cellular characteristics, 10 years pre-treatment for all the other wood properties, whereas the pre-value was used for mechanical properties) to account for differences between individual trees, plots and treatments. If those variables were not significant, they were excluded from the final model. For CPPTM treatment, no pre-value was used for mechanical properties because of a lack of specimens without defects in the pre-harvest section. Collinearity between predictor variables was tested and problematic variables were excluded if the assumption was not met. The same TST of treated plots was attributed to control plots to compare the same calendar year, which limited the potential effect of climate (Pamerleau-Couture *et al.*, 2015). Trees within the blocks were considered as a random effect. A few trees were excluded from the analysis due to visible defects or identification error. The first-order autoregressive correlation (AR-1) was used on the repeated measurement. Square-root transformations were applied when necessary to satisfy the assumptions of normality and homogeneity of variance. Tukey pairwise comparisons test was used to detect the effect of treatment, using the"lsmeans" package and function (Lenth and Hervé, 2015).

Spearman correlation was conducted using the "psych" package in R to evaluate the relationship between intra-ring characteristics in the treated and control plots separately. Because of the large sample size, a Holm correction was applied to the significance level in order to account for the numerous simultaneous tests (Holm, 1979).

Results

Ring width, latewood proportion and wood density

Ring width (RW) increased after each treatment as expected from the pre-selection of trees (Table 2.3; Fig. 2.1). Relative to pre-treatment values, mean RW increased by 40, 47 and 35% after CLVD, CPPTM and CT, respectively (Table 2.3). Compared with control plots, RW was significantly higher by 65, 102 and 63% for CLVD, CPPTM and CT, respectively (Table 2.3; Fig. 2.1). Tree RW was significantly higher than that of control trees starting at year 3 for CLVD and CT and at year 4 for CPPTM (Fig. 2.1). Latewood proportion (LWP) was, on average, 4% lower in treated than control trees after the three partial cutting treatments but no significant differences were observed (Fig. 2.1; Tables 2.3 & 2.4). Earlywood density (EWD) in treated trees was significantly lower than that of control trees after CPPTM (7%) and CT (4%) (Tables 2.3 & 2.4; Fig. 2.1). EWD slightly increased after CLVD (4%) but was statistically similar to that of control trees (Tables 2.3 & 2.4; Fig. 2.1). Instead, latewood density (LWD) was higher in treated trees than control trees after CLVD (11%) and CT (1%) but they were not statistically different than control trees (Tables 2.3 & 2.4; Fig. 2.1). For CPPTM, LWD slightly decreased during the first three years after treatment, but when considering all post-treatment annual rings, LWD increased by 6% and treated trees significantly differed from that of control trees (Tables 2.3 & 2.4; Fig. 2.1). No significant differences were observed between the controls and the three treatments, even if decreases of 3 and 4% in ring density were observed after CPPTM and CT, respectively, and a 4% increase after CLVD (Tables 2.3 & 2.4; Fig. 2.1).

Tracheid properties

Earlywood lumen area (EW LA) was 4 and 10% smaller after CLVD and CPPTM respectively, compared with control trees, while it was 6% larger after CT. However, only CPPTM was associated with significant differences compared with control trees at year 7 (Tables 2.3 & 2.4; Fig. 2.2). After CT, latewood lumen area (LW LA) was 3% larger than pre-harvest values but treated trees were not significantly different from control trees (Tables 2.3 & 2.4; Fig. 2.2). Earlywood cell walls (EW WT) were thinner after CPPTM (3%) and CT (6%) but similar decreases were also observed in their respective controls, so that treated and control trees were statistically similar (Table 2.4). Latewood cell walls thickness (LW WT) slightly increased after the three partial cuttings (2-6%), particularly for CT that was associated with significant differences between treated and control trees at years 5 and 8 (Tables 2.3 & 2.4; Fig. 2.2). Tracheid length decreased after CLDV (4%) and CPPTM (3%), and was associated with significant differences between treated and control trees (Tables 2.3 & 2.4; Fig. 2.2).

Mechanical properties

Modulus of elasticity (MOE) and modulus of rupture (MOR) increased in all treated and control trees (Table 2.3; Fig. 2.3). However, compared with control trees, values of

MOE (24%) and MOR (17%) were significantly lower after CPPTM (Tables 2.3 & 2.4). CT treated trees had lower MOR values (10%) than control trees, although this difference was not significant (Tables 2.3 & 2.4; Fig. 2.3). There were no significant differences between CLVD and control trees (Table 2.4; Fig. 2.3).

Correlation among traits

Correlation coefficients were calculated for the 13 measured traits for treated and control trees separately. Twenty-one significant correlation coefficients were obtained for treated trees and 27 for control trees (Table 2.5). Among these significant correlation coefficients, 14 concerned the same traits between treated and control trees.

For both treated and control trees, ring density was positively correlated with earlywood and latewood density, the correlation with earlywood density being stronger (Table 2.5). Ring density and latewood density were also correlated with LWP for both treated and control trees. Earlywood density was negatively correlated with EW LA for control trees, but not for treated trees.

A positive correlation was observed between ring width (RW) and LWD, but RW and LWP were negatively correlated for both treated and control trees. Contrary to treated trees, RW of control trees was positively correlated with all tracheid properties except EW WT. Tracheid length was positively correlated with early- and latewood lumen area for treated trees and with EW LA for control trees (Table 2.5).

For treated trees, MOE was not correlated with RW or RD but MOR was negatively correlated with RW. RD and RW were not correlated with MOE and MOR for control trees (Table 2.5).

Discussion

As expected from the tree selection, mean RW increased by 40, 47 and 35% after CLVD, CPPTM and CT, respectively, compared with pre-harvest values (Table 2.3). Such growth increases after partial cutting have already been observed in black spruce stands (e.g.Vincent *et al.*, 2009; Krause *et al.*, 2011; Pamerleau-Couture *et al.*, 2015).

An increase in radial growth is usually associated with a decrease in average ring density (RD) (e.g. Makinen *et al.*, 2002a; Xiang *et al.*, 2014) caused particularly by a decrease in latewood proportion (LWP) (Zhang, 1998; Wang *et al.*, 2002). In our study, RW had a negative correlation with LWP (Table 2.5) but only a slight decrease (3 to 7%) was observed after CLVD, CPPTM and CT, with no significant differences from control trees (Fig. 2.1; Table 2.4). Krause *et al.* (2011) found no changes in LWP after commercial thinning in black spruce stands. Similarly, Makinen and Hynynen (2014) found only small changes in LWP (0-3%) after thinning and fertilization in Scots pine (*Pinus sylvestris* L.). Otherwise, despite a slight decrease in RD after CPPTM (3%) and CT (4%) and a small increase after CLVD (4%), the values were not significantly different from control trees (Fig. 2.1; Table 2.4). Similar results were found by Vincent *et al.* (2011), who reported a ~2% non significant decrease in RD of black spruce trees after CT. Peltola *et al.* (2007) and Makinen and Hynynen (2014) also found very small changes (2-8%) in Scots pine average wood density after thinning. Post-treatment wood density (430-475 kg m^{-3}) is in the same range as that observed in natural forests (400-450 kg m^{-3}) (Zhang and Koubaa, 2009), suggesting that the forest industries should not suffer adverse repercussions from the application of these treatments.

Koubaa *et al.* (2000) observed that the negative effect of a high radial growth on wood density decreases when trees reach maturity. Accordingly, in our study, trees were mature and no significant correlations were found between RW (or GR) and RD for either treated or control trees (Table 2.5). Nevertheless, a ~20% decrease in RD was found in mature wood of conifer trees, but it was associated with an unusually high growth increase (100-200%) after fertilization in Norway spruce (*Picea abies* (L.) Karst.) (Makinen *et al.*, 2002a). Therefore, for mature black spruce trees, exceptional increases in growth beyond those found after the three partial cutting treatments might be necessary to observe a significant decrease in average ring density.

A decrease in earlywood (EWD) and latewood density (LWD) has previously been associated with an increased growth after fertilization in Norway spruce (Makinen *et al.*, 2002a). However, while EWD of treated trees was significantly lower than control trees after CPPTM (7%) and CT (4%) and negatively correlated with RW ($p<0.05$ for control plots), LWD significantly increased with increasing RW and was significantly higher after CPPTM (6%) (Fig. 2.1; Tables 2.3 & 2.4). Other studies have also found that an increase in radial growth was associated with a decrease in EWD and with an increase in LWD in Scots pine (Peltola *et al.*, 2007) and Norway spruce (Jyske *et al.*, 2010). By increasing water availability during the end of the growing season by reducing tree competition, partial cuttings can enhance latewood production (Paul, 1958; Smith and Wilse, 1961), thus limiting the negative effect of wider ring growth on LWP and LWD. Alternatively, the decreased stand density could increase soil evaporation at the end of the growing season and limit water availability for the residual trees, resulting in thicker cell wall to prevent cavitation (Sperry *et al.*, 2006; Jyske *et al.*, 2010; D'Orangeville *et al.*, 2013).

Although EWD and LWD were previously related to tracheid properties in Norway spruce (Jaakkola *et al.*, 2007), no correlation was found in this study except for weak correlations between EWD (negative) and EW lumen area (EW LA) for control trees, between EWD (positive) and EW WT for treated trees and between LWD (positive) and LW WT for control and treated trees (Table 2.5). Jaakkola *et al.* (2007) found that an increase in cell wall thickness was positively correlated with EWD. However, after CPPTM and CT, EW WT was not significantly lower than control trees and was therefore only slightly correlated with the decreased EWD. This means that other factors, such as cell wall composition, might have an effect on EWD. Some studies reported a higher lignin concentration associated with increased growth (e.g. Anttonen *et al.*, 2002; Kostiainen *et al.*, 2004), but the reverse has also been observed (e.g. Kirst *et al.*, 2004; Novaes *et al.*, 2010). Given that the density of lignin is lower than that of cellulose and hemicellulose, a change in cell wall composition can have a negative impact on wood density (see Gardiner *et al.*, 2014). While samples were taken close to each other, tracheid properties and ring density were not measured at exactly the same location, which might have caused a lack of correspondence between these two variables. This said, wood density is probably not entirely related to fiber dimensions (Makinen *et al.*, 2002a).

The effects of an increased growth after the three partial cutting treatments on tracheid properties were, overall, small (Fig. 2.2; Table 2.3). While some studies found that an increased growth was linked to wider cells with thinner walls (Makinen *et al.*, 2002b), as well as shorter tracheids (Dutilleul *et al.*, 1998; Kang *et al.*, 2004), other studies found only little or no effects after silvicultural treatments (e.g. Jaakkola *et al.*, 2005; Krause *et al.*, 2011). Compared with pre-treatment values, a marginal increase in LW WT (3%) after CT, a slight decrease in EW LA (0.2%) after CPPTM and a decrease in tracheid length (3-4%) after CLVD and CPPTM were observed, and were the only significant difference compared with control trees (Table 2.4). Differences of similar magnitude were found in tracheid length (0 to 6%) after treatments in Norway spruce (Jaakkola *et al.*, 2005) and Scots pine (Makinen and Hynynen, 2014). Also, Krause *et al.* (2011) did not find any changes in lumen area and cell wall thickness related to an increased growth after CT in black spruce stands, except for very large increases in growth (>100%) that led to an increase in LW LA. Similarly, Makinen *et al.* (2002a) found that tracheid length could decrease by an average of 17% when ring width doubled or tripled in Norway spruce. In this study, there were no correlations between cell properties and ring width for the treated trees, except for a negative correlation between growth ratio and EW LA. Therefore, an exceptional growth increase might also be necessary in order to observe a significant difference. In fact, tracheid properties seem to be mostly determined by cambial age, whereas growth rate is likely a secondary factor (Sirvio and Karenlampi, 2001).

Mechanical properties (MOE and MOR) should be closely linked to wood characteristics such as wood density and cell properties. However, MOE and MOR were not correlated with any other wood characteristics, including growth and RD, except for a weak negative correlation between MOR and ring width for the treated trees only (Table 2.5). Even so, compared with control trees, CPPTM treated trees were associated with lower MOE (24%) and MOR (17%) (Table 2.4). No differences in mechanical properties were observed for CLVD and CT (Fig. 2.3). Vincent *et al.* (2011) also found that RW was unrelated to MOE and that MOE of thinned black spruce trees was similar to that of control trees. While RW and RD had little to no impact on mechanical properties of black spruce trees, Alteyrac *et al.* (2006) found that a large part of MOE and MOR variations was due to microfibril angles (MFA). Generally, MOE and MOR increase with cambial age as MFA decrease. Indeed, high MFA confer low stiffness on young saplings, giving them the flexibility required to prevent breaking in strong winds (Barnett and Bonham, 2004). In addition, MFA of fast-growing trees are generally higher than that of slow-growing trees (Herman *et al.*, 1999). Therefore, even without changes in the wood properties measured in this study, an increase in MFA could be responsible for the lower mechanical properties after CPPTM compared with control trees.

Tree mechanical properties (MOE) were higher in CT plots (even-aged stands) compared to CPPTM and CLVD (uneven-aged stands). To explain this difference between even-aged and uneven-aged stands, Torquato *et al.* (2014) hypothesized that the recruitment of new canopy trees through layering in uneven-aged stands was associated with physiological changes during the transformation of branches into stems that might be responsible for the difference in wood characteristics and mechanical properties. Also, the more complex wind effect in uneven-aged stands produces a higher proportion of mild to heavy compression wood (Torquato *et al.*, 2014). Compression wood is composed of wider and shorter tracheids with high MFA, which are associated with lower mechanical properties (down to 3–5 times less than normal) (Timell, 1986). Therefore, the higher wood mechanical properties found after CT compared with other treatments was likely related to the initial stand age structure rather than to the treatment itself.

Overall, intra-tree variation is more important than inter-tree variation, as all the wood and tracheid properties are closely related to cambial age and tree height (Alteyrac *et al.*, 2006). Given the small changes in wood and tracheid properties observed in this study and the lack of differences from the control trees, the practical implications of these results are limited since the changes remain within the natural variations for black spruce.

Conclusion

The main conclusion of this study on the short-term effect of an increased growth on wood and tracheid properties is that partial cutting treatments in black spruce stands can significantly increase radial growth with only negligible detrimental effects on wood properties. Small changes in wood properties were observed in this study. However, these changes were within the natural variations for black spruce. Modulus of elasticity was observed to be lower after CPPTM and CLVD compared with CT, but this was likely related to the uneven-aged structure of the stands in which these treatments were applied. Therefore, for lumber end-uses, CT applied in even-aged stands is a sound investment in terms of wood properties. However, further studies are needed to enhance our knowledge, notably on the effect of partial cuttings along the entire stem, on other wood characteristics (e.g. branch diameter, stem shape, juvenile wood proportion) and over a longer time period.

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Conflict of interest statement

None declared

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Table 2.1. Mean and standard deviation (SD) of trees with an increased growth of 20% or more at 0.2 m after the treatment compared with 10 years prior for n trees in each treated and control plot (p) within the three partial cutting treatments.

		CLVD		CPPTM		CT	
		Treated (p=4, n=157)	Control (p=4, n=150	Treated (p=3, n=88)	Control (p=3, n=94)	Treated (p=4, n=165)	Control (p=4, n=148)
Increased growth	**Mean**	**30**	**25.7**	**67.2**	**29.4**	**63.6**	**30.9**
(% trees/plot)	SD	11.4	16.3	7.8	7	21.4	28.6

Table 2.2. Mean, standard deviation (SD), minimum and maximum diameter at 1.3 m (DBH), age, height, crown ratio, stand basal area and stand density with the time since treatment (TST) and site index (SI), for n trees in each treated and control plot (p) within the three partial treatments.

			CLVD		CPPTM		CT	
			Treated (p=4 n=20)	Control (p=4 n=20)	Treated (p=3 n=15)	Control (p=3 n=15)	Treated (p=4 n=20)	Control (p=4 n=20)
DBH	cm	**Mean**	**11.1**	**11.8**	**10.3**	**12.0**	**16.3**	**15.8**
		SD	5.4	4.3	3.3	2.8	2.8	3.0
		Min	4.7	6.2	6.4	7.5	10.8	11.2
		Max	21.8	20.4	17.8	16.6	20.5	21.6
Age	years	**Mean**	**104**	**92**	**96**	**132**	**80**	**105**
		SD	29	23	17	38	21	42
		Min	75	66	67	84	55	74
		Max	201	142	122	218	159	195
Height	m	**Mean**	**8.1**	**9.0**	**7.1**	**9.8**	**13.3**	**14.6**
		SD	4.0	2.9	2.5	1.7	2.1	2.8
		Min	2.6	4.6	4.2	6.5	9.4	10.7
		Max	15.4	15.5	13.1	12.3	17.9	19.8
Crown ratio		**Mean**	**0.65**	**0.61**	**0.71**	**0.47**	**0.60**	**0.43**
		SD	0.19	0.16	0.09	0.10	0.12	0.14
		Min	0.22	0.31	0.56	0.32	0.35	0.18
		Max	1.00	0.82	0.88	0.66	0.79	0.67
Stand basal area	$m^2\ ha^{-1}$	**Mean**	**11.9**	**23.3**	**13.3**	**31.9**	**26.5**	**46.0**
		SD	7.7	3.7	8.8	13.8	6.5	12.6
		Min	5.8	19.0	5.1	16.7	20.4	34.9
		Max	23.2	27.6	22.6	43.6	35.0	63.7
Stand Density	$\#\ ha^{-1}$	**Mean**	**1482**	**2423**	**1299**	**2133**	**1208**	**2798**
		SD	379	358	540	706	117	2090
		Min	1033	1925	975	1600	1075	1175
		Max	1950	2700	1923	2933	1333	5867
TST	years	**Mean**	**5**	**6**	**9**	**10**	**10**	**11**
		SD	1	0	0.6	1	0.5	1.4
		Min	4	6	9	9	10	10
		Max	6	6	10	11	11	13
SI		**Mean**	**4.0**	**8.2**	**4.5**	**8.3**	**10.5**	**12.4**
		SD	5.7	3.6	2.2	1.7	2.4	4.7
		Min	0.1	4.8	2.7	6.4	7.7	8.9
		Max	12.3	13.1	6.9	9.7	13.6	19.1

Table 2.3. Mean and standard deviation (SD) of wood and tracheid properties pre- and post three partial cutting treatments and their controls.

			CLVD				CPPTM				CT			
			Treated		Control		Treated		Control		Treated		Control	
			Pre	**Post**	**Pre**	**Post**	**Pre**	**Post**	**Pre**	**Post**	**Pre**	**Post**	**Pre**	**Post**
RW	mm	Mean	0.73	1.02	0.62	0.62	0.62	0.91	0.41	0.45	0.63	0.85	0.57	0.52
		SD	0.25	0.52	0.42	0.47	0.34	0.54	0.24	0.31	0.31	0.48	0.25	0.23
LWP	%	Mean	29.5	26.5	30.5	30.5	35.6	28.8	34.1	33.4	30.8	27.5	33.3	31.3
		SD	9.7	10.8	14.6	16.1	14.4	11.7	14.0	13.1	11.4	12.0	14.2	13.4
RD	kg m^{-3}	Mean	457.4	475.3	446.4	447.3	446.6	432.2	457.4	454.1	454.5	434.6	460.7	450.1
		SD	48.5	58.4	43.4	44.9	38.9	48.3	28.0	39.2	37.8	34.8	42.5	48.8
EW RD	kg m^{-3}	Mean	397.4	412.2	395.6	398.8	392.9	373.9	403.9	400.7	400.2	375.2	402.8	391.4
		SD	38.0	54.1	36.0	40.5	34.3	38.1	32.5	39.1	36.5	31.0	30.0	33.1
LW RD	kg m^{-3}	Mean	629.4	677.8	614.6	610.8	570.2	605.7	607.3	608.6	612.7	628.8	626.8	624.8
		SD	107.9	102.3	110.3	115.4	88.9	93.8	113.0	111.2	92.9	88.0	99.5	120.1
EW LA	μm^2	Mean	473.6	462.7	461.6	481.2	420.6	419.7	472.6	465.3	628.2	611.6	586.2	578.9
		SD	167.1	156.1	136.5	153.6	114.6	87.5	93.6	99.1	109.8	99.3	126.0	120.4
LW LA	μm^2	Mean	92.0	80.4	96.1	91.6	90.4	94.5	79.5	86.6	109.7	112.7	103.9	97.6
		SD	28.2	28.4	34.7	29.6	29.0	29.3	24.6	32.3	29.5	36.7	31.0	29.9
EW WT	µm	Mean	2.35	2.33	2.44	2.48	2.38	2.31	2.38	2.30	2.49	2.33	2.38	2.27
		SD	0.36	0.37	0.40	0.44	0.43	0.32	0.34	0.40	0.26	0.28	0.31	0.30
LW WT	µm	Mean	4.14	4.23	3.92	3.76	3.98	4.20	3.94	3.93	4.00	4.12	3.75	3.80
		SD	0.77	0.94	0.62	0.71	0.53	0.46	0.68	0.82	0.58	0.58	0.50	0.63
TL	mm	Mean	2.55	2.44	2.7	2.67	2.35	2.28	2.67	2.72	2.93	2.92	2.93	3.00
		SD	0.43	0.40	0.36	0.40	0.38	0.30	0.26	0.31	0.28	0.30	0.19	0.19
MOE	MPa	Mean	6033.8	7874.6	6500.0	8413.4	6852.4	7370.1	6100.3	9639.1	8784.8	9731.6	8869.2	9531.9
		SD	1659.4	1657.5	1968.1	1708.9	2311.8	2514.6	777.3	2122.7	2051.8	1292.8	2032.9	1502.6
MOR	MPa	Mean	74.1	88.0	86.4	96.3	79.4	90.0	85.0	109.0	81.3	86.2	92.0	95.3
		SD	14.7	15.6	16.9	14.4	14.0	17.2	10.0	17.1	14.2	13.7	16.8	17.1

RW, ring width; LWP, latewood proportion; RD, ring density; EW, earlywood; LW, latewood; LA, lumen area; WT, wall thickness; TL, tracheid length; MOE, modulus of elasticity; MOR, modulus of rupture.

Table 2.4. Summary of mixed model analysis on ring width, latewood proportion, wood density, lumen area, cell wall thickness, tracheid length, modulus of elasticity and rupture, showing the F-value and P-value of the main fixed effects. See supplementary data (Table S2.1) for the complete table.

	CLVD			CPPTM			CT		
Parameters	DF	F-value	P-value	DF	F-value	P-value	DF	F-value	P-value
Ring width (RW)									
pRW	28	67.3455	**<.0001**	20	48.4937	**<.0001**	32	53.2811	**<.0001**
year	108	5.5157	**0.0001**	211	0.5585	0.8300	288	4.3260	**0.0001**
Tr	28	0.0646	0.8012	20	0.4477	0.5111	32	1.2473	0.2724
Tr X year	108	8.4469	**<.0001**	211	2.6585	**0.0061**	288	2.1664	**0.0301**
Latewood proportion (LWP)									
pLWP	28	37.7743	**<.0001**	19	26.8378	**0.0001**	32	99.9201	**<.0001**
year	96	1.0615	0.3867	181	0.3807	0.9433	273	3.1986	**0.0017**
Tr	28	0.0244	0.8769	19	3.2698	0.0864	32	0.0000	0.9976
Tr X year	96	0.7356	0.5986	181	0.4443	0.9094	273	0.9627	0.4656
Ring density (RD)									
pRD	28	49.8582	**<.0001**	22	11.5305	**0.0026**	32	69.7850	**<.0001**
year	108	1.6959	0.1417	211	0.6604	0.7441	288	4.9834	**<.0001**
Tr	28	1.1870	0.2852	22	1.0386	0.3194	32	0.7074	0.4065
Tr X year	108	0.8790	0.4979	211	1.3786	0.1994	288	0.1541	0.1541
Earlywood density (EWD)									
pEWD	28	85.2079	**<.0001**	21	32.2704	**<.0001**	31	76.7748	**<.0001**
year	96	1.4848	0.2019	181	1.2514	0.2666	273	6.8553	**<.0001**
Tr	28	0.6218	0.4370	21	9.8810	**0.0049**	31	0.5908	0.4479
Tr X year	96	0.5060	0.7711	181	0.7105	0.6988	273	2.1382	**0.0326**
Latewood density (LWD)									
pLWD	28	64.0706	**<.0001**	22	73.4272	**<.0001**	32	200.8795	**<.0001**
year	96	1.5883	0.1707	181	0.5425	0.8421	273	1.7645	0.0840
Tr	28	1.3025	0.2634	22	5.1330	**0.0337**	32	0.8436	0.3652
Tr X year	96	1.8754	0.1057	181	1.1849	0.3071	273	1.1566	0.3258
Earlywood lumen area (EW LA)									
pEW LA	26	97.9350	**<.0001**	25	45.3302	**<.0001**	33	73.1118	**<.0001**
year	36	1.4695	0.2434	147	4.1214	**0.0007**	186	9.8766	**<.0001**
Tr	26	2.8122	0.1055	25	2.4851	0.1275	33	0.2512	0.6195
Tr X year	36	0.7354	0.4864	147	2.5600	**0.0218**	186	0.3822	0.8606
Latewood lumen area (LW LA)									
pLW LA	28	**18.0881**	**0.0002**	25	14.6726	**0.0008**	34	13.7171	**0.0008**
year	9	0.1568	0.8572	146	2.1213	0.0542	186	5.6658	**0.0001**
Tr	28	0.3907	0.5370	25	0.7292	0.4013	34	1.3193	0.2587
Tr X year	9	0.6594	0.5405	146	0.8513	0.5325	186	1.6676	0.1444
Earlywood wall thickness (EW WT)									
pEW WT	28	17.8426	**0.0002**	25	12.9314	**0.0014**	32	22.7264	**<.0001**
year	36	8.4653	**0.0010**	146	0.6954	0.6537	186	3.8646	**0.0024**
Tr	28	1.7785	0.1931	25	0.8492	0.3656	32	1.8589	0.1823
Tr X year	36	0.9412	0.3995	146	1.0304	0.4080	186	0.8927	0.4871

Latewood wall thickness (LW WT)									
pLW WT	28	6.8976	**0.0138**	23	11.1282	**0.0029**	33	44.2501	**<.0001**
year	9	1.4575	0.2829	146	2.1525	0.0509	186	2.6776	**0.0231**
Tr	28	0.0183	0.8933	23	0.6867	0.4158	33	0.3259	0.5719
Tr X year	9	1.6871	0.2387	146	1.2055	0.3067	186	2.3123	**0.0456**
Tracheid length (TL)									
pTL	28	163.8362	**<.0001**	22	46.0023	**<.0001**	34	100.7762	**<.0001**
year	14	0.2798	0.7601	75	2.9476	**0.0382**	109	0.5378	0.6574
Tr	28	7.0977	**0.0127**	22	11.2447	**0.0029**	34	0.3367	0.5656
Tr X year	14	0.1460	0.8654	75	2.6979	0.0518	109	2.1863	0.0938
Modulus of elasticity (MOE)									
pMOE	25	69.5605	**<.0001**	.	.	.	28	5.4519	**0.0269**
Tr	25	0.2503	0.6213	20	8.4448	**0.0087**	28	0.2530	0.6189
Modulus of rupture (MOR)									
pMOR	24	21.5453	**0.0001**	.	.	.	27	0.3569	0.5552
Tr	24	0.2630	0.6128	21	8.3896	**0.0086**	27	0.1608	0.6916

The significant effects ($p<0.05$) are shown in bold type. [a] Pre-harvest values (average of 10 years pre-treatment); Tr, partial cutting treatments.

Table 2.5. Spearman correlation coefficients between all possible pairs of intra-ring traits after the three partial cutting treatments. Upper part, treated plots; lower part, control plots. (See supplementary data (Table S2.2) for the correlation coefficients after the three partial cuttings separately)

	RW	GR	RD	EWD	LWD	LWP	EWLA	LWLA	EWWT	LWWT	TL	MOE	MOR
Ring width (RW)		**0.50**	-0.10	-0.15	**0.40**	**-0.55**	-0.06	0.18	0.16	0.14	-0.20	-0.47	**-0.52**
Growth ratio (GR)	**0.27**		0.02	0.01	0.13	**-0.20**	**-0.63**	-0.18	-0.06	0.06	**-0.73**	-0.38	-0.23
Ring density (RD)	-0.07	0.03		**0.88**	**0.46**	**0.34**	0.03	0.08	**0.28**	0.19	-0.09	-0.17	-0.10
Earlywood density (EWD)	**-0.37**	-0.04	**0.79**		**0.33**	**0.20**	0.07	0.05	**0.25**	0.08	-0.05	-0.14	-0.14
Latewood density (LWD)	**0.56**	0.02	**0.42**	0.11		**-0.47**	0.19	0.15	0.09	**0.24**	0.04	-0.20	-0.46
Latewood proportion (LWP)	**-0.58**	-0.11	**0.19**	**0.23**	**-0.67**		-0.12	-0.06	0.00	-0.01	-0.04	0.10	0.49
Earlywood lumen area (EWLA)	**0.48**	**-0.25**	**-0.24**	**-0.28**	0.21	**-0.42**		**0.50**	0.07	0.03	**0.73**	0.31	-0.34
Latewood lumen area (LWLA)	**0.47**	0.06	-0.09	-0.09	0.15	-0.20	**0.56**		**0.33**	0.14	**0.33**	-0.06	-0.44
Earlywood wall thickness (EWWT)	0.20	0.11	0.10	0.06	-0.05	0.01	**0.26**	**0.28**		**0.46**	0.12	0.30	-0.07
Latewood wall thickness (LWWT)	**0.47**	0.21	0.09	-0.12	**0.28**	-0.19	**0.29**	**0.29**	**0.55**		0.04	0.06	0.08
Tracheid length (TL)	**0.31**	**-0.41**	0.13	0.03	0.22	-0.10	**0.43**	0.26	-0.04	0.04		0.50	-0.17
Modulus of elasticity (MOE)	-0.24	-0.08	0.12	0.16	-0.19	0.27	0.05	-0.04	0.22	-0.08	-0.10		0.41
Modulus of rupture (MOR)	-0.34	-0.25	0.36	0.41	-0.11	0.34	-0.32	-0.19	0.09	-0.03	-0.05	**0.56**	

The significant effects ($p<0.05$) are shown in bold type.*Growth ratio: annual growth increment measured by dividing the annual ring width with the average of the 10 years prior to the treatment.

Supplementary Table S2.1. Mixed model analysis on ring width, latewood proportion, wood density, lumen area, cell wall thickness, tracheid length, modulus of elasticity and rupture, showing the F-value and P-value of the fixed effects.

	CLVD			CPPTM			CT		
Parameters	DF	F-value	P-value	DF	F-value	P-value	DF	F-value	P-value
Ring width (RW)									
pRW[a]	28	67.3455	**<.0001**	20	48.4937	**<.0001**	32	53.2811	**<.0001**
year	108	5.5157	**0.0001**	211	0.5585	0.8300	288	4.3260	**0.0001**
Tr	28	0.0646	0.8012	20	0.4477	0.5111	32	1.2473	0.2724
DBH	.	.	.	.	.	.	.	.	.
CR	.	.	.	.	.	.	.	.	.
TST	.	.	.	20	5.8049	**0.0257**	.	.	.
Age	.	.	.	20	5.1459	**0.0345**	.	.	.
SI	.	.	.	.	.	.	.	.	.
Tr X year	108	8.4469	**<.0001**	211	2.6585	**0.0061**	288	2.1664	**0.0301**
Latewood proportion (LWP)									
pLWP[a]	28	37.7743	**<.0001**	19	26.8378	**0.0001**	32	99.9201	**<.0001**
Year	96	1.0615	0.3867	181	0.3807	0.9433	273	3.1986	**0.0017**
Tr	28	0.0244	0.8769	19	3.2698	0.0864	32	0.00001	0.9976
DBH	.	.	.	.	.	.	.	.	.
CR	.	.	.	19	5.7702	**0.0267**	.	.	.
TST	.	.	.	19	10.2619	**0.0047**	.	.	.
Age	.	.	.	19	8.7952	**0.0079**	.	.	.
SI	.	.	.	.	.	.	.	.	.
Tr X year	96	0.7356	0.5986	181	0.4444	0.9094	273	0.9627	0.4656
Ring density (RD)									
pRD[a]	28	49.8582	**<.0001**	22	11.5305	**0.0026**	32	69.7850	**<.0001**
Year	108	1.6959	0.1417	211	0.6604	0.7441	288	4.9834	**<.0001**
Tr	28	1.1870	0.2852	22	1.0386	0.3194	32	0.7074	0.4065
DBH	.	.	.	.	.	.	.	.	.
CR	.	.	.	.	.	.	.	.	.
TST	.	.	.	.	.	.	.	.	.
Age	.	.	.	.	.	.	.	.	.
SI	.	.	.	.	.	.	.	.	.
Tr X year	108	0.8790	0.4979	211	1.3786	0.1994	288	0.1541	0.1541
Earlywood density (EWD)									
pEWD[a]	28	85.2079	**<.0001**	21	32.2704	**<.0001**	31	76.7748	**<.0001**
Year	96	1.4848	0.2019	181	1.2514	0.2666	273	6.8553	**<.0001**
Tr	28	0.6218	0.4370	21	9.8810	**0.0049**	31	0.5908	0.4479
DBH	.	.	.	.	.	.	.	.	.
CR	.	.	.	21	15.2702	**0.0008**	.	.	.
TST	.	.	.	.	.	.	.	.	.
Age	.	.	.	.	.	.	.	.	.
SI	.	.	.	.	.	.	31	8.2856	**0.0072**
Tr X year	96	0.5060	0.7711	181	0.7105	0.6988	273	2.1382	**0.0326**
Latewood density (LWD)									
pLWD[a]	28	64.0706	**<.0001**	22	73.4272	**<.0001**	32	200.8795	**<.0001**
year	96	1.5883	0.1707	181	0.5425	0.8421	273	1.7645	0.0840

Tr	28	1.3025	0.2634	22	5.1330	**0.0337**	32	0.8436	0.3652
DBH	.	.	.	.	.	.	.	.	.
CR	.	.	.	.	.	.	.	.	.
TST	.	.	.	.	.	.	.	.	.
Age	.	.	.	.	.	.	.	.	.
SI	.	.	.	.	.	.	.	.	.
Tr X year	96	1.8754	0.1057	181	1.1849	0.3071	273	1.1566	0.3258
Earlywood lumen area (EW LA)									
pEW LA[a]	26	97.9350	**<.0001**	25	45.3302	**<.0001**	33	73.1118	**<.0001**
Year	36	1.4695	0.2434	147	4.1214	**0.0007**	186	9.8766	**<.0001**
Tr	26	2.8122	0.1055	25	2.4851	0.1275	33	0.2512	0.6195
DBH	26	12.1920	**0.0017**	.	.	.	.	.	.
CR	.	.	.	.	.	.	.	.	.
TST	26	5.7536	**0.0239**	.	.	.	.	.	.
Age	.	.	.	.	.	.	.	.	.
SI	.	.	.	.	.	.	33	14.0247	**0.0007**
Tr X year	36	0.7354	0.4864	147	2.5600	**0.0218**	186	0.3822	0.8606
Latewood lumen area (LW LA)									
pLW LA[a]	28	**18.0881**	**0.0002**	25	14.6726	**0.0008**	34	13.7170	**0.0008**
Year	9	0.1568	0.8572	146	2.1213	0.0542	186	5.6658	**0.0001**
Tr	28	0.3907	0.5370	25	0.7292	0.4013	34	1.3193	0.2587
DBH	.	.	.	.	.	.	.	.	.
CR	.	.	.	.	.	.	.	.	.
TST	.	.	.	.	.	.	.	.	.
Age	.	.	.	.	.	.	.	.	.
SI	.	.	.	.	.	.	.	.	.
Tr X year	9	0.6594	0.5405	146	0.8513	0.5325	186	1.6676	0.1444
Earlywood wall thickness (EW WT)									
pEW WT[a]	**28**	17.8426	**0.0002**	25	12.9314	**0.0014**	32	22.7264	**<.0001**
Year	36	8.4653	**0.0010**	146	0.6954	0.6537	186	3.8646	**0.0024**
Tr	28	1.7785	0.1931	25	0.8492	0.3656	32	1.8589	0.1823
DBH	.	.	.	.	.	.	32	4.1891	**0.0490**
CR	.	.	.	.	.	.	.	.	.
TST	.	.	.	.	.	.	32	5.9081	**0.0209**
Age	.	.	.	.	.	.	.	.	.
SI	.	.	.	.	.	.	.	.	.
Tr X year	36	0.9412	0.3995	146	1.0304	0.4080	186	0.8927	0.4871
Latewood wall thickness (LW WT)									
pLW WT[a]	28	6.8976	**0.0138**	23	11.1282	**0.0029**	33	44.2501	**<.0001**
Year	9	1.4575	0.2829	146	2.1525	0.0509	186	2.6776	**0.0231**
Tr	28	0.0183	0.8933	23	0.6867	0.4158	33	0.3259	0.5719
DBH	.	.	.	.	.	.	.	.	.
CR	.	.	.	.	.	.	.	.	.
TST	.	.	.	23	4.4528	**0.0459**	.	.	.
Age	.	.	.	23	5.0721	**0.0342**	33	8.0693	**0.0077**
SI	.	.	.	.	.	.	.	.	.
Tr X year	9	1.6871	0.2387	146	1.2055	0.3067	186	2.3123	**0.0456**
Tracheid length (TL)									
pTL[a]	28	163.8362	**<.0001**	22	46.0023	**<.0001**	34	100.7762	**<.0001**
Year	14	0.2798	0.7601	75	2.9476	**0.0382**	109	0.5378	0.6574
Tr	28	7.0977	**0.0127**	22	11.2447	**0.0029**	34	0.3367	0.5656
DBH	.	.	.	.	.	.	.	.	.
CR	.	.	.	.	.	.	.	.	.

TST	28	13.8099	**0.0009**	22	5.5090	**0.0283**	.	.	.
Age	.	.	.	.	.	.	.	.	.
SI	.	.	.	.	.	.	.	.	.
Tr X year	14	0.1460	0.8654	75	2.6979	0.0518	109	2.1863	0.0938
Modulus of elasticity (MOE)									
pMOE[a]	25	69.5605	**<.0001**	.	.	.	28	5.4519	**0.0269**
Tr	25	0.2503	0.6213	20	8.4448	**0.0087**	28	0.2530	0.6189
DBH	.	.	.	20	6.9558	**0.0158**	.	.	.
CR	.	.	.	.	.	.	.	.	.
TST	.	.	.	.	.	.	.	.	.
Age	.	.	.	.	.	.	.	.	.
SI	.	.	.	.	.	.	.	.	.
Modulus of rupture (MOR)									
pMOR[a]	24	21.5453	**0.0001**	.	.	.	27	0.3569	0.5552
Tr	24	0.2630	0.6128	21	8.3896	**0.0086**	27	0.1608	0.6916
DBH	24	7.4588	**0.0116**	.	.	.	.	.	.
CR	.	.	.	.	.	.	.	.	.
TST	.	.	.	.	.	.	.	.	.
Age	.	.	.	.	.	.	27	10.6932	**0.0029**
SI	.	.	.	.	.	.	.	.	.

The significant effects ($p<0.05$) are shown in bold type. [a] Pre-harvest values (average of 10 years pre-treatment); Tr, partial cutting treatments. DBH, diameter at breast height; CR, crown ratio ; TST, time since treatment; SI, site index.

Supplementary Table S2.2. Correlation coefficients between all possible pairs of intra-ring traits after the three partial cutting treatments A) CPPTM, B) CLVD, C) CT. Upper part, treated plots; lower part, control plots.

A) CPPTM

	RW	GR	RD	EWD	LWD	LWP	EWLA	LWLA	EWWT	LWWT	TL	MOE	MOR
Ring width (RW)		**0.67**	-0.05	-0.13	**0.46**	**-0.57**	0.22	**0.45**	0.20	0.17	-0.07	-0.35	-0.44
Growth ratio (GR)	**0.66**		-0.08	-0.18	0.18	-0.30	-0.02	0.17	-0.15	0.09	-0.57	-0.67	-0.43
Ring density (RD)	-0.05	-0.06		**0.90**	**0.58**	0.30	0.07	-0.12	0.19	0.23	0.09	0.21	-0.31
Earlywood density (EWD)	**-0.36**	0.01	**0.71**		**0.49**	0.14	0.00	-0.14	0.24	0.19	0.03	0.12	-0.35
Latewood density (LWD)	**0.79**	0.27	0.17	-0.31		**-0.40**	0.32	0.11	0.12	0.27	0.22	-0.19	-0.41
Latewood proportion (LWP)	**-0.76**	-0.29	0.21	**0.38**	**-0.78**		-0.01	-0.18	-0.08	0.05	0.09	0.26	0.20
Earlywood lumen area (EWLA)	**0.67**	**0.46**	-0.23	-0.37	**0.42**	**-0.61**		**0.51**	0.05	0.19	**0.45**	-0.33	-0.36
Latewood lumen area (LWLA)	**0.63**	**0.48**	-0.02	-0.06	0.33	-0.37	**0.60**		0.33	0.28	0.00	-0.40	-0.45
Earlywood wall thickness (EWWT)	0.11	0.05	**0.41**	**0.49**	0.08	-0.15	0.10	0.23		**0.53**	0.01	0.60	0.15
Latewood wall thickness (LWWT)	**0.56**	**0.42**	0.28	-0.02	**0.47**	**-0.45**	**0.52**	**0.53**	**0.53**		0.03	-0.12	0.05
Tracheid length (TL)	**0.66**	0.44	0.10	-0.31	0.28	-0.15	**0.48**	0.42	-0.09	0.37		0.34	0.06
Modulus of elasticity (MOE)	-0.56	-0.24	0.03	0.57	-0.70	0.60	-0.55	-0.33	0.33	-0.38	-0.71		0.70
Modulus of rupture (MOR)	-0.63	-0.33	0.06	0.69	-0.66	0.58	-0.43	-0.20	0.38	-0.31	-0.46	0.62	

B) CLVD

	RW	GR	RD	EWD	LWD	LWP	EWLA	LWLA	EWWT	LWWT	TL	MOE	MOR
Ring width (RW)		**0.84**	-0.40	-0.24	-0.07	**-0.56**	0.20	0.26	0.01	-0.18	0.37	-0.30	-0.39
Growth ratio (GR)	**0.61**		-0.28	-0.17	-0.06	**-0.47**	0.22	0.21	0.22	0.15	0.19	-0.04	-0.18
Ring density (RD)	-0.27	-0.16		**0.91**	**0.56**	0.33	0.26	0.42	0.55	0.17	0.23	-0.48	-0.42
Earlywood density (EWD)	**-0.45**	-0.36	**0.83**		**0.51**	0.08	0.70	0.64	0.48	-0.07	0.38	-0.42	-0.63
Latewood density (LWD)	**0.38**	-0.18	**0.43**	0.31		-0.25	0.06	0.01	0.39	0.25	0.19	-0.25	-0.51
Latewood proportion (LWP)	**-0.60**	0.00	0.31	0.23	**-0.57**		-0.50	-0.41	-0.62	-0.26	-0.15	-0.04	0.23
Earlywood lumen area (EWLA)	0.48	-0.33	0.10	-0.07	**0.79**	**-0.73**		0.48	0.38	0.19	0.63	0.03	-0.64
Latewood lumen area (LWLA)	0.57	0.13	0.15	0.09	0.37	-0.23	0.54		0.33	-0.06	0.30	-0.74	-0.79

Earlywood wall thickness (EWWT)	0.36	0.19	0.02	-0.16	-0.11	0.32	0.04	0.44		0.43	0.29	0.09	-0.27
Latewood wall thickness (LWWT)	0.36	0.09	0.04	-0.04	0.23	0.16	0.22	0.60	0.51		0.15	0.22	0.18
Tracheid length (TL)	0.08	-0.49	0.23	0.10	0.48	-0.25	0.78	0.50	0.15	0.28		-0.12	-0.56
Modulus of elasticity (MOE)	-0.34	-0.33	0.44	0.32	-0.02	0.36	0.11	0.16	0.17	0.01	0.21		0.42
Modulus of rupture (MOR)	-0.23	-0.15	0.39	0.25	0.21	0.27	0.15	0.16	0.40	0.29	0.15	**0.78**	

C) CT

	RW	GR	RD	EWD	LWD	LWP	EWLA	LWLA	EWWT	LWWT	TL	MOE	MOR
Ring width (RW)		**0.99**	-0.12	-0.24	**0.49**	**-0.53**	-0.26	0.13	0.21	0.24	-0.48	-0.65	-0.64
Growth ratio (GR)	**0.97**		-0.23	**-0.34**	**0.44**	**-0.57**	-0.26	0.09	0.17	0.22	-0.49	-0.23	-0.05
Ring density (RD)	0.03	-0.17		**0.81**	**0.29**	**0.41**	0.07	0.26	0.34	0.16	-0.08	0.36	0.36
Earlywood density (EWD)	**-0.34**	**-0.54**	**0.78**		0.11	**0.31**	0.07	0.18	0.24	0.00	-0.10	0.33	0.41
Latewood density (LWD)	**0.44**	**0.29**	**0.60**	**0.32**		**-0.58**	0.11	0.20	0.03	0.26	-0.07	-0.17	-0.52
Latewood proportion (LWP)	**-0.38**	**-0.41**	0.09	0.14	**-0.62**		-0.09	0.04	0.12	-0.04	0.07	0.25	0.59
Earlywood lumen area (EWLA)	0.26	**0.35**	-0.25	-0.26	-0.04	-0.25		**0.44**	-0.20	-0.12	0.36	0.26	-0.04
Latewood lumen area (LWLA)	0.29	0.31	-0.14	-0.12	0.01	-0.11	**0.57**		0.28	0.06	0.29	-0.02	-0.11
Earlywood wall thickness (EWWT)	0.30	**0.34**	-0.17	-0.29	-0.15	0.07	**0.51**	**0.32**		**0.38**	0.06	0.09	0.05
Latewood wall thickness (LWWT)	**0.42**	**0.43**	-0.08	-0.27	0.14	-0.09	0.28	0.05	**0.64**		0.09	0.24	0.13
Tracheid length (TL)	-0.19	-0.24	0.30	0.27	0.09	-0.01	0.03	-0.08	-0.01	-0.17		0.64	0.23
Modulus of elasticity (MOE)	0.36	0.22	-0.14	-0.48	-0.04	-0.10	0.07	-0.04	0.24	0.17	-0.38		0.64
Modulus of rupture (MOR)	0.05	-0.35	0.31	0.06	0.26	-0.08	-0.38	-0.46	-0.44	-0.24	0.21	0.44	

The significant effects ($p<0.05$) are shown in bold type.*Growth ratio: annual growth increment measured by dividing the annual ring width with the average of the 10 years prior to the treatment.

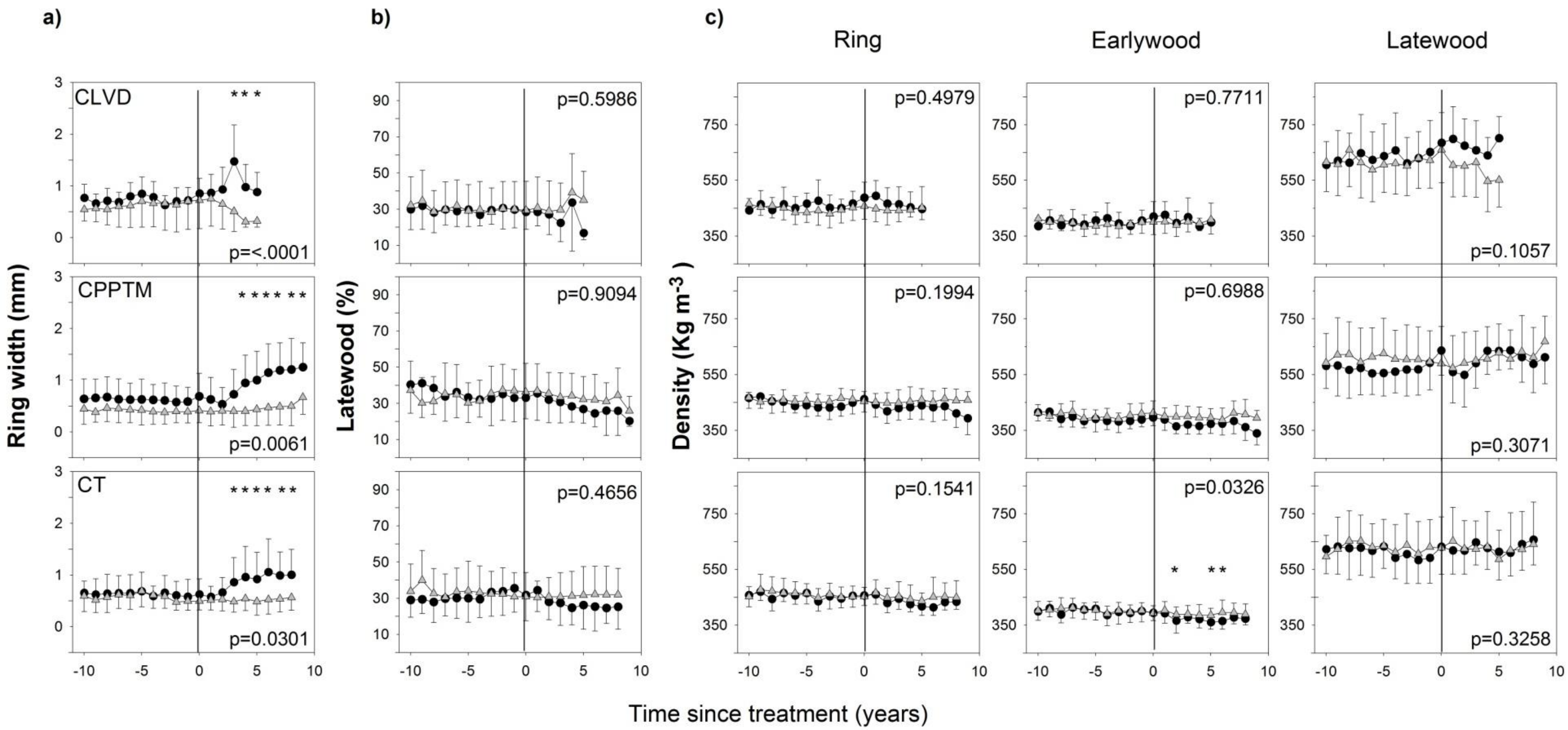

Figure 2.1. Average a) ring width, b) latewood proportion and c) ring, early- and latewood density per year, measured at 1.3 m for each treatment (black circles) with their controls (grey triangles). The vertical lines, at year 0, indicate year of partial cutting. Vertical bars represent the standard deviation. P-values are the results from the treatment and year interaction. * shows years where treated trees differ from control trees (p<0.05).

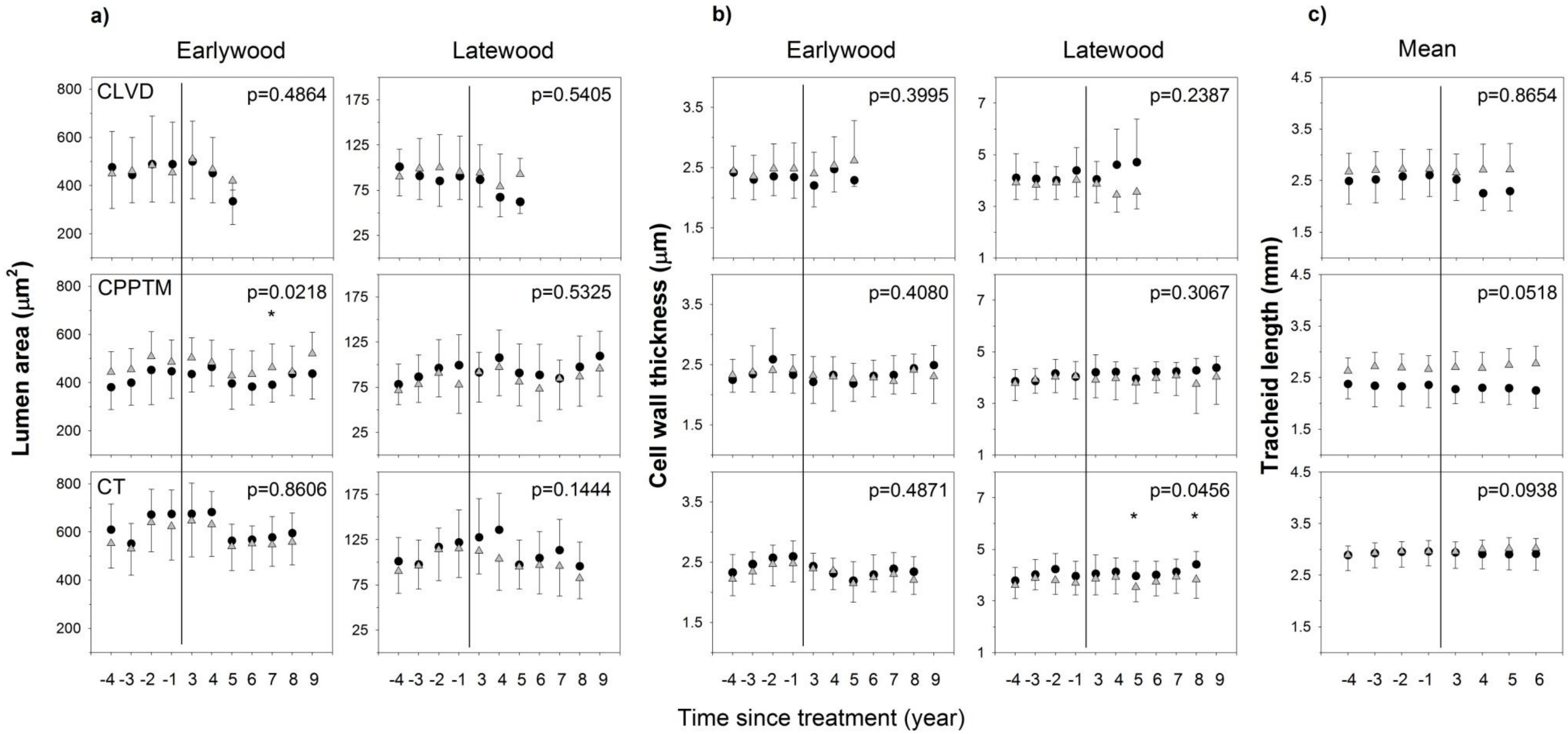

Figure 2.2. Early- and latewood average a) lumen area and b) cell wall thickness and average ring c) tracheid length per year, measured at 1.3 m for each treatment (black circles) with their controls (grey triangles). The vertical lines, at year 0, indicate year of partial cutting. Vertical bars represent the standard deviation. P-values are the results from the treatment and year interaction. * shows years where treated trees differ from control trees ($p<0.05$).

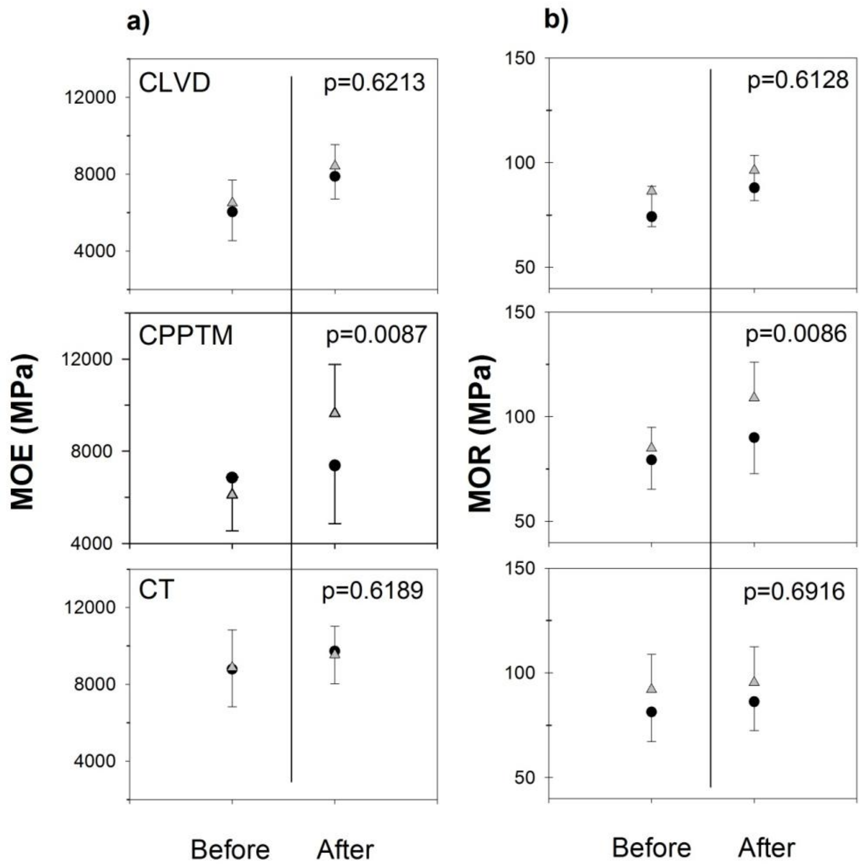

Figure 2.3. Average a) modulus of elasticity (MOE) and b) modulus of rupture (MOR) measured between 0.5 and 1 m, before and after each treatment (black circles) with their controls (grey triangles). Vertical bars represent the standard deviation. P-values are the results from the treatment.

CHAPITRE 3

VARIATION IN RING WIDTH, WOOD DENSITY AND BRANCH DIAMETER ALONG THE STEM OF RESIDUAL BLACK SPRUCE TREES AFTER THREE PARTIAL CUTTING TREATMENTS IN NORTH-EASTERN QUEBEC

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Variation in ring width, wood density and branch diameter along the stem of residual black spruce trees after three partial cutting treatments in north-eastern Quebec

Abstract

Partial cuttings are increasingly used in the boreal forest of eastern Canada. The change in environmental conditions following partial cutting should increase residual trees radial growth and lead to lower wood quality. However, differences can be expected in wood properties with stem height. The effects of increased growth on wood density and branch diameter after three partial cutting treatments were therefore investigated at different sampling heights. The partial cutting treatments were commercial thinning (CT), careful logging around small merchantable stems (CPPTM) and careful logging around stems with variable diameter (CLVD). We sampled 60 black spruce trees among those presenting wider growth rings in treated plots, and 60 black spruces from all trees in control plots. Wood density was evaluated in three different height classes, while branch diameters were evaluated in five sections of the live crown. For each height class, tree rings were, on average, 34, 88 and 45% wider compared to control trees in CLVD, CPPTM and CT, respectively. This increase was greater in the bottom part of the trees after CPPTM. Partial cutting treatments similarly affected wood density parameters along the stem. Only a slight overall decrease in earlywood density after CPPTM (3%) and CT (6%), an increase in latewood density (5%) and a decrease in latewood proportion after CPPTM (4%) were observed compared with control trees. Branch diameter was influenced by tree DBH and crown ratio. Compared to control trees, branches were 3.4, 0.8 and 2.2 mm larger in CLVD, CPPTM and CT, respectively, but significant differences were only detected between control trees and both CPPTM and CT. The overall results suggest that, after partial cutting treatments in black spruce stands, an increased radial growth should not have a negative effect on wood quality along the stem.

Keywords: Partial cuttings, wood density, latewood proportion, ring width, branch diameter, black spruce.

Introduction

Partial cutting treatments are increasingly used in black spruce (*Picea mariana* (Mill.) B.S.P.) even- and uneven-aged stands of the Canadian north-eastern boreal forest. As a result of these treatments, tree growth is generally improved by the decreased inter-tree competition (Pamerleau-Couture *et al.*, 2015). Increased radial growth is usually associated with a decrease in average ring density (e.g. Makinen *et al.*, 2002; Xiang *et al.*, 2014), which could greatly influence tree mechanical properties, such as strength and elasticity (Saranpää, 2003). This reduced ring density is generally induced by a decrease in the latewood proportion (Zhang, 1998; Wang *et al.*, 2002). Changes in tracheid dimensions can also lead to a decrease in earlywood and latewood densities (Makinen *et al.*, 2002). For black spruce trees, an increased growth after partial cutting treatments has been associated with only negligible detrimental effects on wood properties (Pamerleau-Couture *et al.*, submitted, Vincent *et al*., 2011). However, these studies did not evaluate the effect of partial cuttings on wood properties along the entire stem.

Wood properties vary more strongly with tree height and cambial age than with stand density (Alteyrac *et al.*, 2005). As an example, for the same cambial age, narrower rings were observed in the upper stem as diameter growth rate decreased from the base to the top of a tree (Alteyrac *et al.*, 2005). Many studies found that with decreasing stand density, the higher radial growth of the butt log resulted in higher stem taper (e.g. Tasissa and Burkhart, 1997; Sharma and Zhang, 2004), which could strongly affect volume and product recovery. Also, the upper stem is mainly composed of juvenile wood that decreases wood quality because of its lower density, larger ring width, smaller tracheids with thinner cell walls, and larger microfibrils angles (Shmulsky and Jones, 2011). For black spruce trees, the cambial age at which the transition between juvenile and mature wood occurs is generally observed between the 11^{th} and 21^{st} ring (Yang and Hazenberg, 1994; Alteyrac *et al.*, 2006). However, this transition age decreases with increasing stem height in natural forests, possibly due to a reduction of crown volume with tree aging or a low activity of lower branches after canopy closure (Alteyrac *et al.*, 2006). By opening the canopy and decreasing stand density, silvicultural treatments may delay crown recession (Brix, 1981; Gillespie *et al.*, 1994) and thus extend the juvenile period in the upper tree.

The delayed crown recession after silvicultural treatment might also have an effect on branch diameter. Crown structure and characteristics of individual branches affect tree growth by controlling resource acquisition. However, the number and size of branches could affect the grading of black spruce logs. Branches influence log strength as well as the appearance of the wood product (Shmulsky and Jones, 2011). Branch diameters tend to increase with decreasing stand density after silvicultural treatment (Weiskittel *et al.*, 2007; Hein *et al.*, 2008), because they are influenced by the same factors that increase stem growth. As they already received full sunlight, branches in the upper part of the crown of dominant trees are not affected by thinning intensities (Makinen and Hein, 2006; Weiskittel *et al.*, 2007). The effect of partial cutting treatments might therefore be more important in the lower part of the crown. However, the foliage distribution on a tree varies with its social position, size and age (Kantola and Makela, 2004; Garber and Maguire, 2005; Weiskittel *et al.*, 2007), so the type of silvicultural treatment and stand structure (even or uneven-aged stand) might affect branch characteristics differently.

While commercial thinning is a well known partial cutting treatment used in even-aged forests, partial cutting treatments are also now being applied to uneven-aged forests according to the ecosystem-based management. Little is still known about the effect of large ring width induced by a broad range of partial cutting intensities on wood quality (Bose *et al.*, 2014). This study therefore evaluated the effect of increased tree growth on wood and branch properties along the stem after three different partial cutting treatments applied in even- and uneven-aged black spruce stands in the boreal forest of eastern Canada. The studied effects were wood density (ring, early- and latewood density), latewood proportion and branch diameter at different stem heights. The working hypothesis is that increased growth after partial cuttings will negatively affect all wood properties with a more pronounced effect in the lower part of the trees.

Methods

Study sites

The study was conducted on residual black spruce trees after the application of three partial cutting treatments: Careful logging around small merchantable stems (CPPTM in Québec, a variant of HARP in Ontario), Careful Logging around stems with Variable Diameters (CLVD, coupe avec protection des tiges à diamètre variables in Quebec), both applied in uneven-aged forest, and Commercial Thinning from below (CT) applied in even-aged forest. While CPPTM and CLVD are diameter limit cuttings removing all trees with a diameter at breast height larger than 14 cm, CPPTM removes between 70 and 90% of stand basal area whereas CLVD can remove up to 95%. CT removes between 30 and 35% of stand basal area (see Pamerleau-Couture *et al.*, (2015) for more details on the treatments). Four, three and five blocks were sampled for CLVD, CPPTM and CT, respectively. A block corresponds to one treated plot combined with one control plot (located within a 1-km radius), both of which with a basal area of at least 50% in black spruce. Each block was selected in the managed forest of Saguenay Lac-Saint-Jean region (Quebec, Canada) between 47°51' and 50°25' N and 70°13' and 72°11' W. For details on stand basal area and stem density, see supplementary data (Table S3.1).

In each treated plot, five black spruce trees were randomly selected among those presenting a post-treatment radial growth at least 20% greater than that in the 10-year pre-treatment period (Vincent *et al.*, 2009), whereas the selection was made among all trees in control plots (Pamerleau-Couture *et al.*, submitted). According to wood cores sampled from every black spruce tree in each treated and control plot (minimum of 35 per plot), an average of 36, 67 and 64% of residual trees increased their growth after the application of CLVD, CPPTM and CT, respectively.

After measuring their diameter at breast height (1.3 m, DBH), the selected trees were felled to measure tree height (TH) and crown ratio (CR=crown length/TH) (Table 3.1). For even-aged stands (CT), the site index (SI) was determined according to an equation developed by Pothier and Savard (1998) for black spruce while the SI of uneven-aged stands (CLVD and CPPTM) was determined using the Ouzennou *et al.* (2008) method (Table 3.1) (Pamerleau-Couture *et al.*, 2015).

Ring width, latewood proportion and ring density

On each felled tree, wood disks were sampled at 0.5 m, 1.3 m, 2 m and then every 2 m up to the tree top. From these disks, 2-mm thick sections were sawn from pith to bark and then extracted with cyclohexane/ethanol (2:1) solution for 24 hours, followed by hot water for a further 24 hours. Ring width (RW), latewood proportion (LWP), average ring density (RD), earlywood density (EWD) and latewood density (LWD) were measured using an X-ray densitometer (QTRS-01X Tree Ring Analyser; QMS Inc., Knoxville, TN). The maximum derivative method, with a six-degree polynomial, was used to detect the transition between early- and latewood (Koubaa *et al.*, 2002).

We used tree relative height to take into account intra-plot differences in tree height, especially in uneven-aged plots. Three classes of relative height (RH) were determined: Class 1) $0\% \leq RH < 25\%$, Class 2) $25\% \leq RH < 50\%$, Class 3) $50\% \leq RH < 100\%$. Class 3 has a larger range because wood disks from the upper tree were only sampled every 2 meters. As the time since treatment differs for the three partial cutting treatments, different time spans, 5, 9 and 8 years after CLVD, CPPTM and CT, respectively, were analyzed for each treatment to include the maximum years since the treatment (Table 3.1).

Branch diameter

For each tree, the crown length was divided into five equal sections. The first section was located at the crown base and the fifth at the top. In each section, the horizontal and vertical diameter of the five biggest branches were measured, avoiding the basal swell, for a total of 25 branches per tree. Maximum branch diameter was also recorded for each tree.

Statistical analysis

The effect of partial cutting treatments was assessed using a linear mixed-model analysis of variance (ANOVA) with a correlation structure (Ar (1)) between height classes for wood density parameters and between crown sections for branch diameters. Using tree within the block as a random effect, ANOVA was performed in R (R Core Team, 2014) ("nlme" package and "lme" function (Pinheiro and Bates, 2007)). Using separate analyses, each partial cutting treatment was compared with specific control trees. To account for differences between trees and plots, the site index (SI), time since treatment (TST) and tree characteristics were added to the models after checking for collinearity. Tree characteristics included cambial age, DBH, crown presence and pre-harvest values (average of 5 years pre-treatment) for wood density parameters while age, DBH and CR were included for branch diameter. Independent variables were excluded from the final model if they were not significantly related to the response variable. To satisfy the assumptions of homogeneity of variance and normality, square-root transformations were applied when necessary. A Tukey pairwise multiple comparison test ("lsmeans" package and function (Lenth and Hervé, 2015)) was used to discriminate the effect of treatment when the ANOVA detected a significant difference between height classes or crown sections. Due to lost samples, a total of 28 trees were analyzed for branch diameters out of a possible 40 trees for CLVD and their controls.

Results

For each height class, the 5, 9 and 8 years pre- and post-treatment wood properties were analyzed for CLVD, CPPTM and CT, respectively. Ring width generally increased with increasing sample height, class 3 having the wider growth rings for both treated and control trees (Table 3.2). However, sample height did not significantly affect all three treatments (Table 3.3). For each sample height class, RW was, on average, 34, 88 and 45% wider for CLVD, CPPTM and CT trees, respectively, compared to control trees (Table 3.2). Partial cutting had a significant effect after CT ($p=0.0019$) and CLVD ($p=<.0001$) for all height classes (Table 3.3). CPPTM had a positive effect on RW in classes 1 and 2 (interaction between treatment and classes: $p=0.0009$), while a non significant decrease in RW was observed in class 3 (Fig. 3.1; Tables 3.2 & 3.3). Compared with pre-treatment values, tree response was stronger in the first two height classes, while almost no changes were observed in the upper part (Fig. 3.1).

LWP was, on average, 9% lower in the upper part (class 3) compared to the lower stem (class 1) after the three partial cuttings (Table 3.2). However, height classes have no significant effect on LWP (Table 3.3). Overall, LWP in CPPTM treated trees was 7.4% less than in control trees ($p=0.0006$) and 3.8% less than pre-treatment values (Tables 3.2 &

3.3), with the most important decrease in the lower stem (class 1) and no change in class 3 (Fig. 3.1). LWP of CT was 2.4% less in treated trees than control trees, but this difference was not statistically significant (p=0.0761; Table 3.3). An increase in LWP was observed in classes 2 and 3 after CLVD compared to pre-treatment values (Fig. 3.1), while a 2% decrease was observed in class 1 (Table 3.2) without being significant (p=0.5826; Table 3.3).

While the treatments had no significant effect on the average ring density (RD) compared to control trees (Table 3.3), the RD in treated trees generally decreased by an average of 2% and 4% after CPPTM and CT, respectively, compared to pre-treatment values (Table 3.2), with the greater decrease in the upper tree (class 3) (Fig. 3.1). EWD was lower after the three treatments compared to control trees, but the treatment was only significant for CPPTM and CT (Table 3.3). Compared to pre-treatment values, CT (-8%) and CPPTM (-5%) trees had the largest decrease in EWD in the upper part (class 3) (Fig. 3.1; Table 3.2). LWD increased after each partial cutting, but the only significant treatment effect was detected between CPPTM and control trees (Table 3.3). Compared to pre-treatment values, LWD increased after CPPTM mostly in the first two classes with an average increase of 6% (Fig. 3.1; Table 3.2).

Branch diameter

While tree branches were slightly bigger in the second crown section, branch diameter generally decreased with increasing crown height for all treated and control trees ($p<0.0001$; Table 3.4; Fig. 3.2). Branch diameters ranged from 10 to 18 mm in the lowest crown section compared to 6 to 11 mm in the highest section (Fig. 3.2). After each partial cutting treatment, average branch diameter was generally larger compared to control trees (Fig. 3.2). On average, branches were 3.4, 0.8 and 2.2 mm bigger in treated trees than in control trees for CLVD, CPPTM and CT, respectively. For CLVD, the difference from control trees was constant across crown sections, but the treatment had no significant effect ($p=0.1121$; Table 3.5; Fig. 3.2). For CPPTM and CT, the interaction between treatment and crown sections was significant ($p<0.0001$; Table 3.5; Fig. 3.2). For CPPTM, the most important difference (1.8 mm) from control trees was in sections 2 and 3 while for CT it was in sections 1, 2 and 4 with an average of 2.8 mm (Fig. 3.2). However, the pairwise Tukey test did not detect significant differences between corresponding sections of treated and control plots ($p>0.05$). For all treatments, tree DBH and CR had a significant effect on branch diameters while age only had an effect in CLVD (Table 3.5).

The maximum branch diameter was 4.3, 2.3 and 6.2 mm larger after CLVD, CPPTM and CT, respectively, compared to control trees (Table 3.4). The treatment had a significant effect after CPPTM ($p=0.0030$) and CT ($p=0.0243$), but no significant effect on CLVD trees ($p=0.2134$) (Table 3.5).

Discussion

Ring width, latewood proportion and ring density

Ring width significantly increased, 5, 9 and 8 years after CLVD, CPPTM and CT, respectively, as expected from the tree selection (Fig. 3.1; Table 3.3). By removing surrounding neighbors, partial cuttings generally increase light availability, soil temperature and nutrient cycling (Thibodeau *et al.*, 2000), which positively affect radial growth of residual trees (Vincent *et al.*, 2009; Krause *et al.*, 2011). The growth increase was larger in the two lower parts compared to the upper tree, especially after CPPTM. These differences in radial growth along the stem produced changes in stem taper as already observed after thinning (Tasissa and Burkhart, 1997; Sharma and Zhang, 2004). However, Vincent (2010) found no change in stem taper of black spruce trees after commercial thinning. In the present study, while larger ring widths were observed in the lower half of the trees after all three partial cutting treatments, a significant interaction was only detected between height classes in CPPTM and its specific control trees (Table 3.3). The increased growth after CPPTM in the lower stem could be explained by the need of residual trees to increase their mechanical stability to resist the increased wind exposure (Dean and Long, 1986). Indeed, after high intensity partial cutting such as CPPTM, there is a high mortality rate by windthrow (Gardiner *et al.*, 1997; Riopel *et al.*, 2010), which is not observed after CT because of a higher residual stand density and after CLVD due to greater presence of tree clusters (Pamerleau-Couture *et al.*, 2015). Changes in stem taper following CPPTM could have an important impact on volume and product recovery predictions.

Increased radial growth is usually associated with a decrease in average ring density (e.g. Makinen *et al.*, 2002; Xiang *et al.*, 2014) caused by a decrease in latewood proportion (LWP). Despite the increased ring width, very few changes were observed in the other wood characteristics (LWP, RD, EWD, LWD) after all three treatments, regardless of the sampling height. The most significant effects were observed after CPPTM which was associated with the highest RW increase (Fig. 3.1). Even though we observed a slight decrease in EWD after CPPTM (3%) and CT (6%) and a decrease in LWP after CPPTM (4%), average wood density was not significantly different than control trees after the three partial cutting treatments (Table 3.3). The increase in LWD after CPPTM (5%) and CT

(2%) might have been counteracted by their effect on wood density, even though it was only significantly different from control trees after CPPTM (Table 3.3). Water availability at the end of the growing season might be responsible for the increased LWD (Paul, 1958; Smith and Wilse, 1961, Sperry *et al.*, 2006; D'Orangeville *et al.*, 2013). Accordingly, an increase in radial growth has been associated with a decrease in EWD and with an increase in LWD in Scots pine (*Pinus sylvestris* L.) (Peltola *et al.*, 2007) and Norway spruce (*Picea abies* (L.) Karst.) (Jyske *et al.*, 2010). Very small changes in average wood density were also reported after CT in black spruce stands (2%) (Vincent *et al.*, 2011) and Scots pine stands (2-8%) (Peltola *et al.*, 2007; Makinen and Hynynen, 2014). Since mechanical properties, such as strength and elasticity, are greatly influenced by wood density (Saranpää, 2003), the three partial cutting treatments should not have a short-term effect on wood quality of black spruce. Long-term studies are necessary to ensure that this conclusion remain until the year of the final harvest.

The treatments did not significantly affect the wood characteristics (LWP, RD, EWD, LWD) differently according to sampling height (Table 3.3), which suggests that the entire stem should not be negatively affected by these treatments. However, wood properties do naturally vary along the stem. For both treated and control trees, RW was larger in the upper tree (class 3), while LWP, RD, EWD and LWD were lower compared with the butt section. These characteristics can be associated with the juvenile wood (JW) formed under the strong influence of the active living crown. Compared to mature wood, JW is considered of lesser quality because of the marked differences in strength properties partly related to the earlywood predominance, which leads to an overall lower wood density (Mansfield *et al.*, 2009). Other JW characteristics (e.g. higher microfibril angle, larger spiral grain angles) can also cause serious problems for quality products because of low bending strength and dimensional instability upon drying (Shmulsky and Jones, 2011). The delayed crown recession and increased growth rate (Koubaa *et al.*, 2005; Alteyrac *et al.*, 2006) after partial cutting treatments could potentially extend the juvenile period in the upper part of the tree. However, contradictory results have been reported (e.g. Gartner *et al.*, 2002). In this study, while wood density is lower in the upper part of the tree, the lack of difference from control trees suggests that partial cutting treatments did not lengthen the period of JW formation. Although the transition age was not evaluated in this study, we could speculate that even if the number of JW rings was unaffected by treatments, the larger ring width observed in the upper part of partially cut trees will ultimately lead to a higher JW area, which would affect the overall wood quality. Nevertheless, considering that the increased ring width in the upper part was lower than in the rest of the tree (Fig. 3.1), the JW area should not have a considerable effect on black spruce after these partial cutting treatments.

Branch diameter

After the three treatments, branches were larger than those on control trees (Fig. 3.2), but the differences were not significant after CLVD likely because of the lack of samples or the limited time since treatment. Nevertheless, these results suggest that the general factors influencing tree growth also influence branch growth (Hein *et al.*, 2008). Many studies observed similar results in which silvicultural treatments influence branch diameters (e.g. Maguire *et al.*, 1991; Weiskittel *et al.*, 2007). Partial cuttings increase the space available for crown expansion as well as the light intensity on the lower crown, which results in larger branches and extended branch retention (Makinen and Hein, 2006; Weiskittel *et al.*, 2007). For all treated and control trees, branch diameter increased with increasing tree DBH and crown ratio (Table 3.5).

Makinen and Hein (2006) and Weiskittel *et al.* (2007) observed that branches in the lower crown were more affected than those in the upper part after thinning. In this study, even if the pairwise Tukey test did not detect significant differences between corresponding sections of treated and control trees, the mid-part of the crown seems to be primarily affected after CPPTM, while the lower sections are more affected after CT (Fig. 3.2). Residual trees after partial cutting applied in even- and uneven-aged stands formerly belonged to different social positions. For example, with the removal of dominant trees, CPPTM leaves the formerly suppressed trees in the residual stand while the reverse is true for CT. Garber and Maguire (2005) showed that trees have different foliage distributions according to social position. Dominant trees tend to have their maximum foliage density lower than suppressed trees (Makela and Vanninen, 2001), which might explain the higher effect of the treatment on the lower stem after CT.

Tree branch size is an important factor in determining log and lumber grades. The visual grading system is the most commonly used method for grading lumber in North America (Zhang *et al.*, 2002). Lumbers are graded based on various mechanical and biological defects such as maximum knot size and are classified in grades from highest to lowest value (Table 3.6; NLGA, 2008). After CPPTM and CT, the maximum branch diameter was higher than that on control trees (Table 3.4). However, according to Zhang *et al.* (2002) and Benjamin *et al.* (2007), less than 10% of black spruce trees are declassified because of the size of the knots. If trees were harvested now, CPPTM would not be declassified based on knot size except for the SS (select structural) in 2 by 3 and CT could only be classified as 2 by 4, No.1 and 2 (Table 3.6). Although we measured branches outside the stem surface, which overestimates knot diameter, these values gave a good overview of the effect of treatment on wood quality. Since trees would be harvested in around 50 years, branch diameters could potentially be bigger at that time. However, the effect of partial cutting treatments should diminish with time as branch annual rings follow a negative exponential growth from pith to bark (e.g. Makinen, 1999) and stand density should slowly close.

Conclusion

Increased growth was observed after the three partial cutting treatments. However, the treatments did not affect wood quality parameters differently depending on the sampling height. While some slight changes were observed in earlywood density and latewood proportion, average wood density was not affected by the three treatments. Branch diameters were slightly larger than those on control trees after CPPTM and CT. These results indicate that partial cutting treatments applied to black spruce dominated stands should not produce detrimental effects on wood mechanical properties nor on lumber grading. Further studies that included longer time period since treatment should confirm this conclusion.

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Conflict of interest statement

None declared.

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Table 3.1. Mean, standard deviation (SD), minimum and maximum diameter at 1.3 m (DBH), age, height, crown ratio with time since treatment (TST) and site index (SI), for n trees in each p treated and control plot within the three partial cutting treatments.

		CLVD		CPPTM		CT	
		Treated (p=4 n=20)	Control (p=4 n=20)	Treated (p=3 n=15)	Control (p=3 n=15)	Treated (p=5 n=25)	Control (p=5 n=25)
DBH	**Mean**	**11.1**	**11.8**	**10.3**	**12.0**	**17.2**	**16.0**
(cm)	SD	5.4	4.3	3.3	2.8	3.3	3.2
	Min	4.7	6.2	6.4	7.5	10.8	11.2
	Max	21.8	20.4	17.8	16.6	25.4	23.0
Age	**Mean**	**104**	**92**	**96**	**132**	**80**	**100**
(years)	SD	29	23	17	38	19	39
	Min	75	66	55	84	55	74
	Max	201	142	159	218	159	195
Height	**Mean**	**8.1**	**9.0**	**7.1**	**9.8**	**14.6**	**15.0**
(m)	SD	4.0	2.9	2.5	1.7	3.2	2.9
	Min	2.6	4.6	4.2	6.5	9.4	10.7
	Max	15.4	15.5	13.1	12.3	20.4	20.6
Crown	**Mean**	**0.65**	**0.61**	**0.71**	**0.47**	**0.59**	**0.41**
ratio	SD	0.19	0.16	0.09	0.10	0.13	0.15
	Min	0.22	0.31	0.56	0.32	0.31	0.10
	Max	1.00	0.82	0.88	0.66	0.79	0.67
TST	**Mean**	**5**	**6**	**9**	**10**	**10**	**11**
(years)	SD	1	0	0.6	1	0.5	1.5
	Min	4	6	9	9	10	10
	Max	6	6	10	11	11	13
SI	**Mean**	**4.0**	**8.2**	**4.5**	**8.3**	**11.7**	**13.4**
	SD	5.7	3.6	2.2	1.7	3.5	4.5
	Min	0.1	4.8	2.7	6.4	7.7	8.9
	Max	12.3	13.1	6.9	9.7	16.7	19.2

Table 3.2. Mean and standard deviation (SD) of wood properties pre- and post- three partial cutting treatments and their controls.

				CLVD				CPPTM				CT			
				Treated		Control		Treated		Control		Treated		Control	
Parameters		Classes		Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Ring width	mm	**1**	**Mean**	**0.69**	**0.94**	**0.74**	**0.66**	**0.68**	**1.13**	**0.44**	**0.54**	**0.66**	**0.86**	**0.61**	**0.56**
			SD	0.31	0.51	0.55	0.44	0.28	0.36	0.24	0.37	0.27	0.37	0.26	0.26
		2	**Mean**	**0.80**	**0.93**	**0.76**	**0.63**	**0.75**	**1.17**	**0.53**	**0.57**	**0.83**	**1.07**	**0.76**	**0.70**
			SD	0.32	0.43	0.60	0.42	0.35	0.52	0.34	0.41	0.39	0.53	0.45	0.31
		3	**Mean**	**1.11**	**0.98**	**1.02**	**0.88**	**1.25**	**1.10**	**0.78**	**0.73**	**1.29**	**1.34**	**1.21**	**1.04**
			SD	0.42	0.23	0.61	0.58	0.34	0.21	0.53	0.55	0.48	0.49	0.56	0.45
Latewood	%	**1**	**Mean**	**30.5**	**28.6**	**29.1**	**30.2**	**35.8**	**29.1**	**35.2**	**35.4**	**31.6**	**29.4**	**34.1**	**33.9**
			SD	11.4	11.4	13.7	15.4	9.3	5.5	10.4	10.4	8.4	7.4	8.3	8.2
		2	**Mean**	**26.7**	**28.0**	**28.5**	**25.7**	**31.4**	**26.7**	**35.1**	**34.5**	**30.7**	**28.4**	**32.0**	**30.9**
			SD	10.4	13.8	13.2	10.7	10.2	5.7	12.8	12.7	9.5	9.3	9.4	8.8
		3	**Mean**	**21.7**	**25.5**	**21.6**	**24.9**	**24.7**	**24.7**	**35.4**	**32.9**	**25.5**	**22.9**	**24.9**	**23.1**
			SD	7.3	14.1	5.4	12.2	6.9	6.8	12.6	9.8	5.0	3.6	5.7	6.1
Ring density	kg m^{-3}	**1**	**Mean**	**463.4**	**463.1**	**443.2**	**453.0**	**459.0**	**450.3**	**460.6**	**456.1**	**466.8**	**449.3**	**462.7**	**454.4**
			SD	51.0	58.8	44.8	48.8	25.7	19.3	17.3	24.3	29.1	34.5	31.8	31.5
		2	**Mean**	**447.6**	**447.4**	**444.9**	**446.9**	**436.2**	**428.6**	**452.0**	**446.2**	**451.2**	**442.2**	**444.7**	**442.8**
			SD	37.6	50.3	35.0	45.0	19.0	30.1	16.5	15.1	23.6	21.0	21.8	24.8
		3	**Mean**	**426.2**	**410.6**	**448.8**	**442.9**	**448.6**	**436.6**	**436.2**	**415.6**	**451.6**	**423.8**	**447.1**	**431.1**
			SD	29.0	39.8	27.7	35.7	13.3	16.8	25.8	34.1	18.7	15.7	18.5	15.9
Earlywood density	kg m^{-3}	**1**	**Mean**	**399.5**	**394.3**	**389.9**	**400.0**	**398.5**	**388.6**	**407.9**	**405.4**	**404.3**	**383.2**	**403.9**	**396.9**
			SD	38.4	50.5	36.6	39.8	20.7	18.4	25.4	28.1	25.0	28.7	22.6	26.3
		2	**Mean**	**391.1**	**385.0**	**396.3**	**399.3**	**385.6**	**373.0**	**400.0**	**397.6**	**393.1**	**378.6**	**387.1**	**380.9**
			SD	31.8	46.0	24.4	33.3	17.1	25.1	16.0	18.2	18.6	15.6	13.3	20.8
		3	**Mean**	**378.3**	**357.4**	**402.1**	**398.5**	**401.8**	**382.9**	**392.7**	**373.3**	**401.8**	**369.9**	**397.7**	**379.1**
			SD	25.6	31.8	27.0	27.6	17.5	19.4	24.5	30.1	22.2	14.3	17.7	14.4
Latewood density	kg m^{-3}	**1**	**Mean**	**632.6**	**653.8**	**611.7**	**603.9**	**590.7**	**629.7**	**597**	**589.5**	**636.0**	**645.5**	**610.3**	**600.3**
			SD	109.3	115.3	90.9	101.7	54.2	42.0	82.9	88.4	66.2	48.3	70.3	79.5
		2	**Mean**	**631.2**	**639.4**	**620.7**	**620.8**	**579.8**	**610.8**	**585.6**	**580.7**	**616.8**	**640.8**	**601.8**	**615.2**
			SD	71.0	94.0	89.9	93.2	94.4	65.2	90.1	88.0	79.6	79.1	68.9	66.8
		3	**Mean**	**627.2**	**608.1**	**641.9**	**615.5**	**611.2**	**624.0**	**552.5**	**538.1**	**617.1**	**627.0**	**626.6**	**635.5**
			SD	71.8	110.9	62.2	90.9	63.1	67.5	86.2	97.1	39.6	40.4	52.7	54.3

Class 1) 0% ≤ relative height (RH) < 25%, Class 2) 25% ≤ RH < 50%, Class 3) 50% ≤ RH < 100%.

Table 3.3. Summary of mixed model analysis on ring width, latewood proportion, ring density, early- and latewood density showing the F-value and P-value of the main fixed effects. See supplementary data (Table S3.2) for the complete table.

	CLVD			CPPTM			CT		
Parameters	DF	F-value	P-value	DF	F-value	P-value	DF	F-value	P-value
Ring width (RW)									
pRW[a]	44	60.7888	**<.0001**	36	91.4762	**<.0001**	88	138.8380	**<.0001**
Classes	44	1.1734	0.3188	36	1.5702	0.2219	88	1.5499	0.2180
Tr	32	23.4285	**<.0001**	25	29.4102	**<.0001**	43	10.9869	**0.0019**
Tr X Classes	44	2.6142	0.0846	36	8.5796	**0.0009**	88	1.6508	0.1978
Latewood proportion (LWP)									
pLWP[a]	44	45.8894	**<.0001**	36	133.6403	**<.0001**	89	210.2300	**<.0001**
Classes	44	1.6074	0.2120	36	1.0685	0.3542	89	2.6922	0.0732
Tr	32	0.3082	0.5826	25	15.2631	**0.0006**	44	3.3002	0.0761
Tr X Classes	44	1.1416	0.3286	36	0.9976	0.3787	89	2.4462	0.0924
Ring density (RD)									
pRD[a]	43	47.6648	**<.0001**	37	22.2537	**<.0001**	89	84.2471	**<.0001**
Classes	43	0.0045	0.9955	37	4.4214	**0.0190**	89	8.8623	**0.0003**
Tr	32	1.4846	0.2320	25	0.7430	0.3969	43	0.9539	0.3342
Tr X Classes	43	0.8024	0.4549	37	1.2136	0.3087	89	0.4654	0.6294
Earlywood density (EWD)									
pEWD[a]	43	73.3556	**<.0001**	37	21.9665	**<.0001**	89	89.5915	**<.0001**
Classes	43	0.0834	0.9201	37	4.6847	**0.0154**	89	6.8791	**0.0017**
Tr	31	1.3941	0.2467	25	11.2660	**0.0025**	43	6.4096	**0.0151**
Tr X Classes	43	1.4856	0.2378	37	1.2822	0.2895	89	1.2601	0.2886
Latewood density (LWD)									
pLWD[a]	44	90.6469	**<.0001**	36	130.3154	**<.0001**	89	122.2331	**<.0001**
Classes	44	0.7625	0.4726	36	0.5182	0.6000	89	0.7860	0.4588
Tr	32	1.9641	0.1707	25	13.3030	**0.0012**	43	1.2257	0.2744
Tr X Classes	44	0.2821	0.7555	36	0.5748	0.5679	89	1.5412	0.2198

The significant effects ($p<0.05$) are in bold type. [a] Pre-harvest values (average of 5 years pre-treatment); Tr, treated vs control trees per partial cutting treatment; Classes, three relative height divisions.

Table 3.4. Mean, standard deviation (SD), minimum and maximum of the maximum branch diameter per partial cuttings and their controls.

		CLVD		CPPTM		CT	
		Treated	Control	Treated	Control	Treated	Control
Maximum branch diameter (mm)	**Mean**	**18.0**	**13.7**	**19.6**	**17.3**	**27.8**	**21.6**
	SD	5.8	5.5	4.5	3.3	8.2	6.4
	Min	11.0	7.6	14.3	11.9	14.8	9.4
	Max	32.0	26.9	33.5	22.5	52.0	35.4

Table 3.5. Mixed model analysis on branch diameter and maximal branch diameter, showing the F-value and P-value of the fixed effects.

	CLVD			CPPTM			CT		
Parameters	DF	F-value	P-value	DF	F-value	P-value	DF	F-value	P-value
Branch diameter									
Sections	556	51.1508	**<.0001**	663	128.7207	**<.0001**	1034	76.7830	**<.0001**
Tr	20	2.7626	0.1121	26	0.0726	0.7897	42	0.1150	0.7365
CR	20	12.1665	**0.0023**	663	9.2510	**0.0024**	1034	26.2190	**<.0001**
DBH	20	58.4433	**<.0001**	663	76.1405	**<.0001**	1034	147.1270	**<.0001**
Age	20	5.2933	**0.0323**	.	.	.	.	.	.
SI	.	.	.	.	.	.	.	.	.
TST	.	.	.	.	.	.	.	.	.
Tr X Sections	556	0.8293	0.5069	663	8.5944	**<.0001**	1034	7.1390	**<.0001**
Branch maximal									
Tr	21	1.6465	0.2134	25	10.8281	**0.0030**	41	5.4710	**0.0243**
CR	21	4.8030	**0.0398**						
DBH	21	47.2167	**<.0001**	25	27.7822	**<.0001**	41	34.3310	**<.0001**
Age	.	.	.	.	.	.	.	.	.
SI	.	.	.	.	.	.	.	.	.
TST	.	.	.	.	.	.	.	.	.

The significant effects ($p<0.05$) are in bold type. Sections, five equal live crown sections; Tr, treated vs control trees per partial cutting treatment; CR, crown ratio; DBH, diameter at breast height; SI, site index; TST, time since treatment.

Table 3.6. Knot size restriction required by the Nation Lumber Grade Authority (NLGA, 2008) for different grades of nominal lumber widths.

Nominal lumber width (in)	**Grades**	**Allowable knot size (mm)**	
		Edge	**Centerline**
2 X 3	SS	12.7	12.7
	No.1	19.1	19.1
	No.2	22.2	22.2
2 X 4	SS.	19	22.2
	No.1	25.4	38.1
	No.2	31.8	50.8
2 X 6	SS	28.6	47.6
	No.1	38.1	57.2
	No.2	47.6	73.0

Supplementary Table S3.1. Mean, standard deviation (SD), minimum and maximum stand basal area and stand density, for each p treated and control plot within the three partial cutting treatments.

			CLVD		CPPTM		CT	
			Treated (p=4)	Control (p=4)	Treated (p=3)	Control (p=3)	Treated (p=5)	Control (p=5)
Basal area	m^2 ha^{-1}	**Mean**	**11.9**	**23.3**	**13.3**	**31.9**	**29.0**	**48.4**
		SD	7.7	3.7	8.8	13.8	7.9	12.1
		Min	5.8	19	5.1	16.7	20.4	34.9
		Max	23.2	27.6	22.6	43.6	38.8	63.7
Density	# ha^{-1}	**Mean**	**1482**	**2423**	**1299**	**2133**	**1273**	**2612**
		SD	379	358	540	706	176	1857
		Min	1033	1925	975	1600	1075	1175
		Max	1950	2700	1923	2933	1529	5867

Supplementary Table S3.2. Mixed model analysis on ring width, latewood proportion, average, early- and latewood density showing the F-value and P-value of the main fixed effects.

	CLVD			CPPTM			CT		
Parameters	DF	F-value	P-value	DF	F-value	P-value	DF	F-value	P-value
Ring width (RW)									
pRW[a]	44	60.7888	**<.0001**	36	91.4762	**<.0001**	88	138.8380	**<.0001**
Classes	44	1.1734	0.3188	36	1.5702	0.2219	88	1.5499	0.2180
Tr	32	23.4285	**<.0001**	25	29.4102	**<.0001**	43	10.9869	**0.0019**
CP									
DBH				36	5.8655	**0.0206**	88	4.8844	**0.0297**
CA									
SI				25	6.7179	**0.0157**	43	13.5713	**0.0006**
TST									
Tr X Classes	44	2.6142	0.0846	36	8.5796	**0.0009**	88	1.6508	0.1978
Latewood proportion (LWP)									
pLWP[a]	44	45.8894	**<.0001**	36	133.6403	**<.0001**	89	210.2300	**<.0001**
Classes	44	1.6074	0.2120	36	1.0685	0.3542	89	2.6922	0.0732
Tr	32	0.3082	0.5826	25	15.2631	**0.0006**	44	3.3002	0.0761
CP									
DBH				36	5.8190	**0.0211**			
CA									
SI				25	7.7500	**0.0101**			
TST									
Tr X Classes	44	1.1416	0.3286	36	0.9976	0.3787	89	2.4462	0.0924
Ring density (RD)									
pRD[a]	43	47.6648	**<.0001**	37	22.2537	**<.0001**	89	84.2471	**<.0001**
Classes	43	0.0045	0.9955	37	4.4214	**0.0190**	89	8.8623	**0.0003**
Tr	32	1.4846	0.2320	25	0.7430	0.3969	43	0.9539	0.3342
CP									
DBH									
CA	43	4.9321	**0.0317**						
SI							43	8.2719	**0.0062**
TST				25	5.0521	**0.0337**			
Tr X Classes	43	0.8024	0.4549	37	1.2136	0.3087	89	0.4654	0.6294
Earlywood density (EWD)									
pEWD[a]	43	73.3556	**<.0001**	37	21.9665	**<.0001**	89	89.5915	**<.0001**
Classes	43	0.0834	0.9201	37	4.6847	**0.0154**	89	6.8791	**0.0017**
Tr	31	1.3941	0.2467	25	11.2660	**0.0025**	43	6.4096	**0.0151**
CP									
DBH									
CA	43	6.8146	**0.0124**						
SI	31	3.0706	0.0896	25	11.1991	**0.0026**	43	14.9781	**0.0004**
TST									
Tr X Classes	43	1.4856	0.2378	37	1.2822	0.2895	89	1.2601	0.2886
Latewood density (LWD)									
pLWD[a]	44	90.6469	**<.0001**	36	130.3154	**<.0001**	89	122.2331	**<.0001**
Classes	44	0.7625	0.4726	36	0.5182	0.6000	89	0.7860	0.4588

Tr	32	1.9641	0.1707	25	13.3030	**0.0012**	43	1.2257	0.2744
CP									
DBH				36	3.6908	0.0627			
CA									
SI				25	4.1332	0.0528			
TST							43	4.8002	**0.0339**
Tr X Classes	44	0.2821	0.7555	36	0.5748	0.5679	89	1.5412	0.2198

The significant effects ($p<0.05$) are in bold type. [a] Pre-harvest values (average of 5 years pre-treatment); Classes, three relative height divisions; Tr, partial cutting treatments; CP, crown presence; DBH, diameter at breast height; CA, cambial age; SI, site index, TST, time since treatment.

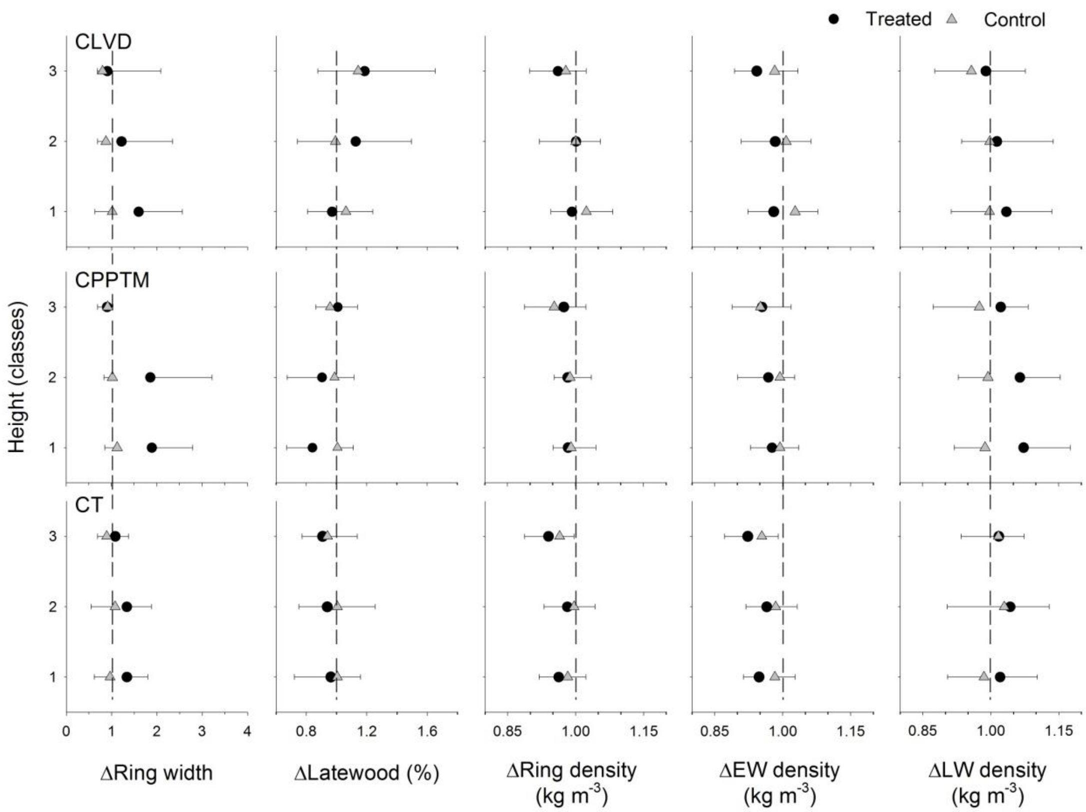

Figure 3.1. Ratio between post and pre-treatment value for ring width, latewood proportion and ring, early- (EW) and latewood (LW) density for each treatment (black circles) with their control (grey triangles). The vertical line represents a ratio of 1, meaning no change between pre- and post-treatment value. Horizontal bars represent standard deviations.

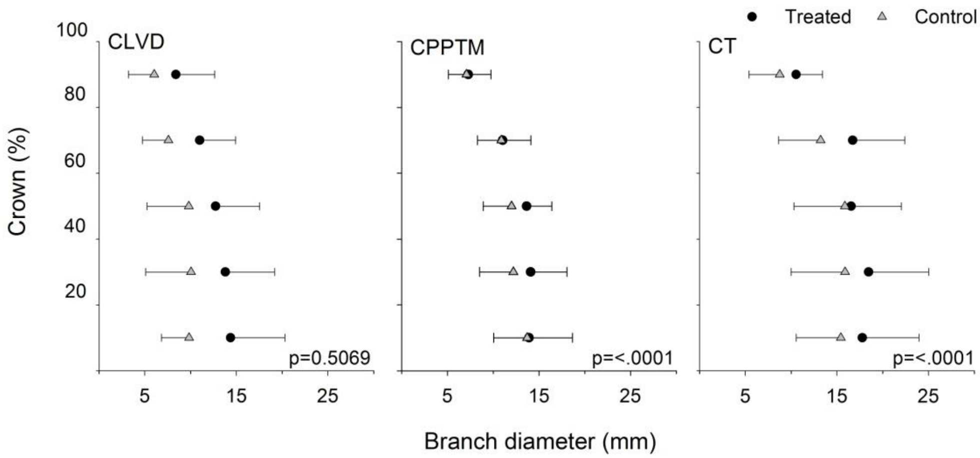

Figure 3.2. Average branch diameter per crown section after each treatment (black circles) with their controls (grey triangles) at sample year. Horizontal bars represent the standard deviation. P-values are the results from the treatment and sections interaction.

CONCLUSION GÉNÉRALE

L’objectif de cette thèse était d'évaluer l’effet des coupes partielles sur la structure des peuplements, la croissance radiale et la qualité du bois de l’épinette noire, en peuplements équiens et inéquiens, contribuant ainsi à fournir des informations essentielles afin de promouvoir un aménagement durable des forêts. L'évaluation de différentes coupes partielles, couplées à des peuplements témoins, est, à notre connaissance, une première dans les peuplements d'épinette noire de l'Est du Canada, ce qui contribue à l'originalité de ce projet. De plus, malgré l'omniprésence de l'épinette noire au Québec, nous ne disposons que de très peu de connaissances sur la qualité du bois des arbres résiduels à la suite de diverses coupes partielles. Cette thèse de doctorat contribue ainsi à combler le manque actuel de connaissance, en plus d’améliorer la compréhension générale quant à la réaction des arbres à des coupes partielles.

Principaux résultats

Structure des peuplements et croissance des arbres résiduels

Les résultats de cette thèse ont démontré qu’après l'application de la coupe avec protection des tiges à diamètre variable (CPTDV), de la coupe avec protection des petites tiges marchandes (CPPTM) et de l'éclaircie commerciale (EC), les écarts entre les forêts naturelles et aménagées étaient réduits, respectant ainsi le principe d'aménagement écosystémique. En effet, la structure d'âge des arbres résiduels ainsi que la distribution de leur diamètre étaient semblables à celles retrouvées dans les peuplements témoins (Chapitre 1). Toutefois, conséquemment à ces interventions, la faible quantité de bois mort observée, particulièrement celui de grandes dimensions, ainsi que la diminution de la densité des peuplements, pourraient mener à une perte de biodiversité.

La CPPTM ainsi que l'EC ont démontré leur capacité à augmenter la croissance radiale moyenne des arbres résiduels (Chapitre 1), ce qui contribue à la viabilité de ces coupes pour l'industrie. Ces résultats sont en accord avec d'autres études sur l'épinette noire à la suite de l'EC (Vincent *et al.*, 2009) et de la CPPTM (Thorpe *et al.*, 2007). La répartition spatiale plus uniforme des arbres résiduels, à la suite des coupes, est partiellement responsable de cette augmentation de croissance. En contrepartie, à la suite de la CPTDV, l'augmentation de croissance radiale est limitée par une plus grande occurrence de grappes d'arbres résiduels, la compétition étant un facteur important limitant l'accroissement radial. Après les interventions sylvicoles, les arbres résiduels ne réagissent pas tous de la même façon. En fait, il existe une grande variabilité d'accroissement en diamètre (Chapitre 1). Cette thèse a démontré que l'augmentation du diamètre des arbres, après une coupe partielle, était influencée positivement par le temps passé depuis le traitement et par la longueur du houppier, mais négativement affectée par la compétition et l'âge des arbres. La croissance radiale augmente davantage à la base de l'arbre comparativement à la moitié supérieure de la tige (Chapitre 3). Il s'agit d'un ajustement des arbres à l'ouverture du peuplement ayant comme but d'augmenter leur stabilité mécanique (Dean et Long, 1986). Cette différence est plus importante à la suite de la CPPTM (Chapitre 3), où un taux élevé de mortalité par chablis a été observé (Riopel *et al.*, 2010).

Grâce à une approche multidimensionnelle, les résultats présentés dans le chapitre 1 ont permis d'observer l'effet des coupes partielles sur la structure des peuplements et la croissance des arbres résiduels, et d'établir un lien entre les deux. Jusqu'à présent, peu d'études se sont intéressées à la répartition spatiale des arbres résiduels et à son impact sur l'accroissement radial des arbres à la suite d'interventions sylvicoles, car l'emphase est davantage portée sur la composition des peuplements ainsi que sur leur structure verticale (Gauthier *et al.*, 2008). La répartition spatiale des arbres est directement reliée à la dynamique des peuplements, notamment à cause de son influence sur la croissance et la mortalité des arbres. De ce fait, les résultats du chapitre 1 sont d'une grande importance et participent aux connaissances générales nécessaires à l'élaboration d'interventions sylvicoles favorisant autant la productivité des peuplements que leur diversité structurale. Bien que l'étude de la mortalité à la suite de coupes partielles gagne en intérêt vu son importance écologique et économique, très peu d'information est disponible sur la quantité et la qualité du bois mort retrouvées après des coupes partielles dans les peuplements d'épinette noire, comparativement à des peuplements témoins. Le chapitre 1 apporte donc de nouveaux résultats sur une problématique grandissante.

Qualité du bois

Tandis que d'autres études ont observé une diminution de la qualité du bois associée à des traitements sylvicoles diminuant la densité des peuplements, dû à des changements dans ses caractéristiques intrinsèques, pour différentes espèces de la forêt boréale (Dutilleul *et al.*, 1998; Makinen *et al.*, 2002), la qualité de l'épinette noire ne semble pas négativement affectée par l'augmentation de croissance radiale, et ce, sur l'ensemble de sa tige (Chapitres 2 & 3). En intégrant de multiples indicateurs de qualité du bois, cette étude est une des premières, en peuplement d'épinette noire, à établir une relation entre les caractéristiques cellulaires, densitométriques et mécaniques. Seuls de faibles changements ont été observés à la suite des coupes partielles, et les changements demeuraient dans les limites de la variation naturelle observée pour l'épinette noire. Une légère diminution de la masse volumique du bois initial a été observée à la suite de la CPPTM et l'EC, mais celle-ci était couplée à une augmentation dans le bois final, ce qui a limité l'effet sur la masse volumique moyenne des cernes de croissance (Chapitres 2 & 3). Bien que les propriétés mécaniques des arbres résiduels après la CPPTM étaient moins élevées que celles des témoins, seule une faible corrélation négative entre le module de rupture et la croissance radiale a été décelée. De plus, les coupes partielles n'ont pas affecté la masse volumique du bois différemment selon la hauteur dans la tige (Chapitre 3). Comme les propriétés mécaniques recherchées du bois sont généralement associées à la masse volumique (Saranpää, 2003), on peut présumer que l'augmentation de croissance radiale, après les interventions sylvicoles évaluées, n'aura pas d'effets négatifs le long de la tige de l'épinette noire.

Très peu d'études se sont intéressées à l'effet des coupes partielles sur les caractéristiques cellulaires de l’épinette noire, particulièrement sur la longueur des trachéides. Il s'agit d'analyses exhaustives qui permettent une caractérisation précise des propriétés du bois. La diminution de la longueur des trachéides observée dans cette étude, à la suite de la CPTDV et la CPPTM, pourrait nuire à la qualité du papier (Chapitre 2). Toutefois, les valeurs demeurent supérieures à la limite établie afin de produire du papier avec une résistance acceptable aux déchirures (Zobel et van Buijtenen, 1989). De légers changements ont été observés, à la suite des coupes partielles, dans l'aire du lumen et la largeur des parois cellulaires, mais aucun lien évident entre ces caractéristiques et les propriétés mécaniques n'a pu être démontré (Chapitre 2).

La diminution de la densité des peuplements, à la suite de coupes partielles, peut ralentir la récession du houppier, car il y a davantage d'espace pour l'expansion du houppier et de lumière qui atteint ses parties inférieures (Brix, 1981; Makinen et Hein, 2006). De ce fait, des branches de plus grand diamètre ont été retrouvées, à la suite des trois coupes partielles, comparativement aux arbres témoins (Chapitre 3). Néanmoins, comme la croissance des branches diminue avec l'âge de celles-ci (Makinen, 1999), l'effet des coupes partielles sur le diamètre des branches devrait s'amoindrir avec le temps, d'autant plus que le peuplement se refermera lentement, et que de moins en moins de lumière atteindra les parties inférieures du houppier.

Les chapitres 2 et 3 offrent des données et des conclusions de grande valeur, notamment du fait de la faible quantité d'études concernant l'effet des coupes partielles sur la qualité du bois de l'épinette noire. L'intégration, au chapitre 2, de plusieurs paramètres de qualité du bois a permis de mieux comprendre les liens existants entre les caractéristiques cellulaires, la masse volumique et les propriétés mécaniques. Le chapitre 3 a, quant à lui, apporté une dimension nouvelle à cette problématique en offrant un aperçu global de l'effet des coupes partielles sur l'ensemble de la tige d'épinette noire.

Limites de l'étude et perspectives de recherche

Pour des raisons pratiques, le temps écoulé depuis l’application des traitements (TDT) variait entre les types de coupe et les blocs d'échantillonnage. Bien que cette variable ait été prise en compte dans les analyses statistiques, il aurait été avantageux d'avoir des TDT similaires afin de mieux comparer l'effet des traitements, notamment sur la structure des peuplements. Bien que les études ayant un recul de plus de 5 ans en Amérique du Nord soient rares, un plus long TDT aurait pu modifier certaines conclusions, considérant qu'il s'agit d'un facteur important dans le développement des peuplements et dans la croissance des arbres résiduels. Par exemple, trois ans après une CPPTM, Cimon-Morin *et al.* (2010) ont constaté que la structure des peuplements s'était simplifiée et qu'elle ressemblait davantage à celle des peuplements équiens. Toutefois, à plus long terme, on peut s'attendre à l'implantation d'une structure de diamètre complexe, grâce à l'augmentation de la surface terrière dans la plupart des classes de diamètre (Groot, 2014), et à la grande variabilité observée entre les arbres résiduels (Chapitre 1). L'augmentation du diamètre des arbres, suivant une coupe partielle, est aussi fortement influencée par le TDT (Chapitre 1). Tel que constaté par plusieurs auteurs, quelques années sont nécessaires avant que l'on observe une augmentation significative de la croissance radiale à la suite d'une coupe partielle (e.g. Vincent *et al.*, 2009). Ce délai varie entre 1 et 3 années (Chapitre 1). L'échantillonnage ayant eu lieu de 3 à 5 ans après la CPTDV, l'effet final de ce traitement sur les arbres résiduels peut ne pas avoir été complètement perçu. Également, à plus long terme (>10 ans), le peuplement se refermera graduellement, augmentant de nouveau la compétition entre les arbres résiduels. Ainsi, l'effet initial de l'ouverture du peuplement sur la croissance et sur certains paramètres de qualité du bois (p. ex. le diamètre des branches) pourrait s'amoindrir avec le temps. De ce fait, l'étude à long terme des peuplements offrirait un meilleur aperçu des effets des coupes autant sur la structure des peuplements que sur la croissance et la qualité des arbres résiduels. Il existe, à ce jour, très peu de connaissances sur le développement des peuplements partiellement récoltés sur une longue échelle temporelle (>10 ans), et la majorité de nos connaissances proviennent d'études récentes (Bose *et al.*, 2014).

Afin de s'assurer d'une bonne productivité des peuplements après une coupe partielle, il est important de maintenir un faible taux de mortalité. Bien que la quantité de bois mort ait été évaluée dans cette étude, aucune donnée n'était disponible quant à l'année de la mort des arbres, la cause de cette mortalité, ainsi que sa vitesse de dégradation. De ce fait, les arbres morts présents pouvaient déjà y être avant la coupe ou bien être le résultat d'une trop grande ouverture du peuplement. Une analyse dendrochronologique permettrait de connaître l'année de la mort de l'arbre, et une caractérisation de son environnement permettrait d'en déterminer la cause (p. ex. le chablis). La mortalité après coupe est une préoccupation majeure pour l'industrie et, afin de minimiser les pertes et ainsi favoriser la viabilité économique des interventions, particulièrement celles des coupes partielles, il est impératif d'élaborer des modèles régionaux de risques de mortalité après des coupes partielles (Bose *et al.*, 2014).

La compréhension des facteurs affectant l'accroissement radial, à la suite d'une coupe partielle, serait garante de sa réussite. Dans cette thèse, les facteurs analysés n'expliquent que 50 % de la variabilité observée. L'étude racinaire des arbres résiduels est une piste intéressante. En effet, Tarroux *et al.* (2010) ont démontré qu'une grande partie de la variabilité de croissance entre les arbres, à la suite d'une éclaircie commerciale en peuplement de pin gris, pouvait être associée aux greffes racinaires, celles-ci permettant aux arbres de se partager des ressources. Bien que rarement observées dans la région à l'étude (Krause, communication personnelle), les greffes racinaires sont possibles chez l'épinette noire bien que leur fonctionnalité n'ait pas encore été démontrée. À la suite d'une EC en peuplement d'épinette noire, la croissance des racines augmente prioritairement par rapport à la tige (Vincent *et al.*, 2009) afin d'en assurer sa stabilité, limitant ainsi l'accroissement radial des arbres. Considérant les différences entre les arbres résiduels des peuplements équiens (dominants) et inéquiens (opprimés), il est possible que la réaction des racines diffère (p. ex. besoin d'ancrage plus important pour les arbres opprimés), expliquant ainsi une partie de la variabilité observée. Finalement, les différentes réactions des arbres résiduels pourraient également être expliquées par leur position par rapport aux sentiers de coupe. En effet, l'ouverture plus importante créée dans ces sentiers permettrait aux arbres à proximité de croître davantage (e.g. Bowering *et al.*, 2006). Les sentiers de coupe n'ont cependant pas été considérés dans cette étude.

Une approche écophysiologique permettrait de mettre en relation le développement cellulaire des arbres résiduels avec les variables environnementales après une coupe partielle, et ainsi créer des modèles régionaux spécifiques. Dans un contexte de changements climatiques, ce type d'approche est particulièrement important. En effet, une augmentation de la température, couplée à des périodes de sécheresse estivale plus importantes, pourrait survenir en Amérique du Nord (Burke *et al.*, 2006; Plummer *et al.*, 2006). La température et les précipitations influencent les processus reliés à la croissance (Deslauriers *et al.*, 2003; Rossi *et al.*, 2008). Par exemple, en période de sécheresse, des cellules de plus petites dimensions avec des parois cellulaires plus épaisses ont été observées pour plusieurs espèces (e.g. Rossi *et al.*, 2009; Jyske *et al.*, 2010). Bien qu'une récente étude expérimentale en forêt mature d'épinette noire ait démontré que la sécheresse n'affectait pas les propriétés cellulaires, cette étude ne considérait pas les effets couplés d'une augmentation de température et de CO_2 atmosphérique avec une diminution des précipitations (Belien, 2015). Par conséquent, il est difficile de prévoir la réaction de l'épinette noire aux changements climatiques dans des peuplements naturels. À la suite d'une coupe partielle, la réaction des arbres à l'ouverture des peuplements pourrait être limitée par les changements de température et de précipitations.

La sélection des arbres pour l'analyse de la qualité du bois s'est effectuée parmi ceux ayant eu une augmentation de croissance d'au moins 20 % comparativement à la moyenne des dix années précédentes. Plusieurs études ont précédemment observé que l'accroissement des cernes de croissance était un facteur nuisant aux propriétés du bois responsables de sa qualité (e.g. Dutilleul *et al.*, 1998; Makinen *et al.*, 2002). Cette sélection d'arbres analysés a donc permis de tester cette hypothèse pour l'épinette noire. De plus, les analyses de qualité, particulièrement les analyses cellulaires, sont très exhaustives, et cette sélection a permis de focaliser notre attention sur une question précise, soit l'effet d'une augmentation de croissance radiale sur la qualité du bois. Toutefois, cette sélection ne permet pas de conclure sur l'effet global des coupes partielles. En effet, certaines études ont observé que seuls les arbres avec une très forte augmentation de croissance ont une diminution de la qualité du bois (Makinen *et al.*, 2002; Krause *et al.*, 2011). Étant donné la grande variabilité d'accroissement radial observée à la suite des coupes partielles (Chapitre 1), une approche intéressante serait d'analyser l'ensemble des arbres d'une station et de les classifier en fonction de leur taux d'accroissement. L'analyse de la masse volumique, par exemple, serait un indicateur intéressant de qualité, considérant son lien avec les propriétés mécaniques, et demanderait peu de temps.

Il y a une augmentation significative de la croissance radiale des arbres résiduels après les coupes partielles (Chapitre 1), et celles-ci ne nuisent pas de façon considérable à la qualité du bois (Chapitres 2 & 3), suggérant ainsi la viabilité économique des interventions. Par contre, cette thèse n'a pas fait l'étude des retombées financières associées à ces interventions. Bien que les coupes partielles aient plusieurs avantages écologiques (diminution des écarts entre les forêts traitées et naturelles) comparativement à la coupe totale, celles-ci ne pourront être utilisées à grande échelle que si les profits sont présents. Liu *et al.* (2007) et Ruel *et al.* (2013) ont démontré que certaines coupes partielles, dont la CPPTM et la coupe de jardinage, étaient économiquement profitables lorsqu'appliquées dans des conditions favorables. Toutefois, les profits peuvent être limités par le coût plus élevé des routes, considérant que deux à trois fois plus de routes doivent être construites pour avoir accès au même volume de bois (Liu *et al.*, 2007). De plus, la profitabilité n'est pas garantie car la valeur du bois dépend également des fluctuations des prix du marché (Brazee et Bulte, 2000; Vincent, 2010). En conséquence, il est d'une grande importance de connaître les conditions idéales à l'application de ces coupes, afin de rentabiliser ces pratiques et ainsi, faire le pont entre les besoins écologiques et économiques.

Il existe une multitude de types de coupe partielle, chacune variant selon leur taux de récolte, le type d'arbres récoltés, la largeur et la distance des sentiers de coupe, etc. Dans cette étude, seuls trois types de coupe ont été évalués. Ces coupes ont été sélectionnées car elles sont présentement appliquées par l'industrie, à une échelle opérationnelle, en peuplement d'épinette noire, et ce, depuis plus de cinq ans. Toutefois, une approche expérimentale permettrait d'évaluer davantage de conditions, en plus de connaître de façon précise les caractéristiques initiales des peuplements. Par exemple, depuis le début des années 2000, un important dispositif expérimental, établi en pessière noire boréale, a été mis en place afin d'évaluer différents systèmes de coupe progressive (Lussier *et al.*, 2016). Ce dispositif vise à analyser les conditions idéales pour une gestion durable des forêts (mortalité, efficacité sylvicole (p. ex. régénération, rendement de récolte), maintien des attributs écologiques, coûts opérationnels), en faisant varier divers paramètres de coupe (p. ex. % de récolte, largeur des sentiers de coupe). Ayant évalué les peuplements avant l'application des coupes (c.-à.-d. hauteur, diamètre et longueur du houppier des arbres, etc.), l'effet réel des coupes peut être observé plusieurs années après. Également, l'approche empirique utilisée dans cette étude ne permet pas de tirer des conclusions générales applicables à différentes conditions. Afin de prendre en compte le grand nombre de combinaisons de structures de peuplement et de modalités de traitements sylvicoles, des analyses de modélisation pourraient être utilisées. De toute évidence, les dispositifs expérimentaux et la modélisation pourront fournir de nombreuses réponses quant à l'application de coupes partielles en peuplement d'épinette noire et contribueront au développement durable des forêts.

Implications des résultats

Les coupes partielles sont de plus en plus appliquées au Québec, afin de maintenir les structures naturelles des forêts suivant le principe d'aménagement écosystémique et d'augmenter la croissance des arbres. Ce faisant, les coupes partielles aspirent autant à des bénéfices écologiques qu'économiques. Les coupes partielles ont un court historique en forêt boréale canadienne, et très peu d'information est disponible, notamment en peuplement d'épinette noire. Ce projet contribue aux connaissances générales sur l'application de coupes partielles en forêt boréale, en décrivant leurs effets sur la structure des peuplements, la croissance des arbres résiduels ainsi que sur la qualité de leur bois. Bien que plusieurs questions demeurent, nous croyons que les coupes partielles analysées dans cette étude sont adéquates en forêt d'épinette noire de l'Est du Canada. En effet, la structure d'âge et la distribution diamétrale des arbres résiduels ne diffèrent pas des peuplements naturels, suggérant le maintien de structures inéquiennes après la CPPTM et la CPTDV. De plus, l'augmentation de la croissance radiale des arbres résiduels n'est pas associée à une perte considérable de qualité du bois, suggérant la viabilité économique des trois interventions. Toutefois, la CPTDV semble moins intéressante que la CPPTM en peuplements inéquiens, car elle accentue la distribution en grappe des arbres, préalablement observée dans les peuplements adéquats pour ce type de coupe. Ceci limite la croissance des arbres résiduels, ce qui pourrait potentiellement nuire au rendement du futur peuplement. De plus, une attention particulière devrait être portée sur la quantité et la qualité du bois mort retrouvé dans les stations traitées par une coupe partielle, afin de limiter les écarts avec les peuplements naturels et les pertes économiques importantes. Nous proposons, entre autres, de limiter l'occurrence de petites grappes d'arbres afin de promouvoir la croissance radiale des arbres et de conserver quelques arbres de fort diamètre dans les stations inéquiennes afin de contribuer au recrutement à long terme de bois mort de grandes dimensions. Ainsi, les coupes partielles pourront contribuer plus efficacement à une gestion durable des écosystèmes forestiers. L'épinette noire est une espèce dominante de la forêt boréale québécoise, il est important d'assurer la pérennité de ces forêts, au bénéfice des générations actuelles et futures (Gagnon et Morin, 2001).

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